California Fish and Wildlife
JOURNAL

SPECIAL ISSUE

Effects of Fire on California's Natural Resources

Journal for the Conservation and Management of California's Species and Ecosystems

California Fish and Wildlife

FIRE SPECIAL ISSUE 2020

California Fish and Wildlife Journal

Contents

Editors for this issue

This issue would not have been possible without the amazing team of guest editors from our Timberland Conservation and Wildfire Resiliency Program who volunteered their time and expertise for this issue.

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Editors for this issue—continued

ANDREW YARUSSO is an Environmental Scientist the Timberland Conservation and Fire Resiliency Program. He reviews Timber Harvesting Plans for consistency with the California Environmental Quality Act and the California Endangered Species Act as well as issues Lake and Streambed Alteration Agreements and provide consultations to evaluate and reduce potential impacts to aquatic, terrestrial, and botanical resources. Andrew joined the Department as a Scientific Aide in 2009 and advanced to his current position in 2012. He obtained a Bachelor of Science in Biology, minor in Chemistry, from Oregon State University. His emphasis in cellular biology quickly landed him employment in medical research, but he realized a desire to work in nature by joining the Arizona Game and Fish Department in 2002 and Oregon Department of Fish and Wildlife in 2004. Since then, he have been involved in multiple projects acquiring almost 13 years of experience in wildlife biology and resource management.

SANDI JACKS is a Senior Environmental Scientist (Specialist) for the North Central Region's Timberland Conservation and Wildfire Resiliency Program. After graduating from California State University, Fresno with a Bachelor of Science in Biology and German, she began her biology career in the late 1990s as a wildlife biologist for the U.S. Forest Service. Over the past 20 plus years, she has worked with our Department and Caltrans and has experience from owl surveys; fisheries projects; wildlife husbandry, handling, and disease surveillance; to experience in document writing and review; permit writing; providing the biology for Fish and Game Code violations, and working with multiple stakeholders of the environment.

KELSEY VELLA is a Senior Environmental Scientist (Specialist) in the Timberland Conservation and Wildfire Resiliency Program in our Region 2 (Rancho Cordova) office. She earned a Bachelor of Science degree in Forestry from Humboldt State University in 2013. While working towards her degree, Kelsey interned at various organizations including Redwood National Park, Sierra Pacific Industries, and Blodgett Forest Research Station. After college, she went to work as an Environmental Scientist at the California Department of Water Resources, managing grant agreements in the Financial Assistance Branch. She then transferred to CDFW's Region 2 Habitat Conservation Program where she worked for two years before joining the Timberland Conservation Program.

SHELBY THOMAS is an Environmental Scientist in the Timberland Conservation and Wildfire Resiliency Program based out of the North Central Region, Rancho Cordova office. She received her bachelor's degree in Anthropology and Archaeology from the University of Oregon and is currently working to complete the Environmental Policy and Management Masters Program at American Public University. She began her career at CDFW in 2017 in the Conserved Lands Program underneath the larger Wildlife Management Program, where she focused predominantly on utilizing adaptive management techniques for fire risk management and trail camera trapping to observe and record baseline wildlife populations on thousands of acres of CDFW's Unstaffed Lands. Currently, she performs timber harvest plan review in various counties throughout the North Central Region.

Introduction

KEVIN SHAFFER, *Fisheries Branch Chief, Wildlife and Fisheries Division, California Department of Fish and Wildlife*

As I write this Introduction to the *Fish and Wildlife Journal*'s Special Issue on Wildland Fire, fire fighters are battling 22 wildfires across the State, five of the top ten largest wildfires (e.g., August, SCU Lightning, LNU Lightning, and North complexes and the Creek Fire) have already occurred this year, and over four million acres have burned. To put the last fact into perspective, the previous top acreage burned in a single wildlife season was just over 1.7 million acres. Additionally, you should know that 17 of the State's 20 largest wildfires have occurred since 2000, and since 2017, 151 Californians have lost their lives in wildfires. Eighty-five people perished in the 2018 Camp Fire alone.

Wildland fires are burning across the western United States in 2020. It is not the first time, but the scale of wildfires, along with the until-recently inconceivable destruction of property, human communities, and human lives, have gotten the attention of the entire nation. And the entire community of fire scientists and fire ecologists.

California may have the greatest range and variation in wildfire behavior, regime, and effects. Most of the State's ecological regions, including oak woodlands, conifer forests, chaparral, and native grass communities are adapted to wildfire. Their very existence and functioning depends on particular attributes of wildfire, often referred to as fire regime. Hundreds of plant species, including those that are key to ecological health (i.e., *Arctostaphylos* ssp., *Ceanothus* spp., *Quercus* spp., *Pinus* spp.) are adapted and dependent on wildfire. Many of the State's rare and endemic species co-exist with wildfire.

Where plants and plant communities go, animals follow. Though animals are not adapted to fire, they do have effective mechanisms to respond to fire. Some animals, included species of birds, rodents, and beetles, prosper for various periods of time only after wildfires occur.

Ecologically, wildfire may be the second in importance only to water in California. Without fire or with greatly altered fire regimes, native plant and animal communities are greatly impacted. Then again, wildfire is an ever-growing concern and impact not only to public lands and wildlife but human communities. The current trajectory of trends in extreme wildfire behavior and larger wildfires has been expected by the fire-fighting community, fire scientists, and fire ecologists. And as our climate continues to change, the future is one of great concern and uncertainty.

This Special Issue is particularly impressive, for several reasons. You will be exposed to 1) the wide range of land management (e.g., water quality, vegetation condition, fire breaks), ecological processes (i.e., post-fire sediment transfer), and biological issues (i.e., effects to native animals, response of native plants) entwined with wildfire, and 2) the wide range of authorship (i.e., forestry, private consultants, environmental organizations, transportation, fire and fuel management, universities and colleges, state and out-of-state field scientists), representing the vast of array of folks involved in wildfire in California. Please read the entire issue. Only then can you begin to understand the complexities of wildfire in California.

I would be remiss not to direct you to other amazing resources addressing wildfire science and management, including the California Fire Science Consortium, http://www.cafiresci.org/, the California Fire Safe Council, https://cafiresafecouncil.org/, the California Department of Forestry and Fire Protection, https://www.fire.ca.gov/, the Department's Wildfire webpage, https://wildlife.ca.gov/Science-Institute/Wildfire-Impacts, UC Press' Fire in California's Ecosystems, Second Edition, van Wagtendonk et al., https://www.ucpress.edu/book/9780520286832/fire-in-californias-ecosystems, and the Association of Fire Ecology, https://fireecology.org/.

I think it is appropriate to end the Introduction to this Special Edition with a huge thank you and accommodation to Angela Baker, Editor-in Chief of the *California Fish and Wildlife Journal*, her associate editors, and the authors. Ange has positioned the Journal in a vital and amazing position to put forth the dynamic sciences necessary to address wildfire in California. No research is more difficult in wildfire science than fire ecology and animal/plant response to fire. She has put together the first issue to tackle this vital subject. And I hope not the last. Thank you, Ange, editors, and authors, for putting the Department and its journal squarely at the center of the role of wildfire to California's fish and wildlife.

Introduction—continued

SUSAN BRITTING, *Executive Director, Sierra Forest Legacy*

California's ecosystems evolved with fire. Lightning and ignitions by Native Americans were the cause of periodic fire with estimates of 4.4 million acres burning annually prior to 1800 in California (Stephens et al. 2007). Many plants developed traits that respond in unique ways to recurrent fire, and various animals evolved to utilize burned habitats. Native Californians understood fire as a dynamic process and intentionally set fires periodically to revitalize and regenerate various plants and the land supporting them (Tripp 2020). With the arrival of explorers and settlers in the 1700s this dynamic began to shift (Taylor et al. 2016). Fire was seen by these new peoples as a destructive process and fire suppression emerged as the dominant response. Other practices like livestock grazing, mining, and logging further shaped California's landscape in ways never before experienced. Over the years, people flooded into California and the population grew from less than 0.5 million before 1800 (Library of Congress 2020) to over 39 million people now. This brings us to the California of today – a frequent-fire landscape in which many, many people live.

The 2020 fire year has been like nothing seen in California's recent history. As of mid-October, wildfire burned over 4.1 million acres, resulted in the death of 31 people, and damaged or destroyed 9,247 structures (CALFIRE 2020). These impacts combined with the weeks to months of smoke impacts affecting most of our population literally takes one's breath away. Clearly, action needs to be taken to better protect people and communities and lower their fire risk. The California legislature is working on solutions now, and we should expect to see investments and policy initiatives in the coming year targeted at reducing human exposure to fire risk and improving the resilience of communities. This special issue of the *Journal* though, is focused on the ecology of California's frequent fire landscape and explores how wildlife, fish and plants respond to fire and fire-related management actions. At the heart of this exploration is the drive to understand how natural resources benefit from fire and what actions can be taken to support these benefits. This exploration also links us back to the demands that people place on the landscape and how best to live with fire while protecting biodiversity.

California is a globally recognized hotspot of biodiversity; this stems from its "exceptional variation in landscape features, latitudinal range, geological substrates and soils, and climatic conditions, resulting in a wide range of ecosystems to support plant and animal species" (CSWAP 2015). Place-based disturbance regimes, whether it be fire, flooding, or some other periodic event, also influence and shape biodiversity. Among the 22 vegetation communities identified in California, scientists have described 56 different fire regimes reflecting the variability in periodicity and severity between and within these communities (Fryer and Luensmann 2012). Evaluation of the expected fire regime of a vegetation community and its current condition is essential to identifying management practices that align with this disturbance process and enhance biodiversity. A case in point is the surplus of fire identified in southern California vegetation communities compared to the deficit of fire in forests and woodlands in northern California (Safford and Van de Water 2014). These patterns help inform where management practices, like prescribed fire, will be beneficial to biodiversity as opposed to creating atypical and less diverse habitats.

It is certain that California will experience wildfires in the years to come. Our challenge is to learn how to live in this frequent-fire landscape. Deepening our understanding about ecological systems and the drivers that enhance native biodiversity, as illustrated by several articles presented in this issue, is one critical element. Another is designing management practices that both reduce the wildfire risk to people while conserving biodiversity. And of equal, and possibly greater importance, is how we site, design, and build our communities to be resilient to wildfire. The good news is that progress on all fronts is possible. What it will require though is increased investment and cooperation between government agencies and stakeholders to ensure success.

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SECTION 1.
Vegetation Treatment and Policy

Tubbs Fire on the morning of 9 October 2017, outside of Healdsburg, CA. Photo Credit: Karen Gaffney, Sonoma County Ag + Open Space

Slash piles being burned after a forest thinning project in El Dorado County, CA. Photo Credit: Kevin Vella, National Wild Turkey Federation

A prescribed burn implemented by CalFire's Vegetation Management Program at Bobcat Ranch in Yolo County, CA. Photo Credit: Kelsey Vella, CDFW

ORIGINAL RESEARCH

Sonoma County Complex Fires of 2017: Remote sensing data and modeling to support ecosystem and community resiliency

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In the western U.S., long-term fire suppression has led to a build-up of surface and ladder fuels, increasing the severity of fires. Coupled with increased home building in the wildland urban interface and global climate change, much of the western U.S. is facing unprecedented risk of catastrophic wildland fires. Given the almost 30 million acres of forestland in California, and the impacts to human community health and safety and natural systems that stem from uncontrolled fires, it is imperative that we understand the underlying processes and conditions in the landscape that determine fire impacts. In October of 2017, Sonoma County, California experienced three significant fires that resulted in loss of life and property, as well as impacts to natural systems. Sonoma County Ag + Open Space—with support from a team of technical consultants and in partnership with NASA and other experts—researched the impacts of the fires to woody vegetation within areas that burned during wind-driven and non-wind driven events. Using high-resolution aerial imagery, we mapped canopy condition of woody vegetation and used machine learning techniques to determine the importance of landscape measures of vegetation structure, land cover type, topography, climate and weather, and nearness to streams as predictors of woody canopy condition for areas that burned during the October 2017 fires. Across the landscapes, riparian and mesic vegetation types exhibited the least canopy damage, followed by upland hardwood forest types. Shrub and upland conifer types exhibited the most canopy damage. Measures of vegetation structure derived from lidar data are the most important predictors of post-fire woody canopy condition, in addi-

tion to slope-aspect, proximate vegetation community types, and distance to streams. In general, the higher the density of shrubs and fire-adapted vegetation types, the higher the density of ladder fuels, and the greater the distance from streams, the higher the canopy damage. This study emphasizes the value of high resolution airborne lidar for mapping vegetation type and structure and building locations at a scale large enough to inform local management decisions. The study also documents pre- and post-fire baseline conditions to support the long-term evaluation of vegetation impacts and provides remote sensing and analysis tools to better plan for, manage, and mitigate future extreme wildfire through the lens of climate and extreme event resiliency, community safety and ecosystem health.

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California's wildlands are critically important in maintaining the state's biological diversity, as well as providing myriad other benefits related to human health and vitality. Forested watersheds provide clean and abundant drinking water for millions of people, sequester substantial amounts of carbon, provide revenue and jobs from the sale of wood products, create opportunities for recreation, and are important scenic attributes in California's tourism economy.

In California, 15 of the most destructive wildfires in the state's history occurred in the last 20 years (CAL FIRE 2019). The underlying causes of these wildfires stem from a variety of factors, including climate change, tree disease, drought, and land-use policies, as well as over 100 years of fire suppression (Keane et al. 2002; Miller 2012; Smith et al. 2016). These landscapes are home to a diversity of plant and animal species as well as millions of people who live in rural watersheds or in the wildland urban interface (WUI). Given the fact that forests cover about a third the California landscape (USDA Forest Service 2014) and forest conditions are influenced by vast temporal and spatial scales, high quality remote sensing data and analysis is critical for efficiently and effectively managing forests for both ecosystem and human community resiliency.

Sonoma County, California is a million-acre county situated at the northern boundary of the San Francisco Bay Area and the southern boundary of the rural North Coast counties of Mendocino, Humboldt, and Del Norte (Figure 1). A biologically rich area with a high degree of endemism, Sonoma County's wildlands are characterized by a relatively undeveloped coastline, a diversity of geologic features, three sizable rivers (Russian, Petaluma, and Gualala), numerous creeks and streams, and a variety of vegetation types including forests, woodlands, grasslands, salt and freshwater wetlands, and the Geysers geothermal area.

In 1990, Sonoma County voters created the Sonoma County Agricultural Preservation and Open Space District (Ag + Open Space) to permanently protect the diverse agricultural, natural resource, and scenic open space lands of Sonoma County for future generations. Along with its partners, the agency has permanently protected over 49,000 ha (121,000 acres) of land in Sonoma County, using the best available science and data to prioritize its actions.
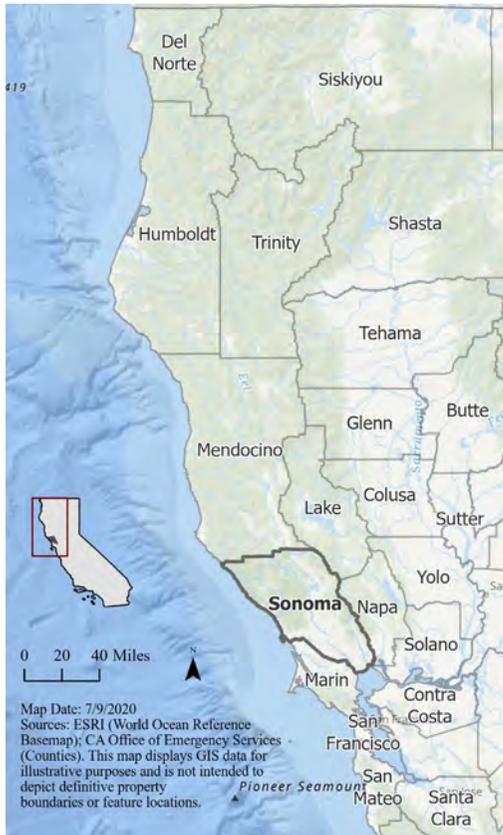
Figure 1. Location of Sonoma County in California, USA.

Sonoma Veg Map: Foundational Data

Ag + Open Space relies on high quality data, ongoing analysis and modeling, and collaboration with a diversity of experts to inform decisions regarding the most important lands to conserve. To this end, Ag + Open Space led and managed the Sonoma County Vegetation Mapping and Lidar Program (Sonoma Veg Map Program) to create a suite of datasets to inform its land conservation objectives, supported by a highly qualified team of consultants including the authors of this paper. In addition to Ag + Open Space funding and staff and consultant contributions, substantial funding and guidance was provided by a consortium of organizations including NASA, California Department of Fish and Wildlife, California Native Plant Society, United States Geological Survey and the Sonoma County Water Agency, as well as two technical committees. In May of 2017, Ag + Open Space completed and provided public access to a robust and comprehensive suite of fine-scale landscape datasets for the entirety of Sonoma and portions of Mendocino Counties.

Based on 2013 high resolution imagery, lidar data and field samples, the datasets provide fine-scale information about the County's topography, land use, vegetation, and hydrology. Specific datasets important for landscape planning and land conservation include forest metrics, digital surface and digital elevation models, ortho-photography, watershed

boundaries, flow accumulation/direction, lifeform, croplands, fine-scale vegetation maps, pervious/impervious surfaces, high resolution building footprints, contours, stream center-lines, and aboveground biomass and carbon. These data are available for download at the Ag + Open Space site sonomavegmap.org.

Sonoma Complex Fires

Wildfires are an integral part of life in Sonoma County and multiple fires have burned across the Sonoma County landscape over the last century (Figure 2). However, over the last decade, the size, frequency, intensity, and costs of wildfires throughout the west have increased as a result of a century of fire exclusion, global climate change, and increased construction in the wildland urban interface (Mitchell 2013; Syphard and Keeley 2015; Mann et al. 2016). On the evening of 8 October 2017, the Tubbs, Nuns, and Pocket Fires (termed the Sonoma Complex Fires) ignited and burned for 20 days, leaving 44,800 ha (110,700 acres) burned, 6,997 structures destroyed, and causing 24 fatalities in Sonoma and Napa Counties.
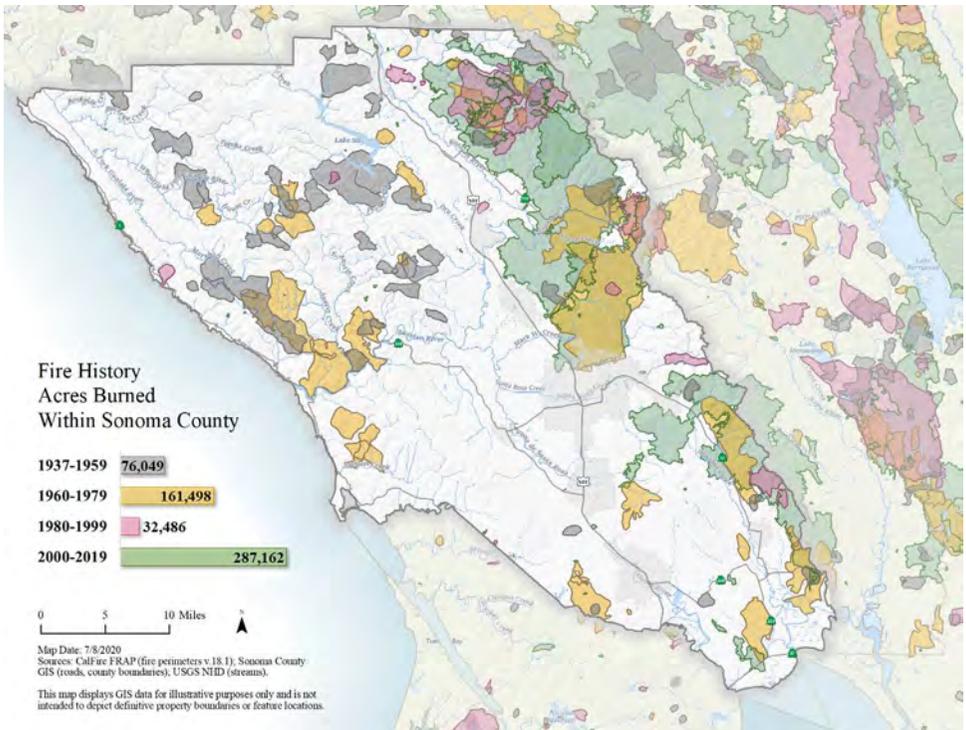
Figure 2. Fire perimeters in Sonoma County and vicinity between 1937 and 2019. Source: Fire and Resource Assessment Program (FRAP) fire perimeter layer developed by BLM, CAL FIRE, NPS, and USFS.

Research objectives

To better plan for future wildfire events and mitigate wildfire risk, Ag + Open Space sought and received NASA Rapid Response Research funding (grant number 80NS-SC18K0683) to employ the Sonoma Veg Map Program and other datasets to better understand

the Sonoma Complex Fires. Research tasks included: (1) mapping woody canopy condition (percent woody canopy damage) as a result of the 2017 fires from pre- and post-fire imagery and lidar data; and (2) discovering and quantifying relationships between post-fire woody canopy condition and landscape characteristics such as weather, vegetation type, fuel loading, land use, and land management patterns. The results of these analyses are being used to inform strategies for land conservation, land use, and land management activities that enhance ecosystem and human community resiliency to wildfire.

This paper summarizes the methods and results of the research effort, and presents the major project conclusions. The first section reviews the methods used to accomplish each research task. The second section reports on research results, and the final sections discuss the impact of the results and present thoughts for future research.

METHODS

Study area

The study area includes portions of the Nuns, Tubbs, and Pocket fires that burned within Sonoma County in 2017 plus portions of Napa County captured by the imagery (Figure 3). All three fires are located primarily in the eastern mountains of Sonoma County. The Pocket fire was located within the Big Sulphur Creek and Middle Russian River watersheds in the northern Mayacamas Mountains, draining into the Alexander Valley. The Tubbs fire was located within the Middle Russian River and Mark West Creek watersheds, with portions of the fire extending into urban areas within the city of Santa Rosa. The Nuns fire was situated in the Sonoma Creek, Napa River, and Carneros Creek watersheds on the west and east flanks of the southern Mayacamas Mountains and portions of the Sonoma Mountains. Areas that burned east of Santa Rosa are within the Santa Rosa Creek watershed. Terrain of the study areas ranges from flat to steep with elevations ranging from 60 to 1,050 m. Vegetation across the study areas is largely comprised of oak woodland, mixed chaparral, mixed hardwood/conifer forest, grassland, and vineyards.

Post-fire woody canopy condition mapping

The first step of this project was to map woody canopy condition following the Sonoma Complex Fires. We acquired 0.305 m (1 foot) resolution stereo, digital airborne, 4-band (red, green, blue, near-infrared) optical imagery over the areas of the Pocket, Tubbs, and Nuns fires in Sonoma County (Figure 4). The imagery was collected using a Vexcel UltraCam Eagle M3 camera flown at 5,054-m (1-foot) altitude on a Beechcraft Airliner twin turboprop aircraft. Airborne imagery was selected over satellite imagery because it can be collected cloud-free and carries no license restrictions, allowing the imagery to be freely shared in the public domain. The imagery was flown by Quantum Spatial (quantumspatial.com) in June of 2018, and provides a smoke- and cloud-free view of all areas within the footprint of the Sonoma Complex Fires in Sonoma County. Following quality control, the post-fire imagery was made available to the public on sonomavegmap.org.

We evaluated the condition of woody canopy for vegetation communities mapped in the Sonoma County Fine-Scale Vegetation and Habitat Map, which characterizes 82 classes of land use and vegetation across the county at the alliance-level with minimum mapping
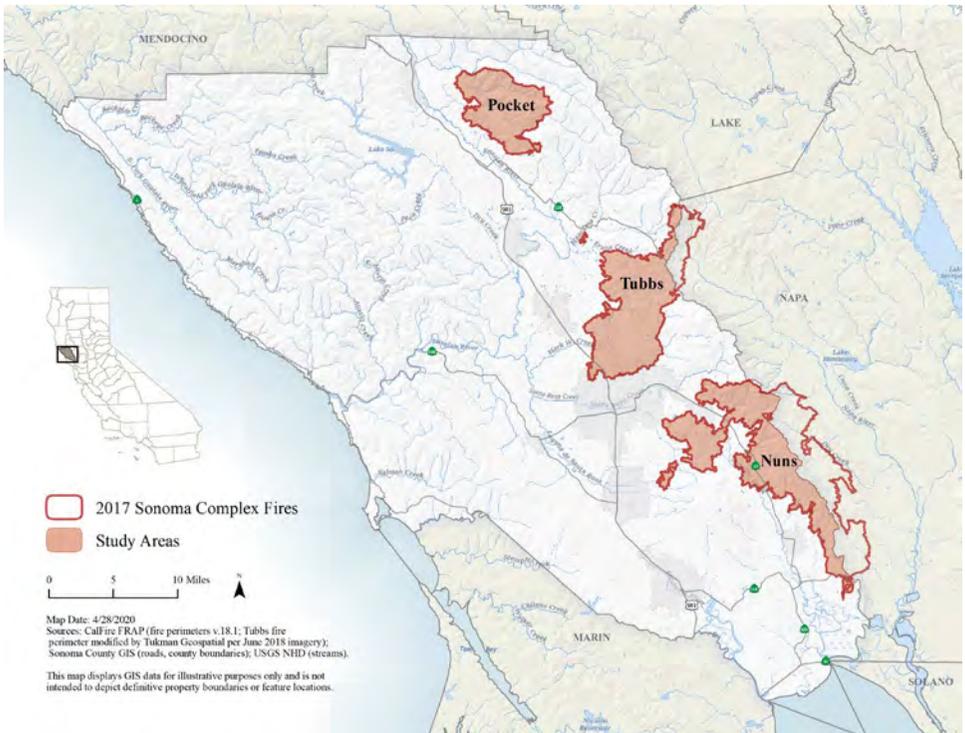
**Figure 3.** The study areas include portions of the Sonoma Complex Fires within Sonoma County, CA.
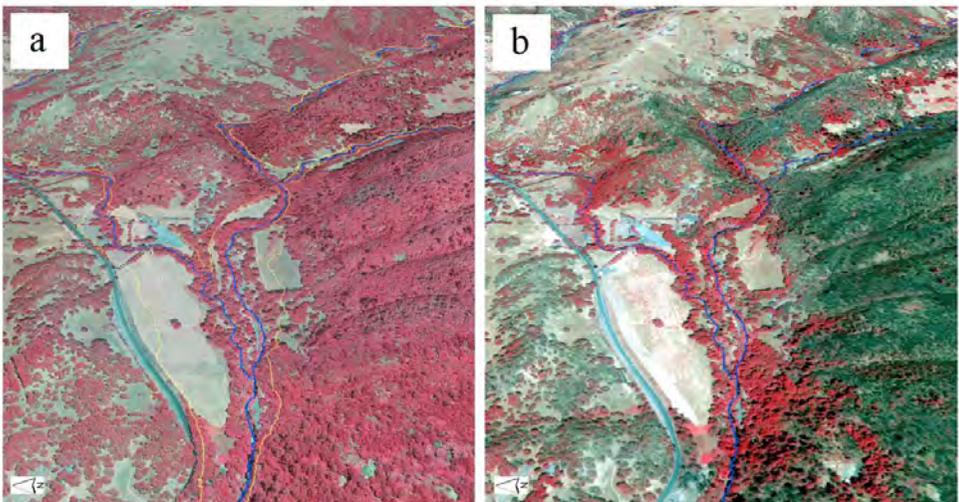

Figure 4. Comparison of 2013 pre-fire imagery (a) to the 2018 post-fire infra-red imagery (b) for the Mark West Creek area of Sonoma County.

units ranging from 0.1–0.4 ha (0.25–1 acre). Please see the Sonoma Vegetation and Habitat Map Final Report for descriptions of each of the map classes (https://sonomaopenspace. egnyte.com/dl/1SWyCSirE9/).

First, due to variability of post-fire woody canopy condition within the fire-affected polygons of the Sonoma County Fine-scale Vegetation and Habitat Map, we created ¼ to 20 acre homogenous sub-polygons based on similar Normalized Difference Vegetation Index (NDVI) values in post-fire imagery using Trimble's eCognition software (http://www. ecognition.com/suite) (Figure 5d).
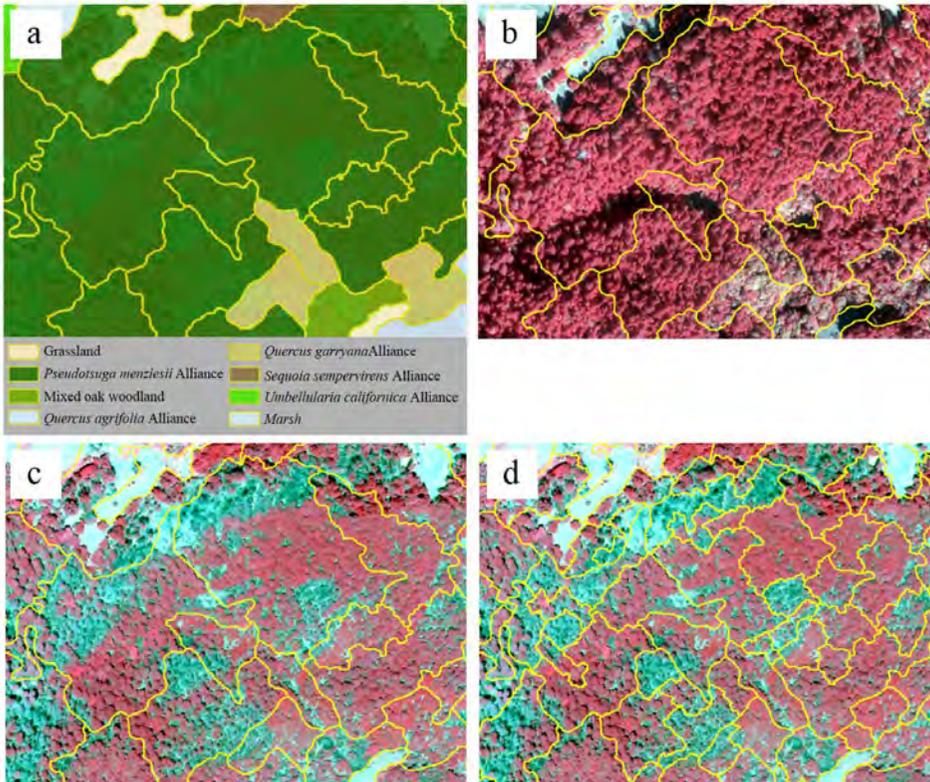
Figure 5. Comparison of the fine-scale vegetation map polygon classes (a), to the fine-scale vegetation polygons over pre-fire 2013 infrared imagery (b), over post-fire 2018 imagery (c), and the sub-polygons of homogeneous damage within the fine-scale polygons (d).

Next, we quantified percent damage of each sub-polygon by calculating the relative proportion of burned versus unburned canopy based on NDVI values from the post-fire imagery. To do this, we further broke the sub-polygons into tiny segments (approximately 0.5-5.5 m^2) in eCognition based on NDVI value (Figure 6a), and classified them as shadowed or illuminated using the average near-infrared band value of the tiny segments. Segments with low near-infrared values were classified as shadowed and segments with high near-infrared were classified as illuminated.

Finally, we established NDVI and Visual Atmospheric Resistance Index (VARI) thresholds to classify the segments as burned versus unburned. Because the thresholds differed for shadowed verses illuminated segments, the thresholds were identified through the use of density slices. Density slicing is the process of binning the range of one band or derivative band of imagery into different classes depending on both the distribution of band values and visual interpretation of the imagery. We then applied separate NDVI/VARI density slices on the illuminated and shadowed tiny segments to label each segment as having damaged or undamaged post-fire woody canopies (Figure 6b). In the NDVI histogram of the Pocket Fire there is a clear bimodal distribution of values distinguishing burned from unburned woody canopies (Figure 7). The histograms of the Tubbs and Nuns Fires are similarly bimodal. We calculated percent woody canopy damage for each sub-polygon based on the relative area of burned tiny segments to unburned tiny segments within a sub-polygon.
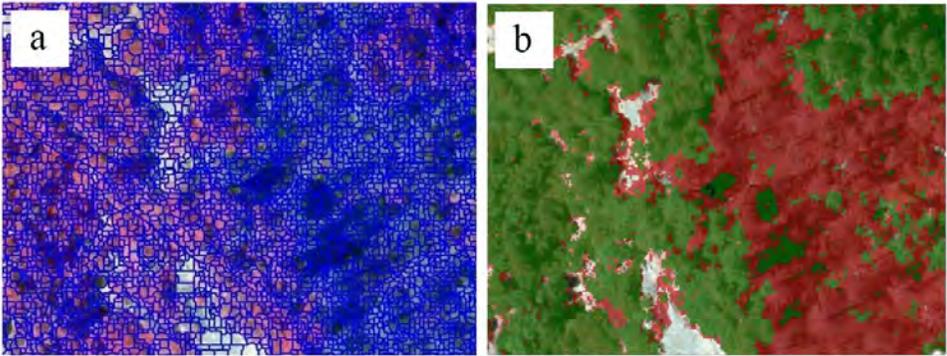
**Figure 6.** Tiny segments within the sub-polygons (a), and the resulting classification of the tiny segments into burned (red) and unburned (green) vegetation (b).
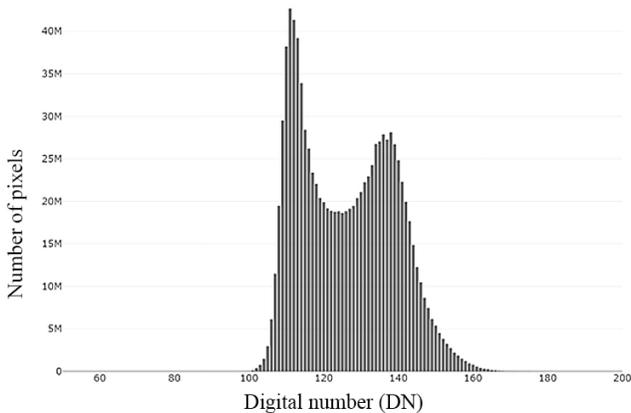

Figure 7. Histogram of NDVI values (converted to a scale from 0-255 and represented as a digital number) for the post-fire imagery of the Pocket Fire area showing a clear bimodal distribution. Damaged canopies have lower NDVI values than undamaged canopies.

Due to the acquisition of aerial imagery in spring following the fire—a time when grasses and forbs have already sprouted and are thus captured as unburned in the post-fire imagery—this project focused on assessing only woody canopy condition within the study area. As a final step in developing the canopy damage maps, we used the 2013 lidar digital surface model to segregate pre-fire woody vegetation (i.e., forests and shrublands) from herbaceous areas based on canopy height of each tiny segment. We classified tiny segments with pre-fire vegetation taller than seven feet as woody vegetation and included these tiny segments in the canopy damage maps. We excluded tiny segments with vegetation height lower than seven feet from the canopy damage maps and subsequent analysis.

We performed an accuracy assessment of the woody canopy condition maps by comparing manually interpreted woody canopy condition (measured in 1% cover increments) from the 2013 and 2018 airborne imagery to the canopy condition map labels for 240 sample sub-polygons (Congalton and Green 2019). Forty samples from each of six canopy condition classes (<5%, 5–20%, 20–40%, 40–60%, 60–80%, 80–100%) were randomly selected. To assure that the analysis was not impacted by spatial autocorrelation, samples were not allowed to be within 365 m (1,200 ft) of one another. Overall accuracy of post-fire woody canopy condition classification was 85%.

Analyzing factors influencing fire behavior and outcomes

The first step in this task involved identifying factors known to affect wildland fire behavior so that measures of these factors could be developed from the Sonoma Veg Map Program and other datasets. Early researchers of fire behavior identified that fire behavior is influenced by factors spanning multiple spatial and temporal scales, and that the most indicative factors were measures of vegetation structure, vegetation type, topography, and climate and weather (Fons 1946; Von Wagner 1969; Rothermel 1972, 1983; Andrews 1986).

Fine scale.—At the finest spatial scale, combustion is controlled by available oxygen, heat, and fuels over seconds (McGranahan and Wonkka 2018). Broadening the scale to a forest stand or vegetation patch, fire behavior is determined by the three-dimensional arrangement of vegetation fuels on the ground and in the canopy, topography, and weather over time. Surface fuels are characterized by size classes, and with all else being equal, smaller-sized fuels (e.g., grasses, shrubs, twigs, leaves) burn more quickly than larger downed wood (Rothermel 1972). For example, "flashy" fuels such as dried grass will burn quickly, but with relatively low intensity. Surface fires will spread more readily with drier fuels and higher wind (Agee et al. 2002). In forests, more severe fires occur when flames reach the tree crown. This generally occurs when surface fires create enough energy to pre-heat and then combust live fuels in the canopy. Crown fires are initiated with "torching" of lower canopy fuels (e.g., branches, leaves, lichen) that "ladder" the fire to the crown. The higher the canopy fuels are above the surface, as determined by crown base height (CBH), or higher canopy moisture content, the less chance of torching (Agee et al. 2002; Agee and Skinner 2005). Once in the crown, the sustained spread of fire to other crowns occurs with high fuel density (i.e., canopy bulk density) and high rate of spread, which increases with wind speed (Agee et al. 2002; Hall and Burke 2006).

Landscape scale.—At the landscape scale of a wildfire, fire behavior is controlled by variation in topography, weather, and the spatial and vertical pattern of fuels (McGranahan and Wonkka 2018). Forested landscapes with heterogenous patches of different fuel types,

moisture content, and natural (e.g., riparian areas) or managed surface fuel breaks can slow fire spread (Weatherspoon and Skinner 1996; Agee et al. 2000; Schmidt et al. 2008).

Regional scale.—At the regional scale, constraints on fire behavior and severity are related to mean climate, patterns of ignition, and broad patterns of vegetation that define fire regimes over decades or longer (McGranahan and Wonkka 2018). In their analysis of Western U.S. forested ecoregions spanning years 2002–2015 and including 2,061 unique fires, Parks and colleagues (2018) found that fire severity at these spatiotemporal scales was primarily determined by variables related to live fuels, followed by variables related to fire weather, climate (i.e., 30-year normals), and topography.

Weather is another critical factor that controls the behavior and severity of a wildland fire over a landscape. In the Western U.S., years with high precipitation in winter and spring can promote vegetation growth, thereby increasing fine-fuel loads, while a dry and hot summer and fall can remove moisture from fuels, making them more combustible (Balch et al. 2018). In California, extreme wind events in the fall can exacerbate pre-existing dry conditions that can lead to more severe fires. For example, the most severe damage inflicted by the Sonoma Complex Fires occurred in the first 14 hours, when strong Diablo winds were channeled by topography through a wind corridor, moving through fuels that had built-up during a wet winter—preconditioned for fire by the warmest summer and autumn on record (Nauslar et al. 2018).

Machine learning

Variable development.—Based on information from the literature and from local wildland fire experts, we used machine learning techniques (Kane et al. 2015) to determine the importance of specific spatial variables for predicting percent woody canopy damage. Machine learning is an artificial intelligence method that analyzes sample data to identify patterns in large, diverse datasets. In this project, the dependent variable in each fire analysis was the percent woody canopy damage of each sub-polygon. We created 66 landscape and weather/climate spatial datasets used as independent variables in the machine learning analysis (Table 1).

There are a total of 46,835 woody canopy condition sub-polygons across the study areas. We calculated landscape and weather/climate variables for each of the sub-polygons using python, pandas and arcpy, and stored these data in a table with each row representing a sub-polygon and each column representing the values of one of the 66 independent variables. Many of the variables were derived from topographic and elevation data from the Sonoma Veg Map Program. For example, based on work by Kramer (Kramer et al. 2014, 2016) and Hoff (Hoff et al. 2019) we used LasTools to create a 20-m resolution ladder fuel proxy derived from the Sonoma County 2013 countywide QL1 (8 points per square meter) lidar point cloud. These data provide information about the density of living and dead vegetation in vertical strata between one and four meters, and from four and eight meters above the ground.

The values of cells in the table represented the mean value for the independent variable for that sub-polygon if the independent variable was continuous, and the plurality value if the independent variable was thematic. In addition to the variables characterizing the sub-polygons themselves, a number of independent variables were created for the sub-polygon plus its surrounding neighborhood. These variables were created in the same manner as those

Table 1. Independent variables used in the machine learning analysis. LC = measure of land cover type; T = measure of topography; S = measure of nearness to streams; V = measure of vegetation structure; C = measure of climate/weather condition

Description of Independent Variables	Abbreviation	Measurement Type
[1]Fine-scale vegetation class of the sub-polygon	Veg	LC
[1]Majority fine-scale vegetation class within 1000 ft (304.8 m) of sub-polygon	MajVeg-1000	LC
[1]Majority fine-scale vegetation class within 500 ft (152.4 m) of sub-polygon	MajVeg-500	LC
[3]Percent of sub-polygon that is impervious	%Imperv	LC
[3]Percent of sub-polygon that is structure	%Struc	LC
[1]Percent of area surrounding sub-polygon that is forest within 1000 ft (304.8 m)	%Surr-For-1000	LC
[1]Percent of area surrounding sub-polygon that is forest 500 ft (152.4 m)	%Surr-For-500	LC
[1]Percent of area surrounding sub-polygon that is impervious within 1000 ft (304.8 m)	%Surr-Imperv-1000	LC
[3]Percent of area surrounding sub-polygon that is impervious 500 ft (152.4 m)	%Surr-Imperv-500	LC
[1]Percent of area surrounding sub-polygon that is shrub within 1000 ft (304.8 m)	%Surr-Shrb-1000	LC
[1]Percent of area surrounding sub-polygon that is shrub 500 ft (152.4 m)	%Surr-Shrb-500	LC
[1]Percent of area surrounding sub-polygon that is not forest or shrub within 1000 ft (304.8 m)	%Surr-NoFor-Shrb-1000	LC
[1]Percent of area surrounding sub-polygon that is not forest or shrub 500 ft (152.4 m)	%Surr-NoForShrb-500	LC
[1]Percent of area surrounding sub-polygon that is vineyard within 1000 ft (304.8 m)	%Surr-Vine-1000	LC
[1]Percent of area surrounding sub-polygon that is vineyard 500 ft (152.4 m)	%Surr-Vine-500	LC
[1]Percent of sub-polygon cone area that is vineyard	%Cone-Vine	LC
[3]Percent of sub-polygon cone area that is structure	%Cone-Struc	LC
[3]Percent of sub-polygon cone area that is impervious	%Cone-Imperv	LC
[1]Area of *Eucalyptus* stand nearest to sub-polygon	Area-Euca	LC
[1]Distance of sub-polygon to nearest *Eucalyptus* stand	Dist-Euca	LC
[1]Distance of sub-polygon to nearest conifer stand	Dist-Conif	LC
[1]Distance of sub-polygon to nearest irrigated area	Dist-Irrig	LC
[1]Distance of sub-polygon to nearest knobcone pine stand	Dist-Knob	LC
[1]Distance of sub-polygon to nearest riparian stand	Dist-Rip	LC
[1]Distance of sub-polygon to nearest shrub stand	Dist-Shrb	LC

Table 1 continued

Description of Independent Variables	Abbreviation	Measurement Type
[1]Distance of sub-polygon to nearest structure	Dist-Struc	LC
[2]Percent of sub-polygon burned in fires from 1939–present	%Burn-39-2020	LC
[2]Percent of sub-polygon burned in fires from 1939–1969	%Burn-39-69	LC
[2]Percent of sub-polygon burned in fires from 1970–1991	%Burn-70-91	LC
[2]Percent of sub-polygon burned in fires from 1992–2017	%Burn-92-17	LC
[4]Distance of sub-polygon to nearest property with a conservation easement	Dist-Ease	LC
[4]Distance of sub-polygon to protected lands (park, preserve etc.)	Dist-Prot	LC
[3]Sub-polygon majority aspect	Maj-Asp	T
[3]Sub-polygon majority 32-class slope aspect index	Maj-SlpAsp	T
[5]Topographic index for majority of the sub-polygon	Maj-TopoInd	T
[3]Sub-polygon mean ground elevation	Mn-Elev	T
[5]Topographic index within 1000 ft (304.8 m) of sub-polygon	TopoInd-1000	T
[5]Topographic index within 500 ft (152.4 m) of sub-polygon	TopoInd-500	T
[3]Sub-polygon mean slope from bare earth DEM	Mn-Slp	T
[3]Sub-polygon mean horizontal distance from nearest stream	Mn-DistStr	S
[3]Sub-polygon mean height above river (relative to nearest large stream)	Mn-HtRiv	S
[3]Sub-polygon [# of lidar returns from 1–4m/# of lidar returns from 0–4 m]	Lad-1-4	V
[3][# of lidar returns from 1–4 m /# of lidar returns from 0–4 m] within 1000 ft (304.8 m) of sub-polygon	Lad-1-4-1000	V
[3][# of lidar returns from 1–4 m /# of lidar returns from 0–4 m] within 500 ft (152.4 m) of sub-polygon	Lad-1-4-500	V
[3]Sub-polygon [# of lidar returns from 4–8 m/# of lidar returns from 0–8 m]	Lad-4-8	V
[3][# of lidar returns from 4–8 m /# of lidar returns from 0–8 m] within 1000 ft (304.8 m) of sub-polygon[3]	Lad-4-8-1000	V
[3][# of lidar returns from 4–8 m /# of lidar returns from 0–8 m] within 500 ft (152.4 m) of sub-polygon	Lad-4-8-500	V
[3]Sub-polygon percent canopy density in the 15–60 ft (4.6–18.3 m) range	%CnpDen-15-60	V

Table 1 continued

Description of Independent Variables	Abbreviation	Measurement Type
[3]Sub-polygon percent canopy density in the 60–100 ft (18.3–30.5 m) range	%CnpDen-60-100	V
[3]Sub-polygon percent canopy density in the 100–150 ft (30.5–45.7 m) range	%CnpDen-100-150	V
[3]Sub-polygon percent canopy density in the 150–200 ft (45.7–61.0 m) range	%CnpDen-150-200	V
[3]Sub-polygon percent canopy density in the 200–250 ft (61.0–76.2 m) range	%CnpDen-200-250	V
[3]Sub-polygon mean absolute canopy cover	Mn-CnpCov	V
[3]Sub-polygon mean canopy height	Mn-CnpHt	V
[3]Sub-polygon mean canopy slope	Mn-CanSlp	V
[3]Standard deviation of sub-polygon canopy cover	SD-CnpCov	V
[3]Standard deviation of sub-polygon canopy height	SD-CnpHt	V
[3]Presence of woody land cover above 6 ft (1.8 m) in height	%Wood>6ft	V
[8]Sub-polygon mean climatic water deficit (September 2017)	Mn-CWD	C
[8]Sub-polygon mean evapotranspiration (1980-2010)	Mn-Evap	C
[6]Sub-polygon mean summer fog (June to August)	Mn-Fog	C
[8]Sub-polygon mean average annual precipitation (1980-2010)	Mn-Precip	C
[6,7]Humidity at the nearest weather station at the time MODIS/VIRS first detected the fire at the sub-polygon	Humid	C
[6,7]Wind direction at nearest weather station at the time MODIS/VIRS first detected the fire at the sub-polygon	WndDir	C
[6,7]Wind speed at nearest weather station at the time MODIS/VIRS first detected the fire at the sub-polygon	WndSpd	C
[6,7]Wind gust speed at nearest weather station at the time MODIS/VIRS first detected the fire at the sub-polygon	WndGustSpd	C

Sources:
[1]Sonoma Veg Map Program Vegetation Products
[2]CAL FIRE
[3]Sonoma Veg Map Program Lidar Products
[4]California Protected Areas Database/ California Conservation Easement Database
[5]California Landscape Conservation Partnership
[6]NASA MODIS/VIIRS
[7]Weather Stations
[8]Basin Characterization Model (270 m) (Flint et al. 2013)

for the sub-polygons, except that the variable values were calculated for areas within a fixed distance radius (152 or 305 m (500 or 1000 ft)) from the sub-polygon and for areas within cones extending a half mile northeast (340 to 120 degrees) from the sub-polygons. Independent variables are grouped into five variable types based on their foundation as follows:

- Measures of land cover type
- Measures of topography
- Measures of nearness to streams
- Measures of vegetation structure
- Measures of climate/weather condition

Initially the sub-polygons were segregated by fire (Nuns, Tubbs, and Pocket fires) and further by the areas where fire progression was wind-driven or not. To determine wind-driven verses non-wind-driven fire areas, we used NASA Moderate Resolution Imaging Spectroradiometer (MODIS) and Visible and Infrared Scanner (VIRS) imagery to map the perimeters of each fire during (1) the extreme wind-driven fire events which spanned from the time of fire ignition on the late evening of 8 October 2017 continuing to early morning on 9 October 2017 and (2) the non-wind-driven fire events which burned from the morning of 9 October 2017 to 18 October 2017 (Figure 8) (Schroeder et al. 2014). Consequently, the machine learning analysis was initially performed separately on six fire events:

- Nuns fire wind-driven event
- Nuns fire non-wind-driven post wind event
- Tubbs fire wind-driven event
- Tubbs fire non-wind-driven post wind event
- Pocket fire wind-driven event
- Pocket fire non-wind-driven post wind event

In addition, the machine learning analysis was performed on a combination of all fires, segregated only by whether the fire was wind-driven or not.

Random Forests Analysis.—Next, we ran a Random Forests (Breiman and Cutler 2014) machine learning regression analysis against the data set to determine which independent variables are most predictive of percent woody canopy damage (measured in 1% increments) resulting from each fire. Random Forests is a supervised ensemble machine learning technique that uses the values of sample data (i.e., training data) to construct multiple decision trees for modelling the relationships between a dependent variable and the independent variables. The final model output of Random Forests is the most common (i.e., modal) prediction from all of the trees (Green et al. 2017).

To complete the analysis, we first implemented multiple runs of Random Forests with R's randomForest package with different parameters (e.g. number of trees, tree depth), and used the caret package to determine the optimal *mtry* parameter for each fire event (i.e., the number of variables available for splitting at each tree node). We chose parameters that resulted in the highest testing accuracy. Second, we ran each of the six fire events through Random Forests 100 times with different random selections of 80% of the sub-polygons for model training and 20% for model testing. Lastly, we calculated the average (for 100 runs per event) R^2 for the linear relationship between predicted and estimated percent woody canopy damage, the root-mean square error (RMSE) of predictions, and the increase in mean squared error of the Random Forests model for when each independent variable was excluded from the model.
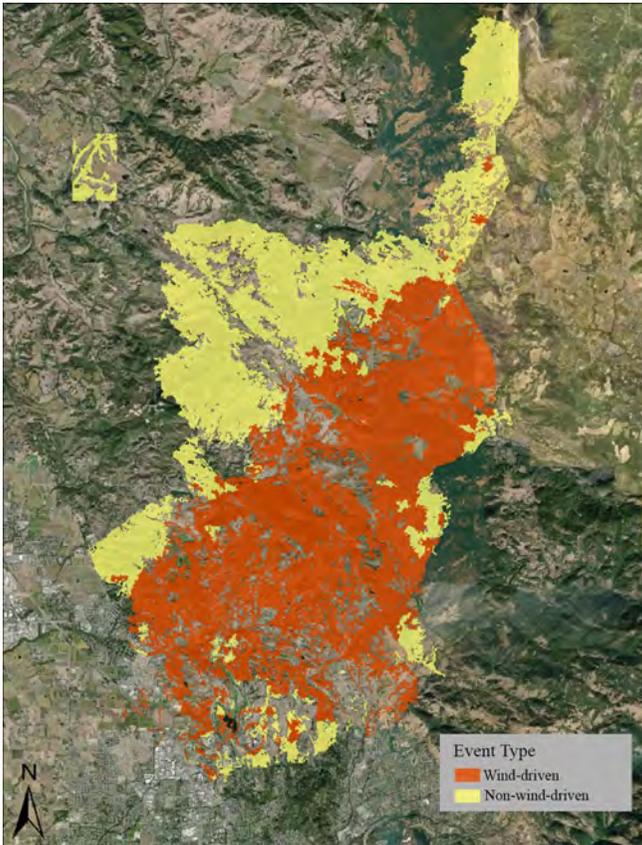
Figure 8. The Tubbs fire segregated into areas that burned during (orange) and after the wind event (yellow).

Finally, we evaluated the importance of each of the 64 independent variables in each of the six fire event models (Genuer et al. 2010). We measured variable importance as the percent increase in mean square error that can be attributed to the exclusion of the variable in the model (Liaw and Wiener 2002). Random Forests calculates this statistic by running the analysis first with the measured value for each variable sample, and then a second time, but letting the value of the variable change randomly. The resulting change in the mean square error measures how the exclusion of a variable decreases the accuracy of the model versus if the variable was included.

RESULTS

Post-fire woody canopy condition mapping

The amount of area in each percent canopy damage classes for the Tubbs and Nuns fires are very similar, with large expanses of higher woody canopy damage; 42–43% of the fire areas are in the 80–100% woody canopy damage percent class. Conversely, the Pocket Fire presents more of a mosaic of woody canopy damage across the landscape with only 19.6 % of the fire area in the 80–100% woody canopy damage percent class (Figure 9).
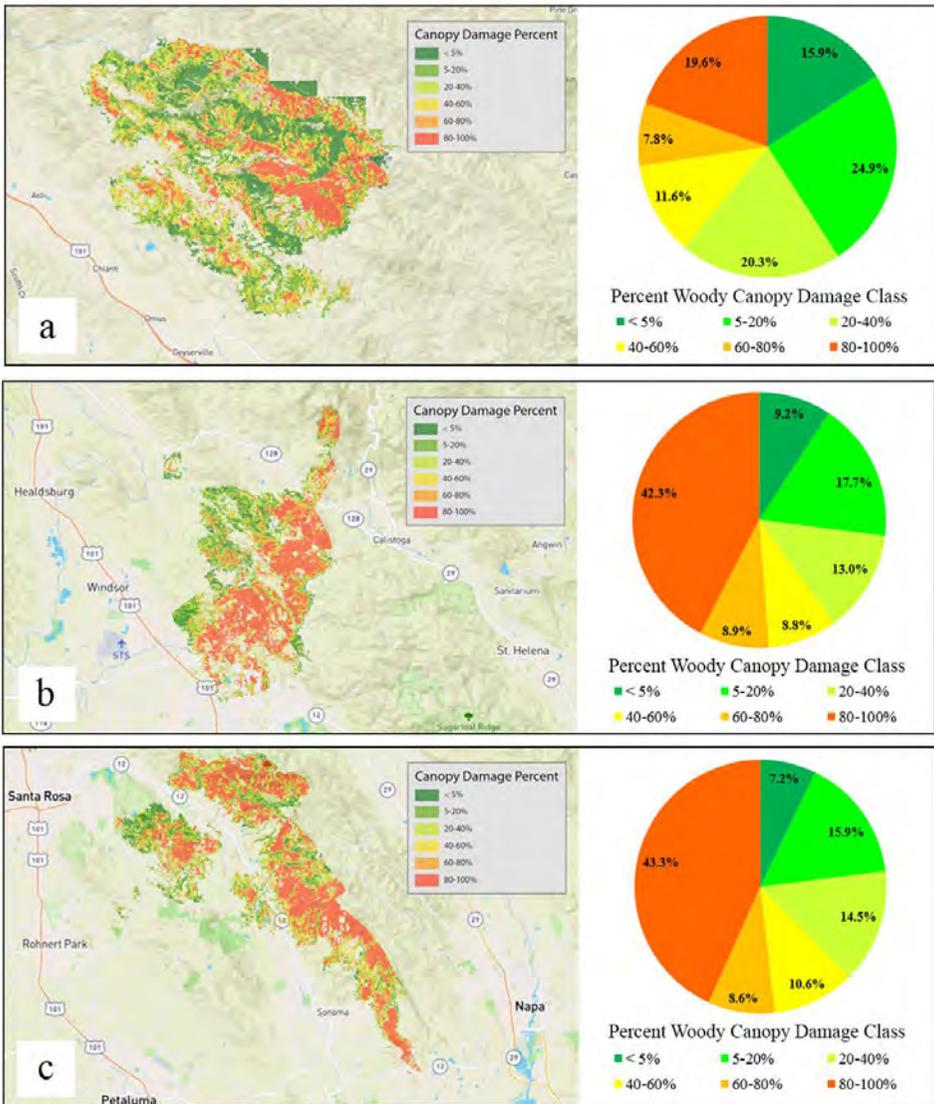
Figure 9. Woody canopy condition maps and proportion of each fire area in each of the percent canopy damage classes for the Pocket (a), Tubbs (b), and Nuns (c) fires. The continuous woody canopy condition values for each of the three fires have been consolidated into percent classes (e.g. <5%, 5–20%, etc.).

Machine learning

Six fire event analysis.— All of the fire events show that a significant amount of variation in woody canopy condition can be explained by the models (Table 2). For each of the six fire events, we determined the 10 most important independent variables in model development and associated percent improvement in mean square error (Figure 10).

Table 2. Comparison of average R^2, RMSE, and MSE for Random Forests models for each of the fire events.

Fire Event	Average R^2	Average RMSE	Average MSE
Nuns Non-Wind	0.55	0.22	0.048
Nuns Wind	0.45	0.24	0.058
Pocket Non-Wind	0.51	0.22	0.048
Pocket Wind	0.50	0.20	0.040
Tubbs Non-Wind	0.56	0.21	0.044
Tubbs Wind	0.52	0.23	0.053

Vegetation structure measures are the most important for all six events and the second most important for all but one event. For example, the ladder fuel metric is 1.5 times more important than the next most important variable (mean canopy height) for the Nuns non-wind-driven event and 1.7 times more important than the next most important variable (horizontal distance to stream) in the Tubbs wind-driven event. Additionally, 32% of the top 10 important variables are measures of vegetation structure.

Climate/weather variables are less important than vegetation structure, but still appear in the top 10 important variables for all six events. Climatic water deficit in 2017, mean evapotranspiration, and wind direction are each listed three times in the top 10 variables. However, wind direction is important only for the non-wind-driven event models which is understandable, as the wind direction during the wind events was fairly constant from the northeast. Measures of how close a sub-polygon is to a stream are in the top 10 important variables for all six events, with the exception of the Tubbs non-wind-driven event. Measures of topography appear as a top 10 variable in only two events. There are more land-cover type variables in Figure 10 than any other variable type, comprising 37% of the ten most important variables. The Pocket wind-driven event is notably different from the other events in that the percent increase in the mean square error attributable to the variables is lower (by a half or a quarter) than that of the top variables of the other events.

While they tend to be less important than vegetation structure measures, there are some additional patterns in the six fire analysis which are of note:
- Distance to nearest *Eucalyptus* polygon is listed as one of the most important variables three times. This was surprising given the small amount of *Eucalyptus* occupying the study area prior to the fires (61 acres).
- Distance to nearest shrub stand appears three times as one of the most important variables.
- Measures of the proximity of a building structure to a sub-polygon appears twice.
- The majority fine-scale vegetation class within 500 or 1000 feet of the sub-polygon appears seven times.
- Distance to knobcone pine stands appears twice.

Combined event analysis.— We removed the stratification of the fires based on location and ran Random Forest on all fires combined, stratifying only by wind-driven or non-wind-driven events. The average variance in the data explained by the models (R^2) increased for both wind- and non-wind-driven events (Table 3), suggesting that the general location of the fires within Sonoma County was not an important factor in fire behavior.
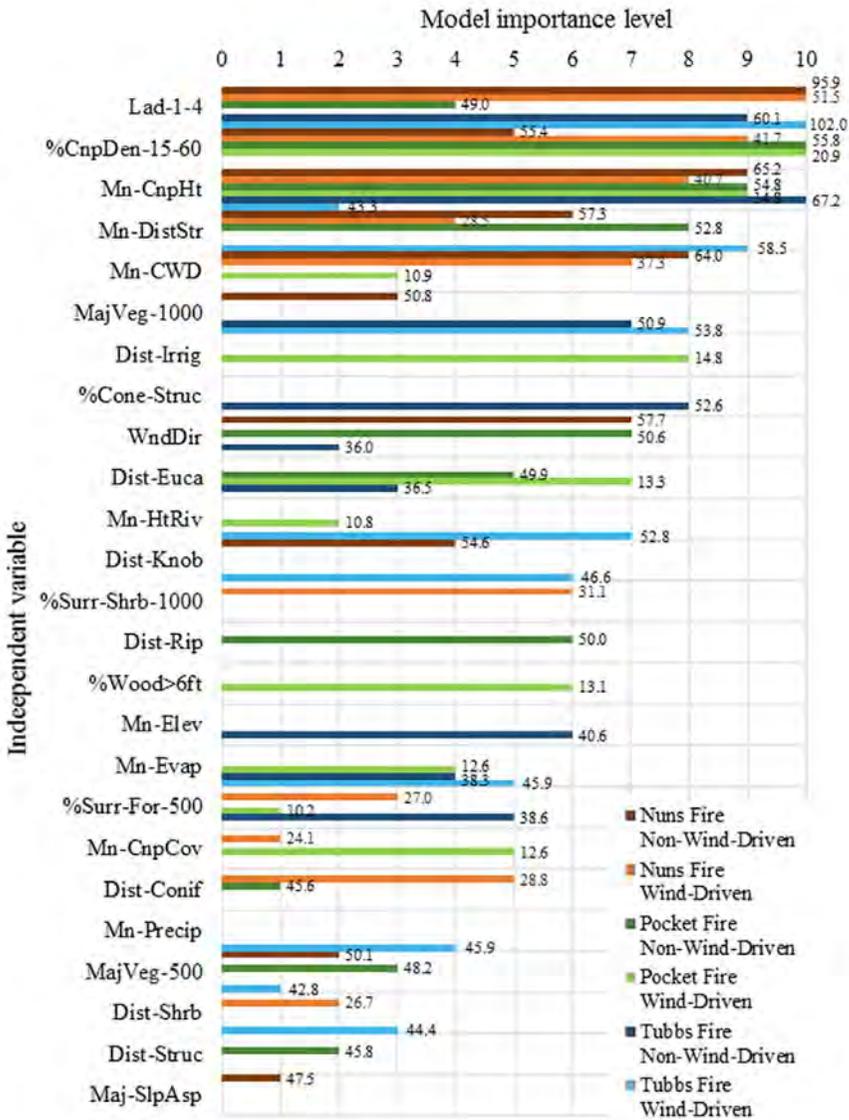
Figure 10. Comparison of the 10 most important independent variables for the six fire events (10 = more important; 1 = less important). Data labels represent the average percent increase in MSE resulting from the exclusion of the variable from the model for 100 runs.

Table 3. Average R², RSME, and MSE for the combined fires Random Forests model runs.

Fire Event	Average R²	Average RMSE	Average MSE
Combined Fires Non-wind-driven	0.63	0.27	0.073
Combined Fires Wind-Driven	0.56	0.29	0.084

For the two-event analysis, where events were stratified by whether or not they were wind- or non-wind-driven, we determined the 10 most important independent variables in model development and associated percent improvement in mean square error (Figure 11). Like the six-event models, measures of vegetation structure, topography, and nearness to streams are the most important variables that affect woody canopy condition, and wind direction is important only in the non-wind event. In contrast to the six-event analysis, the slope-aspect index of the sub-polygon appears at the first (non-wind-driven event) and second position (wind-driven event).
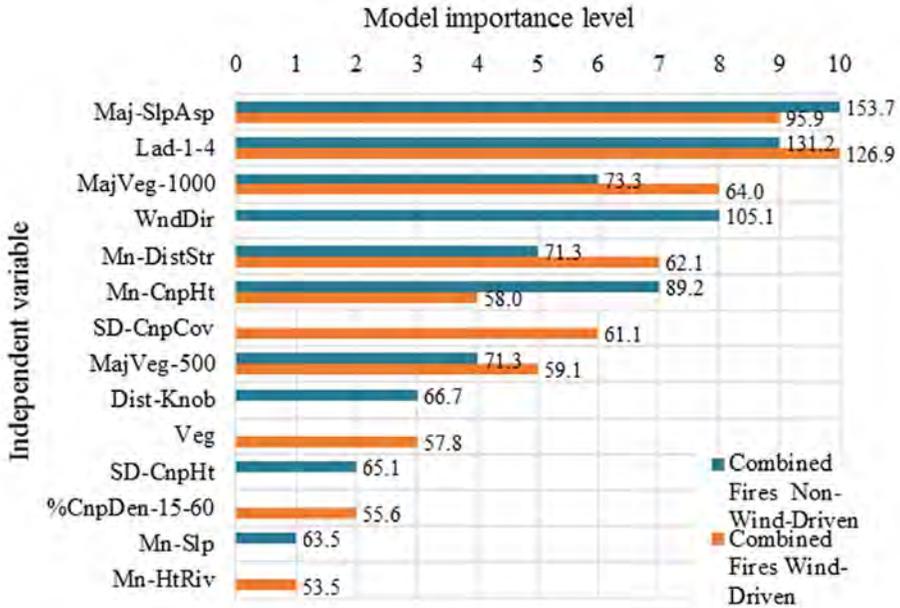

Figure 11. Comparison of the 10 most important independent variables for the two-event analysis (10 = more important; 1 = less important). Data labels represent the average percent increase in MSE resulting from the exclusion of the variable from the model for 100 runs.

There is notably less variability in the measures when comparing the results of the combined fire analysis (Figure 11) versus the six-fire event analysis (Figure 10). For example, only one variable related to nearness to stream appears, rather than the three different variables in Figure 10. Fewer land cover type variables appear to be important and most of those are a measure of the fine-scale vegetation class within 500 or 1000 ft of the sub-polygon. The only climate/weather variable identified as important is wind direction, and it only appears in the non-wind-driven event.

Effect of discontinuous variables

To understand the marginal effect of discontinuous variables, we examined the distribution of the independent variables by percent woody canopy damage. The fine-scale vegetation class is a variant in over 37% of independent variables in Figure 10 (the six event

analysis) and in 30% of the variables in Figure 11 (the combined event analysis). Riparian and mesic types have the lowest percent canopy damage, followed by the open hardwood woodland types such as blue oak (*Quercus douglasii*), black oak (*Quercus kelloggii*), valley oak (*Quercus lobata*), and Oregon white oak (*Quercus garryana*). Shrub and upland conifer types exhibited the most percent canopy damage, including fire-adapted knobcone pine (*Pinus attenuata*) and chamise (*Adenostoma fasciculatum*) vegetation alliances (Table 4).

Table 4. Area weighted average canopy damage by fine-scale vegetation class.

Fine-scale Vegetation Map Class	Percent Canopy Damaged
Populus fremontii Alliance	15%
Vancouverian Riparian Deciduous Forest Group	19%
Southwestern North American Riparian Evergreen and Deciduous	26%
Acer macrophyllum Alliance	28%
Southwestern North American Riparian/Wash Scrub Group	30%
Quercus chrysolepis Alliance	30%
Quercus lobata Alliance	31%
Quercus garryana Alliance	35%
Quercus douglasii Alliance	37%
Quercus kelloggii Alliance	38%
Rubus armeniacus Alliance	39%
Arctostaphylos viscida Alliance	41%
Quercus wislizeni (tree) Alliance	43%
Quercus (agrifolia, douglasii, garryana, kelloggii, lobata, wislizenii) Alliance	43%
Non-native Forest & Woodland	48%
Pseudotsuga menziesii Alliance	48%
Aesculus californica Alliance	48%
Quercus agrifolia Alliance	50%
Umbellularia californica Alliance	52%
Arbutus menziesii Alliance	55%
Hesperocyparis sargentii Alliance	55%
Pseudotsuga menziesii - Notholithocarpus densiflorus Alliance	56%
Sequoia sempervirens Alliance	58%
Hesperocyparis macnabiana Alliance	67%
Non-native Shrub	67%
Eriodictyon californicum - Lupinus albifrons Alliance	69%
Pinus sabiniana / Quercus durata Provisional Alliance	70%
Quercus wislizeni (shrub) Alliance	71%
Notholithocarpus densiflorus Alliance	71%

Table 4. continued

Fine-scale Vegetation Map Class	Percent Canopy Damaged
Pinus ponderosa - Pseudotsuga menziesii Alliance	71%
Eucalyptus (globulus, camaldulensis) Semi-natural Alliance	77%
Ceanothus cuneatus Alliance	80%
Baccharis pilularis Alliance	82%
Quercus durata Alliance	83%
Adenostoma fasciculatum Alliance	89%
Californian Mesic Chaparral Group	90%
Arctostaphylos (canascens, manzanita, stanfordiana) A. glandulosa Mapping Unit	93%
Pinus attenuata Alliance	95%
Pinus lambertiana Alliance	99%
Pinus radiata Alliance	99%
Ceanothus thyrsiflorus Alliance	99%

High proportions of the shrubs (88%) and eucalyptus (77%) in the study areas were damaged in contrast to low proportions of riparian hardwoods (20%) and deciduous hardwoods (36%) (Figure 12).
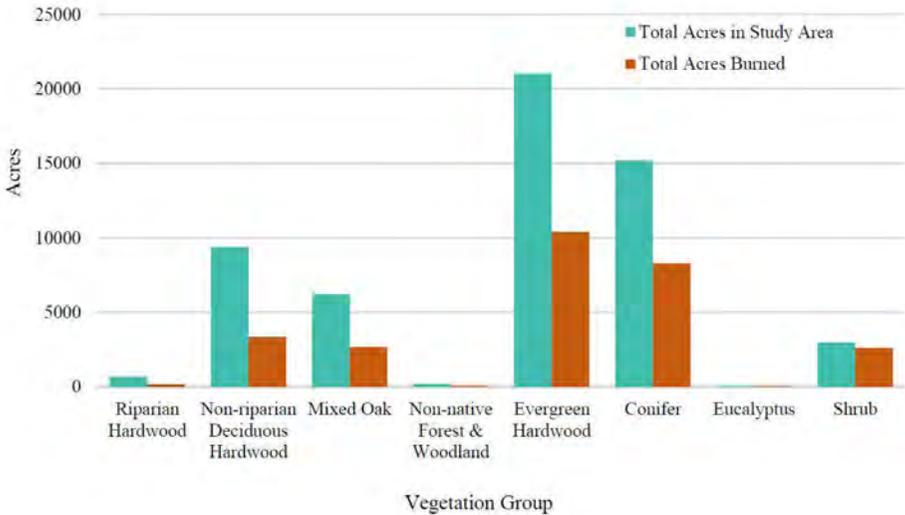
Figure 12. Acres of canopy damage across all fires versus the acres occupied by combined vegetation groups in the study areas before the fires.

While knobcone pine (*Pinus attenuata*) occupies only a small portion of the fire area (1,417 acres or 2.5%), a substantially higher proportion of it (90%) was damaged compared to other conifers such as Douglas fir (*Pseudotsuga menziesii*) (48%) and Sargent cypress (*Hesperocyparis sargentii*) (55%) (Figure 13). Among hardwoods, greater portions of *Eucalyptus* and tanoak (*Notholithocarpus densiflorus*) were damaged, while riparian hardwood communities exhibited the lowest percent woody canopy damage (Figure 14).
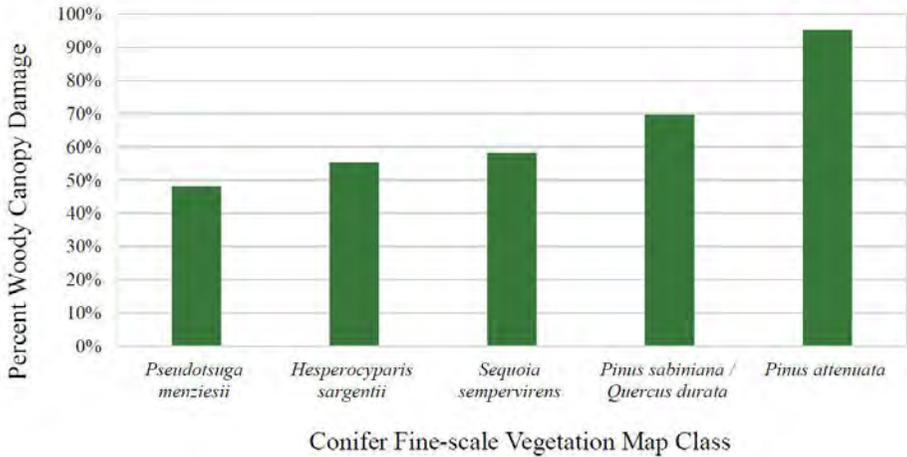
Figure 13. Comparison across conifer vegetation classes of the area damaged by the fires as a percent of total area occupied by the class within the study areas.
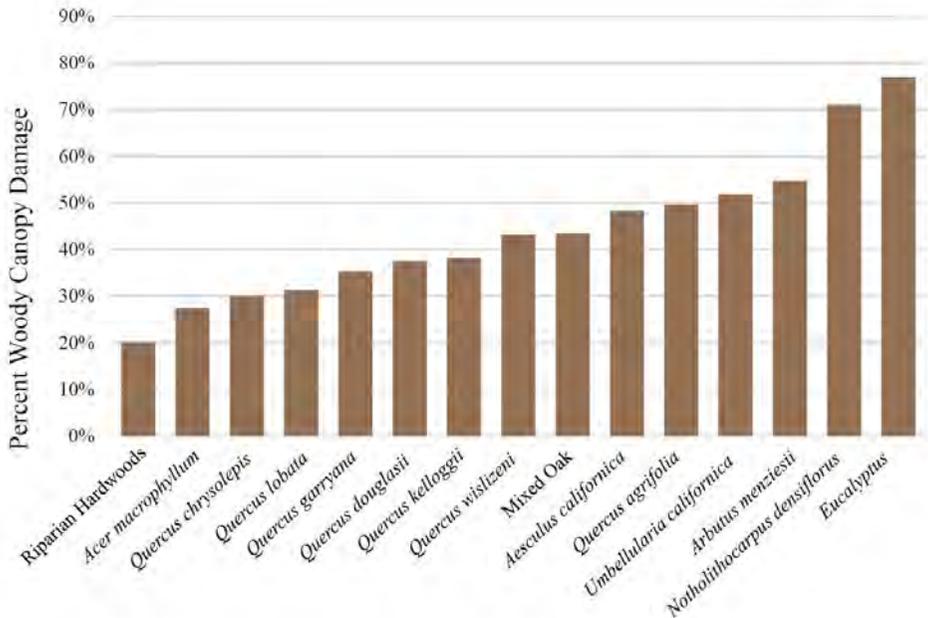
Figure 14. Comparison across hardwood vegetation classes of the area damaged by the fires as a percent of total area occupied within the study areas.

In addition to fine-scale vegetation class, slope-aspect is an important independent variable in the combined event analysis. Sub-polygons with steep south, southwest, and southeast facing slopes experienced the highest percent canopy damage for both the wind-driven and non-wind-driven events (Figures 15 and 16). In addition to ladder fuels, slope

Canopy Damage by Slope-Aspect
Wind-Driven Fires (18,097 acres)
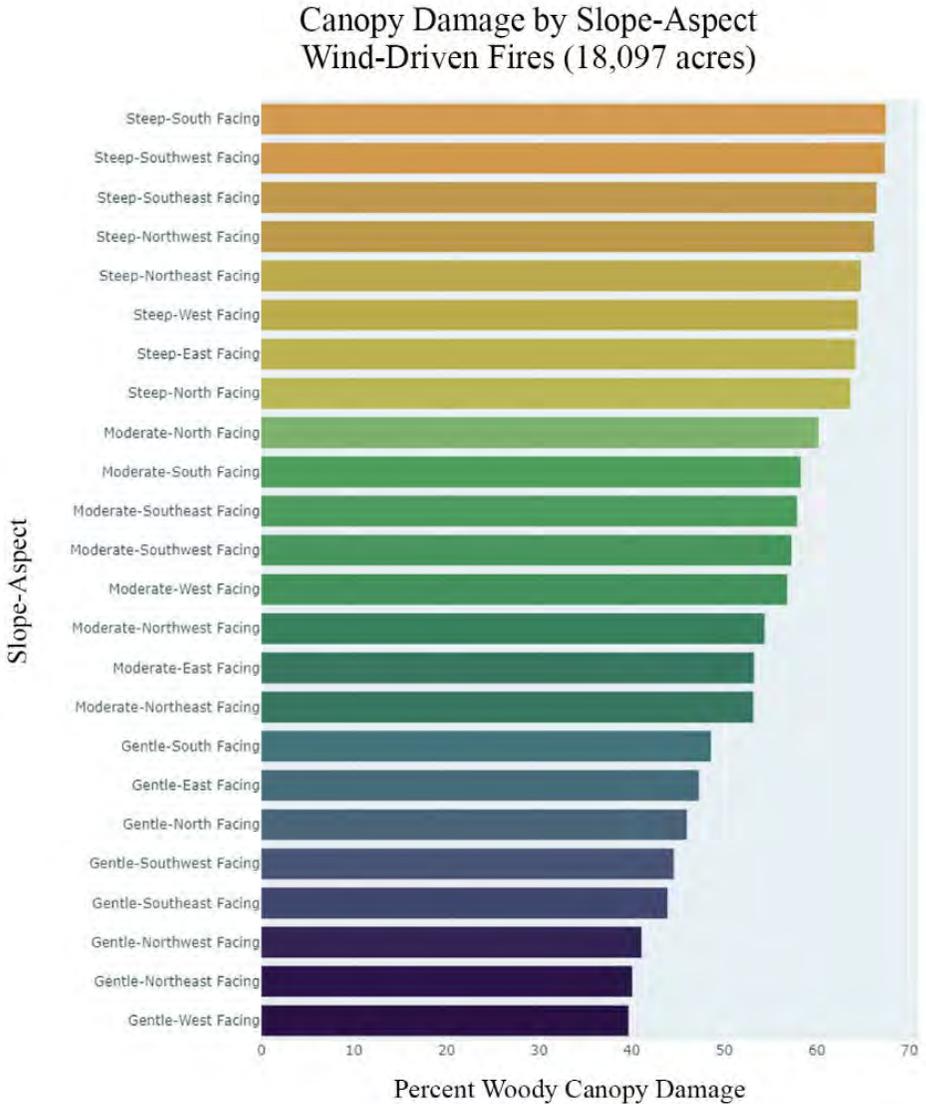
Figure 15. Area weighted average canopy damage by slope-aspect class for the combined wind-driven event.

appears to be the primary driving factor for post-fire canopy condition in the wind-driven fires (Figure 15), with percent canopy damage directly related to slope class—the steeper the slope, the higher the percent damage. Damage in the non-wind-driven fires is much less affected by slope, with steep north and northeast areas sustaining the lowest canopy damage.
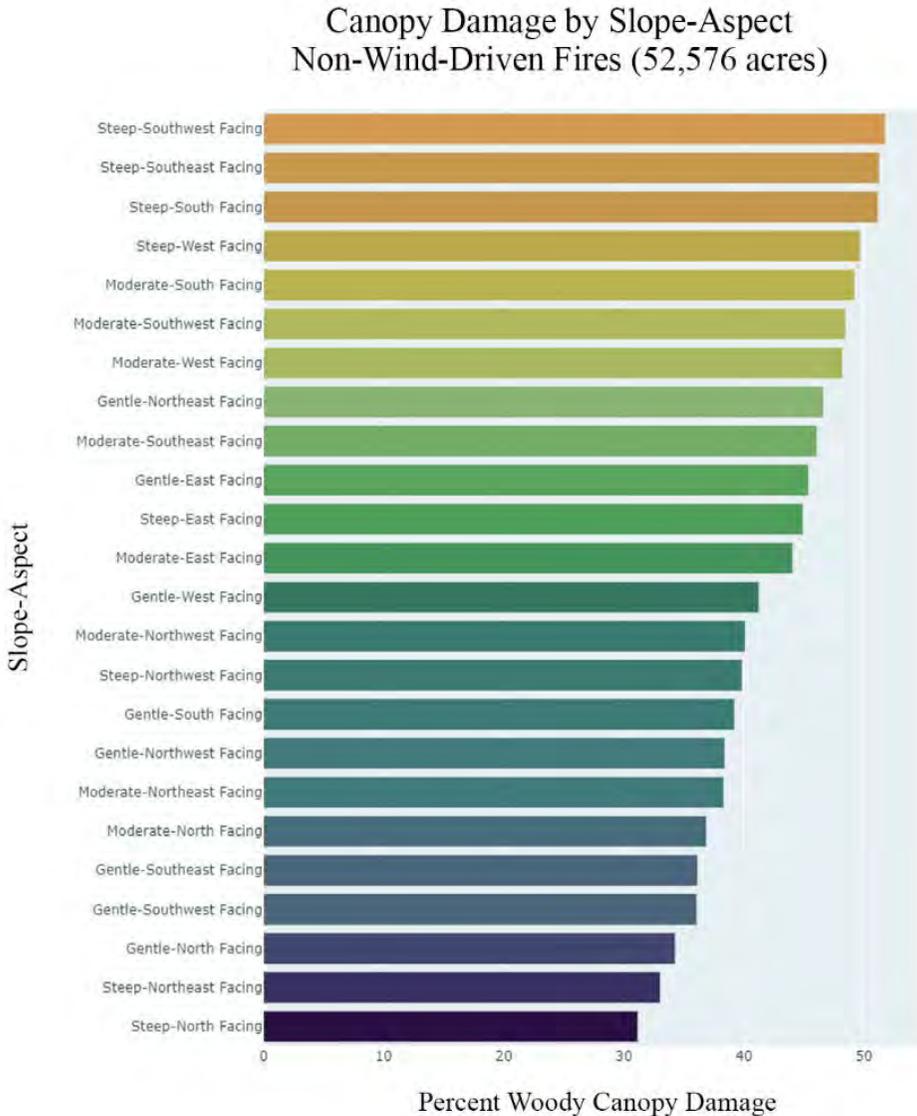
Figure 16. Area weighted average canopy damage by slope-aspect class for the combined non-wind-driven event. Slope was not a strong predictor of damage in non-wind-driven fires.

Effect of continuous variables

To better understand the relationship between the important independent variables and woody canopy condition, we developed partial dependence graphs for the more important continuous independent variables (Figure 17). Partial dependence plots show the marginal effect an independent variable has on the prediction of the dependent variable in Random Forests models, and can help show the direction of the relationship and whether the relationships between dependent and independent variables are linear, quadratic or more complex
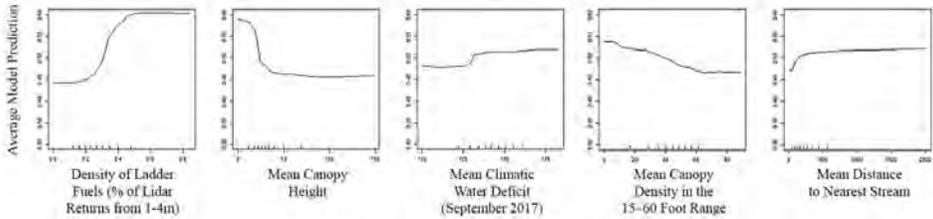
Figure 17. Partial dependence plots for five continuous variables for the six fire events.

(Friedman 2001).

The greater the density of ladder fuels, the higher mean climatic water deficit, and the further away from a stream, the greater the predicted percent canopy damage. The greater the mean canopy height and mean canopy density in the 15–60 ft. range, the lower the predicted percent canopy damage.

Ladder fuels and vegetation type are both important independent variables in all of the machine learning models, and the density of pre-fire ladder fuels varies across vegetation communities within the study area (Figure 18). Knobcone pine (*Pinus attenuata*) and upland shrubs have higher percentages of ladder fuels than other vegetation types in Figure 18, as well as a higher percentage of canopy damage (Table 4).

DISCUSSION

Results of our analysis showed that high resolution airborne imagery and semi-automated techniques can be effectively used to create highly accurate maps of woody canopy condition following a wildfire, and that those maps can be used to better understand how different landscape variables contribute to woody canopy damage from fire. Vegetation structure and type, weather/climate variables, slope, and distance from streams are the primary variables that affect post-fire woody canopy condition in the landscapes of eastern Sonoma County. The higher the density of shrubs and fire-adapted vegetation types, and the higher the density of ladder fuels, the higher the damage. The closer to streams, the lower the damage. During wind-driven fire events, the steepness of slope is also indicative of damage, with steeper slopes experiencing more damage.

Applications for land management, land conservation, land use

The woody canopy condition maps and the replicable approach to mapping and modeling support a wide variety of wildfire recovery and resiliency efforts that protect and
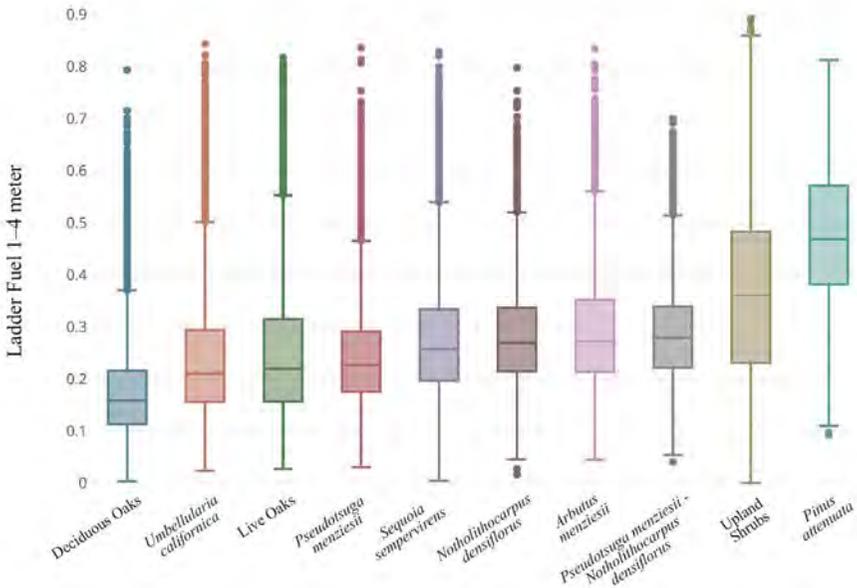
Figure 18. Density of pre-fire ladder fuels by vegetation type within the study areas. Deciduous oaks include blue oak woodland, leather oak chaparral, Oregon white oak woodland, black oak woodland, and valley oak woodland; live oaks include coast live oak woodland, canyon live oak woodland, and interior live oak woodland; upland shrubs include chamise chaparral, hazelnut scrub, Ceanothus chaparral, manzanita chaparral, coyote brush, Californian mesic and maritime chaparral, poison oak scrub, and interior live oak chaparral.

benefit California ecosystems and human communities. Fire behavior experts have long recognized that wildfire behavior is affected by topography, weather, and vegetation type and structure (Finney 1998; Scott and Burgan 2005). This study validates the importance of those variables, but more importantly it offers tools to support the management of those within our control. While we cannot directly manage weather or topography, we can manage wildland fuels, and policy makers can make informed decisions about whether or not valuable assets should be placed in landscapes with heavy fuels and limited access and egress. With this information, we can deploy effective fuel management appropriate for given ecosystem types to promote ecological integrity of the system and support community safety and disaster preparedness. There is neither the funding available nor the need to treat all of the landscape. Now that we can accurately and efficiently map ladder fuels, vegetation type, and vegetation structure, treatments can be prioritized based on the location of heavy fuel loads vis a vis the location of features and assets in need of protection. For example, now that we understand that stream beds are important barriers to fire damage, we can tailor those treatments to account for their importance and the ecological sensitivity of riparian areas. Additionally, fuel reduction efforts such as prescribed or managed fire can be used effectively in these landscapes with less potential damage to nearby structures. Land conservation investments can be targeted in areas of high repetitive fire damage, or in the WUI that surrounds human settlements, and these land conservation easements or fee title purchases can be managed in a way to reduce fuel loading or create fire breaks. Examples

of this might include a conservation easement that is intended for cultivated agriculture, grazing, or riparian corridor protection, or a park that has extensive thinning of ladder fuels. Sonoma County Ag + Open Space and other land conservation partners are using the results of this research to prioritize long term conservation investments that support ecosystem and community resiliency and achieve multiple benefits—including sustaining local food supplies, biodiversity, scenic open space, naturally filtered drinking water, as well as positive climate change action related to adaptation, carbon sequestration, and avoided emissions.

Sonoma County, like the State of California, has a strong land use policy focus on infill, combined with a publicly funded land conservation agency that protects working and natural lands. This research provides additional information to inform elected officials and policy makers about how and where development can take place in a way that meets housing demand, protects agricultural and natural lands, supports climate change action and helps to protect public health and safety due to extreme events such as wildfires.

Shared data and shared learning

One of the most important outcomes from this research has been the ability to share data and analysis methods and results with other entities working on related ecosystem and community issues. Starting with the Sonoma Veg Map Program foundational datasets, and continuing on with the research focused on the Sonoma Complex Fires, our data collection and modeling work has been useful beyond the original intent of informing Sonoma County land conservation, land use policy and land management. Lidar and other data from the Sonoma Veg Map Program have contributed to a wide variety of applications including environmental planning, flood risk assessment, carbon mapping, easement monitoring, habitat assessments and ecological restoration, climate adaptation planning, engineering design, agricultural planning, and scientific research (Green 2017).

This research has enhanced the capacity of conservation organizations, land managers, decision makers, and the public to understand the relationships between landscape characteristics, weather, and wildfire-caused woody canopy damage. As a result, public policy, public outreach strategies, and land conservation and management practices are being modified and informed by the findings of this research. The subsequent canopy condition and fire modeling datasets are supporting multiple applications including the prioritization and location of fuels reduction and vegetation management projects, public safety and evacuation route analysis, and land conservation prioritization. Additionally, the findings from this research have helped spur other regions such as the North Coast and Sierra Nevada, as well as other Bay Area counties (including Santa Clara, San Mateo, Marin, and Santa Cruz) and CAL FIRE to build fine-scale landscape datasets, in part, so they can better plan for, manage, and mitigate future extreme wildfire events.

Recommendations for additional research and analysis

Expand statistical analysis.—This project benefitted from an abundance of high-quality spatial data available in Sonoma County. The data created through the Sonoma Veg Map Program provided detailed datasets available in few other places in the country and this research would not have been possible without it. Yet even with the plethora of data available for inclusion in the modeling, the models do not fully explain the observed

variance and relationship between woody canopy condition and the landscape and weather variables included in the study. More research and funding are needed to determine additional landscape variables that might improve the models, including measures of surface fuels and land management history (including the use of grazing for fuel management). In addition, our research evaluated the importance of vegetation type in predicting canopy damage, but additional research is needed to better understand the impact of the vegetation type variables. Closeness to vegetation type repeatedly appears as an important variable that influences woody canopy condition, but which of those vegetation types increases or decreases the likelihood of woody canopy damage is not fully understood. The distance to vegetation type variables need to be parsed apart (i.e., into groups such as fire-adapted species, versus riparian species, deciduous oaks, shrubs, etc.) and studied in more depth.

Expand scope of study.—This research focused on the variables that impact damage to the woody canopies of forests and shrublands, but additional research is needed to analyze the landscape variables that contribute to building structure damage. Further, fire modeling is just one application for these datasets—there are other critical issues related to extreme events, ecosystem health and community safety that also rely on these types of data, and additional work is needed to identify landscape datasets that are relevant to multiple climate change and extreme event issues—such as emissions reduction/avoidance, fire, flood, drought, public health and safety—and articulate this need to policy and decision makers.

Expand study across space.— In addition, additional resources are needed to expand the analyses into other ecosystems. This research has provided meaningful analysis for wildfires in eastern Sonoma County, and repeating this research in other ecosystems with different dynamics would be useful in prioritizing fuel treatments in those areas and in determining if any statewide patterns emerge.

This research highlights the importance of lidar data in assessing wildfire risk, and expanding this study beyond Sonoma County is contingent upon lidar data being available. Until recently, many of the variables determined to be important in this study were not measurable, including the ladder fuel metrics, distance from fine-scale streams (i.e., both horizontal and vertical distance from the thalweg of streams at high resolution), mean canopy height, and mean canopy density in the 15 to 60 ft range. Additionally, lidar data are a critical input for the creation of the fine-scale vegetation type map which is also an important independent variable in the canopy condition machine learning analysis. Sonoma County is fortunate that its 2013 QL1 lidar collect was substantially funded by NASA research. The National Oceanic and Atmospheric Administration (NOAA) and the United States Geologic Survey (USGS) have done an admirable job supporting QL2 lidar collects in portions of California, but the USGS cost-sharing requirements are often a high hurdle for rural counties. The broad usefulness and value of lidar data demonstrated by this study points to the need for a partnership between federal and state agencies to complete a statewide lidar dataset.

Expand study across time.— In addition, the damage maps are critical in updating fine-scale vegetation maps for fire damage and providing baseline conditions from which we can further evaluate vegetation impacts over time. More funding is needed to remap the burned areas 3–5 years after the fires to fully understand the mid- and long-term impacts of the fires on the landscape. Finally, this study highlights the need for the development of semi-automated fine-scale change monitoring methods. The methods used in this study were highly successful in mapping woody canopy condition; however, the Sonoma datasets are based on 2013 data which are now seven years old. As other counties in California

and regions in the United States migrate to reliance on fine-scale datasets, cost effective methods must be developed for keeping the datasets current. Rather than expensively recreating the datasets from scratch, updating methods should focus only in areas that have changed. Great strides have been made in using Landsat imagery for moderate resolution change monitoring (Huang et al. 2010; Kennedy et al. 2010; Hansen et al. 2013; Zhu and Woodcock 2014). However, fine-scale mapping and monitoring to support local decision making remains expensive, inconsistent, and primarily reliant on manual image interpretation. Research is needed which combines the temporal resolution and scientific calibration of Sentinel and Landsat imagery with the high spatial resolution of commercial imagery to monitor change at fine-scales.

ACKNOWLEDGEMENTS

Author Contributions
Conceived and designed the study: K Green, MT, AS, and K Gaffney
Collected the data: MT and DL
Performed the analysis of the data: MT, DL, and K Green
Authored the manuscript: All authors
Provided critical revision of the manuscript: All authors

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ESSAY

The California Vegetation Treatment Program: integrating biological resource protection into wildfire risk reduction

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Key Words: CAL FIRE, CalVTP, fire, fuels reduction, fuels, mitigation, risk, vegetation management, vegetation treatment, wildfire, wildlife

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California's wildfire crisis is continuing and could worsen with climate change. As noted in a report of California Governor Newsom's Wildfire Strike Force (2019): "Climate change has created a new wildfire reality for California. The state's fire season is now almost year-round. More than 25 million acres of California wildlands are classified as under very high or extreme fire threat. Approximately 25 percent of the state's population—11 million people—lives in that high-risk area." Since 2010, the number of wildfires occurring annually has increased, as has the total land area burned. The largest, most destructive, and deadliest wildfires on record in California history were wind-driven wildfires that occurred in 2018[1] (CAL FIRE 2019a, CAL FIRE 2019b, CAL FIRE 2019c). In addition, thousands of fires occur in the state every year that do not reach catastrophic levels.

The state's response to this crisis includes a comprehensive array of risk reduction and management strategies, such as vegetation treatments, home hardening, expanded evacuation capacity, comprehensive emergency planning, and improved land use practices, as well as investment in new suppression and response equipment and resources, use of technology tools, and establishment of strong utility oversight. In May of 2018, California Governor Brown signed Executive Order B-52-18, which bolstered one of these strategies by substantially increasing the pace and scale of vegetation treatments allowed in the state. Under the order, up to approximately 2,000 km² on nonfederal lands are targeted for treatment each year. This expanded target is a substantial increase compared to the current level of vegetation treatment activity in California. Legislation was subsequently passed in 2018 to expand on this Executive Order, including Senate Bill (SB) 1260, which required a streamlined process under the California Environmental Quality Act (CEQA) to help expedite implementation of vegetation treatments to address wildfire risk.

On 30 December 2019, the California Board of Forestry and Fire Protection (Board) fulfilled the SB 1260 requirement for streamlined CEQA coverage by approving the Cali-

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[1] Since this article was accepted for publication in May 2020, six of the largest fires in California's history burned in the fall of 2020.

fornia Vegetation Treatment Program (CalVTP) after certifying its Program Environmental Impact Report (EIR). The CalVTP was developed by the Board, in collaboration with the California Department of Forestry and Fire Protection (CAL FIRE). The CalVTP directs the implementation of vegetation treatments on up to approximately 1,000 km^2 per year within the treatable landscape of the State Responsibility Area, which encompasses more than 80,000 km^2 of nonfederal land throughout California. Wildfires occurring in steep topography or high fuel load areas, those that move more slowly through the landscape, and wind-driven fires after wind speeds diminish with weather change are fires that can be further slowed or stopped by vegetation treatment implemented under the CalVTP.

The CalVTP Program EIR is available for use by any state, regional, special district, or local government agency that seeks to fund vegetation treatments or implement treatments where it has land ownership, land management, or other regulatory responsibility in the treatable landscape. More than 200 such potential "project proponent" agencies could implement vegetation treatment projects using the Program EIR, including the California Department of Parks and Recreation, the California Department of Fish and Wildlife (CDFW), the California State Lands Commission, cities, counties, water and irrigation districts, conservation districts and conservancies, park and open space districts, universities and colleges, community service districts, utility districts, flood control districts, water agencies, and transportation authorities.

CEQA requires that public agencies implementing vegetation treatments inform decision makers and the public about significant adverse environmental impacts of proposed projects, and how to feasibly reduce those environmental impacts. The Program EIR is a powerful streamlining tool that is available to expedite environmental review under CEQA while providing environmental protections, which helps achieve the state mandates to increase the pace and scale of vegetation treatments and to conserve important habitats and biodiversity in the state. To maximize streamlining, it is designed to cover a full spectrum of potential biological resources impacts (e.g., effects on sensitive plants and animals, sensitive natural communities, and aquatic resources) and mitigation for treatments throughout the state. Because of this comprehensive analysis, many treatment projects can be covered under the CalVTP, so separate CEQA documents (such as a Mitigated Negative Declaration or EIR) will not need to be prepared.

Individual vegetation treatment projects that seek coverage under the CalVTP Program EIR must prepare a project-specific analysis (PSA), which is a checklist-based evaluation of whether a vegetation treatment project falls within the scope of the CalVTP Program EIR. Completing the PSA checklist and supporting analysis provides the documentation of this evaluation required to streamline CEQA review. If the vegetation treatment project is wholly "within the scope" of the CalVTP Program EIR, as documented in the PSA, the public agency may proceed with implementation after project approval. Depending on the complexity of the treatment project, a PSA may be completed in less than one month.

The CalVTP provides a toolbox of treatment types and treatment activities from which project proponents can select to design individual treatment projects. Treatment types are wildland-urban interface fuels reduction, fuel breaks, and ecological restoration. Wildland-urban interface fuels reduction treatments involve the strategic removal of vegetation to prevent or slow the spread of wildfire between structures and wildlands, and vice versa. Fuel break treatments modify flammable vegetation to reduce wildfire spread while providing a safer location for firefighters to fight fires. Ecological restoration treatments occur in areas

that have departed from the natural fire regime as a result of fire exclusion. These treatments restore ecosystem processes, conditions, and resiliency by moderating uncharacteristic wildland fuel conditions to reflect historic vegetative composition, structure, and habitat values.

Treatment activities under the CalVTP are prescribed burning, mechanical treatment, manual treatment, prescribed herbivory, and herbicide application. Prescribed burning treatments involve the intentional application of low-intensity fire to target vegetation in a predetermined area. Typically, control lines or fuel breaks are constructed before prescribed burning is initiated. This treatment activity also includes pile burning, which typically is implemented after vegetation is removed during other treatment activities. Mechanical treatments involve the use of motorized equipment (e.g., tractors, masticators) to cut, mulch, uproot, crush, or chop target vegetation. Manual treatments include the use of hand tools and hand-operated power tools (e.g., chainsaws, loppers, pruners) to cut, clear, or prune herbaceous or woody species. Prescribed herbivory entails the use of domestic livestock (e.g., goats, sheep, cattle) to reduce a target plant population. Herbicide application is implemented through utilizing several ground-application methods.

Treatment activities could be applied within the approximately 80,000-km^2 treatable landscape, which contains a vast variety of habitat types. To address environmental impacts on wildlife, plants, sensitive natural communities, and habitat at this scale, the CalVTP Program EIR was organized geographically into "ecoregions" using the U.S. Forest Service National Hierarchical Framework of Ecological Units to capture areas with similar or recurring patterns of physical and biological characteristics. This approach provided a relevant geographic and ecosystem context for the impact analysis and will increase the efficiency of locating information during project-specific review of later treatments under the CalVTP.

Because the geographic scope of the program is large, over 300 special-status wildlife species, over 1,000 special-status plant species, hundreds of sensitive natural communities, and over 1,800 km^2 of aquatic resources were addressed in the Program EIR impact analysis. The ecoregion organization approach was used to analyze all these sensitive natural resources, and special-status wildlife species were further organized by grouping them into life history categories that respond similarly to the range of treatment activities (Figure 1). It was assumed that life history traits (e.g., breeding ecology, preferred habitat) predict potential impact mechanisms. For example, the tree nesting and cavity nesting category includes arboreal birds, as well as mammals, such as fisher (*Pekania pennanti*), Humboldt marten (*Martes caurina humboldtensis*), and ringtail (*Bassariscus astutus*), because physical modifications to breeding habitat as a result of treatment activities, including loss of tree or cavity habitat, would likely result in similar impacts for all these species.

Implementation of treatment activities would involve the use of prescribed burning, heavy equipment, and fire crews—activities that may adversely affect wildlife present in the treatment area to varying degrees. Impact mechanisms may include loss of active nests or dens when vegetation is removed, burned, or disturbed. Individuals may be injured or killed inadvertently by heavy machinery or fire crews, or by fire if they cannot flee during prescribed burning activities. Wildlife habitat may also be modified or lost during any of the treatment activities.

To address these potential impacts on wildlife and habitat, the CalVTP mitigation strategy was developed in close coordination with resource agencies, including the California Natural Resources Agency, CDFW, and the California Coastal Commission, and considered species and habitat protection, as well as feasibility and efficiency of pro-
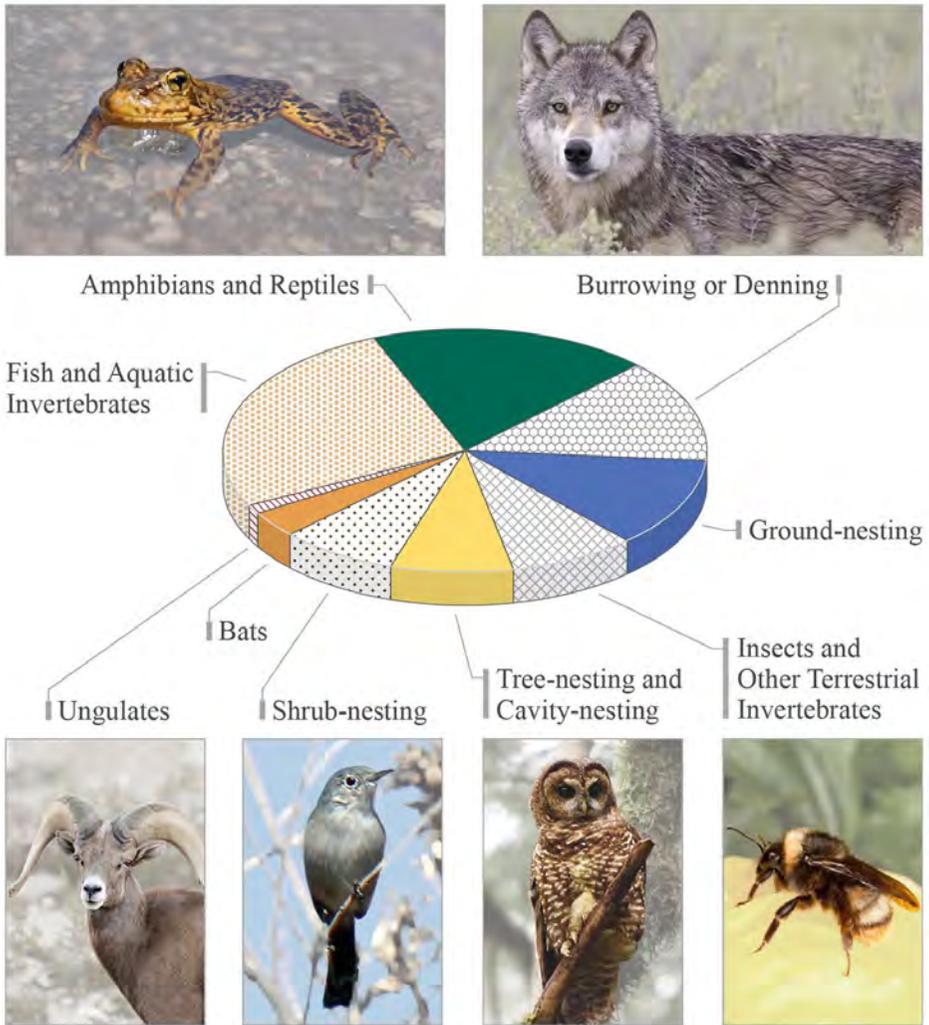
Figure 1. Life history categories considered in analysis of special-status wildlife in the CalVTP Program EIR.

tective measures. This strategy includes Standard Project Requirements (SPRs), which are integrated into treatment design to avoid and minimize impacts and include identification of biological resources through reconnaissance-level surveys and review of data sources (e.g., California Natural Diversity Database), focused or protocol-level surveys, and impact avoidance through physical no-disturbance buffers or seasonal limited operating periods. If, after implementation of SPRs, completion of the PSA identifies residual impacts that are potentially significant, a tiered mitigation approach using performance standards for maintenance of habitat function would be implemented that is tailored to the resource-specific conditions of the treatment project. Maintenance of habitat function includes retention of critical features that are important to wildlife, such as snags, large trees with cavities, and coarse wood debris as well as required canopy cover for species like northern spotted owl (*Strix occidentalis caurina*), California coastal gnatcatcher (*Polioptila californica*), and

fisher. If a treatment project cannot be modified or redesigned to maintain habitat function, compensatory mitigation and incidental take authorization from CDFW or the U.S. Fish and Wildlife Service may be necessary.

Adaptable SPRs and mitigation measures were designed according to listing status to apply to as many species as possible. For example, to mitigate impacts on state-listed or federally listed wildlife species and avoid take, treatments will not be implemented in habitats determined to be occupied by listed wildlife species. Alternatively, CDFW or other applicable responsible agencies (e.g., U.S. Fish and Wildlife Service) will be consulted to determine whether treatments could be implemented in a species' habitat but outside the sensitive period of its life history (e.g., breeding season) to avoid take. Following this tiered approach, if residual impacts would remain significant after implementation of applicable measures to avoid take through elimination of direct impacts and maintenance of habitat function, then consultation with CDFW or other applicable responsible agencies and implementation of compensatory mitigation would be required. Species-specific mitigation measures would be required for some species that did not fit within the overall framework of mitigation by listing status (e.g., bighorn sheep [*Ovis canadensis*], special-status butterflies), because these species may have extremely limited ranges, may occur within very specific habitat types, or may be difficult to detect during reconnaissance-level or focused surveys.

Not all effects of vegetation treatment on wildlife habitats and species are adverse. Some vegetation treatments, especially those that fall under the ecological restoration treatment type, may improve wildlife habitat over variable time scales by restoring habitat degraded by decades of fire suppression; restoring natural fire ecology and processes; and reducing the risk of catastrophic wildfire, which can damage or eliminate wildlife habitat. It is also likely that some wildlife species will be able to flee from fire crews or heavy equipment or could relocate to nearby suitable habitat if habitat on a treatment site is altered or removed.

California is experiencing a wildfire crisis. Vegetation treatments are a critical component of the state's approach to protecting residents, infrastructure, and prized biodiversity from the devastating effects of wildfire. Thorough analysis of impacts at a species, habitat, and treatment activity level, conducted using the best available science, is critical to avoid or minimize environmental impacts on wildlife and to conserve wildlife habitat, in particular for special-status species. The CalVTP Program EIR, especially its PSA checklist for later vegetation treatment projects, SPRs, and mitigation measures, provides a powerful tool to expedite the implementation of vegetation treatments to reduce wildfire risk while conserving biological resource values.

The CalVTP Program EIR and PSA checklist template are available on the Board's website (https://bof.fire.ca.gov/projects-and-programs/calvtp/).

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ESSAY

Caltrans' efforts to reduce the frequency and severity of wildfires while protecting California's valuable resources

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The California Department of Transportation's (Caltrans) mission is to provide a safe, sustainable, integrated, and efficient transportation system to enhance California's economy and livability. Recognizing the important role California's natural environment plays in the State's economy and livability, and during this time of unprecedented climate change, Caltrans Division of Environmental Analysis is motivated and committed to proactively turning innovative ideas into sustainable solutions.

While the history of water issues in California is long and convoluted, one thing is clear—clean, fresh water is undoubtedly one of the State's most precious and vulnerable resources. As wildfire has a measurable impact on water quality, Caltrans performs wildfire fuel reduction activities to reduce the intensity and severity of wildfire events. While Caltrans' existing vegetation management program reduces wildfire fuel within the highway right of way (area adjacent to highway owned by Caltrans), there is potential for a separate and additive effort if Caltrans is able to earn compliance credits as mandated under the National Pollutant Discharge Elimination System (NPDES) Statewide Storm Water Permit (State Water Resources Control Board (SWRCB) Order Number 2012-0011-DWQ, NPDES Number CAS000003), for TMDL (Total Maximum Daily Load) waterways by funding expanded fuel reduction efforts to off-highway projects. TMDLs within the permit are written by the State and Regional Water Quality Control Boards, and/or the U.S Environmental Protection Agency (EPA) (https://www.waterboards.ca.gov/water_issues/programs/tmdl/). A TMDL is the maximum amount of a specified pollutant that can enter a waterbody and have the waterbody meet water quality objectives. TMDLs cover a wide variety of pollutants including trash, temperature, sediment, and toxins such as mercury. Watersheds that feed a waterbody with a TMDL designation are often held to the same standards as the affected waterbody.

The Caltrans Stormwater Program works to ensure compliance with the NPDES Permit through implementation of the Storm Water Management Plan (SWMP). The SWMP provides the framework and guidance to ensure compliance with the permit, including monitoring and reporting, and ensures TMDL compliance.

Caltrans owns over 1,750 km² (434,000 acres) of right of way and maintains approximately 15,000 center-line miles of highway. Many highway facilities are located in TMDL

watersheds and Caltrans is often assigned a waste load allocation for TMDL constituents ranging from temperature and dissolved oxygen, to sediment and specific pollutants like mercury. Fire science has demonstrated that wildfires and the associated runoff is a significant source of pollution, including those covered by TMDLs (Smith et al. 2011). In addition to Best Management Practices (BMPs), including low impact development and bioswales already used to treat roadway runoff, Caltrans proposes fuel reduction activities in TMDL watersheds in high fire-severity zones to provide water quality benefits by reducing the severity and intensity of a wildfire (Caltrans 2017). As these activities are supplementary and offer an opportunity to reduce devastating impacts to water quality after a high severity wildfire, Caltrans proposes earning TMDL compliance credits for these fuel reduction activities.

WILDFIRE IMPACTS TO WATER QUALITY

The first impact of any wildfire is modification of the ecosystem substrate (USFS 2005). After a high severity wildfire, grasses, forbs, and shrubs no longer protect stable sediments from the destructive impact of rainfall. Litter composed of dead leaves, thatch, twigs, and underbrush (duff) is destroyed and no longer cushions the soil surface from rainfall nor filters suspended material from runoff after a wildfire. Under the right circumstances, wildfires can turn into catastrophic high intensity events in the presence of ladder fuels (high density thickets of trees and brush), allowing fires to spread vertically and horizontally, damaging or killing mature trees. In many cases, high intensity wildfires, more than low intensity wildfires, generate more ash and charred vegetation while degrading soil structure and water quality. The biological component of surface soil is linked to the soil physical properties. After a wildfire, some or all roots that bind fine sediments are damaged or destroyed and sediments are more easily eroded. Additionally, high intensity wildfires radically alter the physical properties of soils, creating a hydrophobic layer approximately 15 to 30 centimeters below the soil surface (DeBano 1981; DeBano 1990; Robischaud 2000; USFS 2005; Weiting et al. 2017). This hydrophobic layer reduces infiltration, greatly increases runoff and destabilizes the surface soil, all of which increase sediment transport and magnify impacts from high intensity rainfall runoff (USFS 2005; Paige and Zygmunt 2013).

High intensity wildfires followed by high-intensity rainfall can lead to catastrophic mud and debris flows which can impact the entire watershed. An example of the connection between high intensity wildfire followed by high intensity rainfall occurred in southern California in December 2017 (Thomas Fire). In January 2018, a flash flood passed through an urban area of Montecito CA to the Pacific Ocean, resulting in 20 different debris flows which added more than a million cubic yards of sediment to the surrounding waters. The debris flows overwhelmed Highway 101 (impassable for 10 days), left 23 people dead, 80 homes destroyed, 500 structures damaged, 20 bridges damaged, and more than 50 miles of highway impacted (SB OES 2018). Caltrans alone spent $26 million and replaced three bridges, based on a Directors Order (executed as an emergency contract, Public Contract Code §1102).

Even when catastrophic mud or debris flows do not occur, high intensity wildfires increase surface water sediment loading approximately 10 to 10,000 times, depending on the location, timing and rainfall intensity (Burke et al. 2013; Ice et al. 2004; McNabb and Swanson 1990; Paige and Zygmunt 2013). As climate change and drought worsen, plants can become weaker and more susceptible to wildfire, generating more erosion and sediment impacts on surface water (Sankey et al. 2017).

All wildfires have a measurable impact on water quality (USFS 2005), however high intensity wildfires significantly increase the potential for soil erosion, generating sediment transport that increases turbidity, pH, temperature and reduces dissolved oxygen in surface water (Burke et al. 2013). Post-wildfire runoff not only contains suspended charred organic material, but ash and sediment. Increases in suspended sediment loading also result in increased concentrations of dissolved nutrients, metals, salts, alkalinity and organic compounds, further degrading water quality (USFS 2005; Smith et al. 2011; Paige and Zygmunt 2013; Sham et al. 2013). High temperatures transform hydrated minerals (calcium and magnesium carbonates, gypsum) into dehydrated alkaline oxides that increase pH in runoff (Abraham et al. 2017). Metals, including iron, manganese, mercury, and selenium, are transformed (oxidized) by high-temperature, high-intensity wildfires (USFS 2005; Smith et al. 2011; Burton et al. 2016; Ogidie and Flegal 2017).

Virtually all metals retained by organic matter chelation (cobalt, copper, nickel, lead, zinc) become soluble when organic matter is destroyed, which impacts receiving waters (USFS, 2005; Smith et al. 2011; Abraham et al. 2017). Nitrogen loading to surface water increases by a factor of 5 to 10 times (Chorover et al. 1994; Mast and Clow 2008; Murphy et al. 2008; Smith et al. 2011; Stein et al. 2012; Abraham et al. 2017) and sulfate loading after a wildfire can be as high as 100 times the pre-wildfire levels (Chorover et al. 1994).

Given it takes two to five years after a wildfire for water quality impacts to diminish (Tecle and Neary 2015; Abraham et al. 2017), preventing further degradation is key—thus these findings support the concept of offering TMDL compliance crediting for wildfire-reduction activities by Caltrans in TMDL watersheds. Currently, Caltrans wildfire fuel reduction activities are somewhat limited to existing vegetation control and removal programs in the right of way. If Caltrans were able to earn TMDL compliance credits for fuel reduction activities, more comprehensive off highway fuel reduction efforts could be developed, while also increasing Caltrans' ability to fund external agencies' fuel reduction activities in TMDL watersheds.

MOVING FORWARD

The solution to improving water quality is complex; however, there is clear proof that high intensity wildfires degrade water quality. Managing fuel loads and fuel breaks is achievable through partnerships, funding and prioritization. To lead such efforts to protect our State's valuable aquatic resources, and to support and present a unified voice, Caltrans needs the partnership and expertise of departments such as the California Natural Resources Agencies (CNRA), including the Department of Fish and Wildlife (CDFW) and CAL FIRE, as well as the CalEPA (State and Regional Water Quality Control Boards).

Caltrans has begun a collaborative dialogue with other state agencies to 1) establish support for the TMDL compliance crediting based on wildfire fuel reduction activities, and 2) find the most appropriate, region-specific fuel reduction methods. Fuel reduction is typically accomplished by several methods, including application of fire control strips adjacent to the roadside shoulder, tree removal, thinning/felling trees in place, often followed by mastication and/or mowing. From a technical perspective, scientists, ecologists, firefighters and engineers support more frequent, less intense wildfires, however implementing this approach is costly, time consuming and will require a broad multiagency effort. Ultimately, the public must weigh in as well through the CEQA process for each individual project.

Caltrans aims to take a collaborative approach working with the various departments that have expertise in this field within the California Natural Resource Agencies such as CDFW and CAL FIRE, and the CalEPA.

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SECTION 2.
Fire Impacts on Plants

Conifer forest habitat in the Slate Creek watershed during summer 2019 burned during the 2018 Delta Fire, Shasta County, CA. Photo Credit: Len Lindstrand, III, Sierra Pacific Industries.

Shasta snow-wreath (*Neviusia cliftonii*) flower with petal at Ellery Creek during April 2020, Shasta County, CA. Photo Credit: Len Lindstrand, III, Sierra Pacific Industries.

Shrub and understory cover returns two years after the 2013 Rim Fire in a large high severity burn area in Stanislaus National Forest. At the time, the Rim Fire was the third-largest wildlife in California history at over 257,000 acres (at the time of publication, this fire is now the tenth-largest). Photo Credit: Cristin Walters, CDFW.

ORIGINAL RESEARCH

Effects of a firebreak on plants and wildlife at Pine Hill, a biodiversity hotspot, El Dorado County, California

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We examined the effects of hand clearing and pile burning of chaparral on plants and wildlife on the perimeter of Pine Hill 1–2 years after clearing. Pine Hill is home to four federally listed plant species, necessitating botanical surveys prior to clearing activities to prevent harming these species. We found over 65 new locations for the listed plants. We compared vegetation within burn scars, in cleared only plots, and in intact chaparral (control) and the germination and survival of a listed species, *Ceanothus roderickii* (Pine Hill Ceanothus). The density of *C. roderickii* seedlings was far lower in the cleared, unburned treatment than in the burned treatments, while mature *C. roderickii* was only present in unburned treatments and mature chaparral. Intact chaparral had higher cover but lower species richness of both native and exotic species than all disturbed treatments. The cleared only treatment had almost three times the cover by exotic grasses as did the burned treatments, and cover by presumably palatable, native and exotic species, was almost twice that of the burned treatments; mature chaparral contained few palatable plants, i.e. those identified as having wildlife value by Conrad (1987). Increased availability of palatable plants in treated areas may have contributed to 3–4 times higher probabilities of detection by cameras of herbivores in treated versus intact chaparral; which may have attracted smaller predators (bobcats [*Lynx rufus*] and grey foxes [*Urocyon cinereoargenteus*]) that were positively associated with western grey squirrel (*Sciurus griseus*) detections. Large carnivore detections were higher in areas with higher mule deer (*Odocoileus hemionus*) detections. Larger animals (pumas [*Puma concolor*], black bears [*Ursus americanus*], and mule deer) were detected 2–4 times more in treated areas, likely due to the physical impediment of mature chaparral. Invasion of nonnative grasses and increased wildlife usage may have been accelerated through the creation of firebreaks; continued monitoring will investigate long-term effects.

Natural fire regimes have long been altered in California (Syphard et al. 2007; Steel et al. 2015). In areas around the WUI (Wildland Urban Interface), this is even more pronounced because of the inherent danger fire represents as a management tool close to homes (Adams 2005). Since fire is frequently not an option in the WUI, fuel loads are often reduced through mastication and/or bull dozers; this disturbs soils, causes erosion (Dasmann et al. 1967; Backer et al. 2004), and provides noxious weeds a chance to become established (Giessow and Zedler 1996; Keeley 2001; Merriam et al. 2006). Additionally, plants that require a fire cue for germination may not benefit from this type of disturbance as it will not break seed dormancy (Keeley and Fotheringham 2000). Finally, the disturbance by heavy equipment may have negative effects on local wildlife populations (Bull et al. 2001; Russell et al. 2009).

The Pine Hill unit of the Pine Hill Ecological Reserve, (hereafter Pine Hill), owned and operated by the California Department of Fish and Wildlife (CDFW) in western El Dorado County, is an example of a dense, mature chaparral community in the WUI. Pine Hill is surrounded by mostly residential five-acre property parcels. To protect the surrounding private properties and Pine Hill from uncontrolled wildfire, CDFW planned to create a 20−25 m firebreak along the 4.25-km perimeter in 2017, and it was completed in 2019. This was considered necessary as uncontrolled fire may have grave ramifications on the local flora and fauna (Bennett 2003) and private property. The area is home to six special status plants that may be affected by the creation of firebreaks. Moreover, Pine Hill is landlocked and difficult to access with equipment.

The approach for creating this firebreak included measures to reduce the effects on local ecosystems that are commonly associated with firebreaks (Backer et al. 2004). We selected hand clearing and pile burning to potentially generate positive habitat effects for both plant and wildlife resources and minimize soil disturbance. In this study we examined the effects of these methods on both botanical and wildlife resources using plant surveys, vegetation plots, and trail cameras. Replicated, independent burn sites presented the opportunity to conduct research on vegetation recovery, weed invasion, and recruitment of obligately seeding plants over time.

METHODS

Study area

We conducted these studies on the perimeter of Pine Hill which is located in the center of a 120-km^2 gabbro soil island in western El Dorado County, California (Figure 1). The soil of the gabbro island is derived from the magma chamber of an ancient volcano that was pushed into the Sierra Nevada foothills by plate tectonics resulting in a soil distinctly different from the metamorphic, sediment derived soils to the west and the granitic soils of the Sierra Nevada uplift to the east (Medeiros et al. 2015). This gabbro island is home to almost 750 plant species making it one of the most botanically diverse areas on Earth (Wilson et al. 2009). Among the botanical riches are six rare species, a few of which are found nowhere else in the world; five are federally protected under the Endangered Spe-

cies Act. The six rare plants are *Calystegia stebbinsii* Brummitt (Stebbins' morning-glory, hereafter CAST), *Ceanothus roderickii* W. Knight (Pine Hill Ceanothus, hereafter CERO), *Galium californicum* Hook. & Arn. ssp. *Sierrae*, Dempster & Stebbins (El Dorado bedstraw, hereafter GACAS), *Fremontodendron decumbens* R. M. Lloyd (Pine Hill Flannelbush, hereafter FRDE), *Packera layneae* (Greene) W.A. Weber & A. Love (Layne's butterweed, hereafter PALA), and *Wyethia reticulata* Greene (El Dorado mule-ears, hereafter WYRE); the first five are federally listed as threatened and/or endangered, in addition, WYRE is a federal species of concern (Table 1-1 in U. S. Fish and Wildlife Service 2002).

Pine Hill is 0.983 km^2 in size and 609 m in elevation. All rare species except CAST occur on Pine Hill mostly associated with chaparral that covers most of its aspects; the exception is GACAS which is found in or near oak woodland on the east. There is no record of when Pine Hill's perimeter last burned, and the last fire was likely many decades ago.
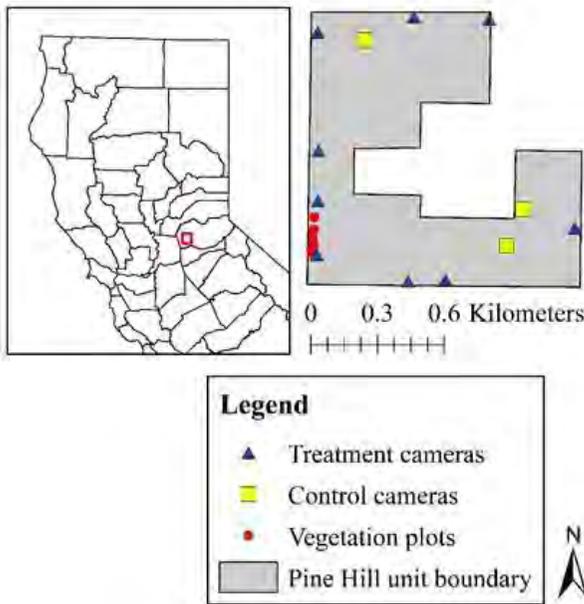
Figure 1. The locations of camera sites and vegetation plots (2017−2019) in the Pine Hill unit of the Pine Hill Ecological Reserve, El Dorado County, California are shown. The symbols used are depicted in the legend. Treatment cameras were located within burned and cleared areas in the firebreaks along the perimeter of the property, and the control cameras were located within unburned and uncleared areas of the property. The entire perimeter was surveyed for rare plants by botanists from the California Native Plant Society (CNPS). The location of the property in relation to northern California counties is outlined in the upper left.

Precipitation and seasonality are typical for a Mediterranean climate: the mean summer (June–September) temperature during the study period was 23.7°C and the mean winter (December–March) temperature was 8.8°C with average annual precipitation of 86.1 cm for 2017–2019 (NOAA 2020). On the sunnier east, south, and west slopes, chaparral shrub vegetation, dominated by white leaf manzanita (*Arctostaphylos viscida*) and chamise (*Adenostoma fasciculatum*), is found. Cooler, wetter exposures on the upper east sides and the north slopes give rise to oak woodland where black oak (*Quercus kelloggii*) and poison oak (*Toxicodendron diversilobum*) flourish.

Chaparral, a shrub-dominated plant community found in abundance throughout California, is composed of fire adapted species. These plants, including the rare species, can survive and regenerate following fire due to underground roots and stems (resprouters) or heat-tolerant seed in the soil that requires a cue to germinate by heat or chemicals released by charred wood (seeders) (Keeley and Fotheringham 2000).

No past surveys of wildlife had previously been completed at Pine Hill; however, field observations by CDFW personnel included mule deer, wild turkeys (*Meleagris gallopavo*), coyotes (*Canis latrans*), grey fox, rabbits (*Lepus* spp. and *Sylvilagus* spp.), and western grey squirrel. Further, neighboring property owner reports and observed wildlife signs suggested that the area might also be used by pumas and black bears.

Data collection

Pre- and post- clearing plant surveys .—In 2017, three 1-m wide survey paths were cut with hand tools. The paths were approximately 8 m apart while circumventing the perimeter within the footprint of the final cleared firebreak. Paths were necessary because the area did not allow for any rare plant surveying due to dense, impassable chaparral. After the trails were completed, CNPS botanists identified burn locations as well as plants of interest with a special concern for FRDE plants because of its rarity and much taller stature (>30 cm) in comparison to all the other plants. As low growing CERO was to be spared hand clearing, due to its endangered status, all plants shorter than 30 cm were left, and vegetation was cut above 30 cm. Hand clearing of chaparral and understory shrubs began in 2017 and continued to 2019; shrub piles (maximum size 10 m²) were burned in 2017, 2018, and 2019 in locations identified as free of rare species by the CNPS botanists (see Ayres et al. 2020, this issue for survey methods). During the clearing CDFW biologists monitored Cal Fire (California Department of Forestry and Fire Protection) crews to help avoid flagged plants and to place burn piles in previously identified locations. Field assessment estimated a total of 10% of the perimeter area had experienced fire on the ground in burn piles, the remaining perimeter area was cleared only. Teams of four to six botanists surveyed the cleared perimeter for rare species in 2019-2020 and mapped new locations of CERO, FRDE, GACAS, PALA, and WYRE. The occurrence of species, and their growth stage – re-sprouting or seedling germination – within and adjacent to burned sites was noted as well.

Vegetation recovery, weed invasion, and recruitment by Ceanothus roderickii.— In May 2019, plots were established along the western perimeter in cleared areas with piles burned in 2017 (5 plots) and 2018 (3 plots); the 2017 and 2018 burn areas were next to each other and thus allowed us to compare first-year and second-year plant responses to fire within the same site. Plots sizes were the circular area of the burn pile and this area was matched in size by a cleared but unburned plot in a random direction, which was determined by the second-hand sweep of a watch, within 1 m of the burned edges (8 plots). Average plot size was 7.8 m²; and plot sizes ranged from 4.3 to 12.65 m². Burned plots were selected to contain seedlings of CERO, as this rare plant is a fire obligate seeder (Boyd 2007). Rebar with a labeled PVC sleeve was placed in the center of the plots to allow ease of relocation. The diameters of the plots were measured, and plot edges were pin flagged. To assess the undisturbed chaparral vegetation, a meter tape was run into the intact chaparral parallel to the clearing and four 10 m by 10 m plots were located at 10 m intervals along the tape. An old bulldozed road/fuel break ran throughout the western aspect, approximately parallel to the western perimeter.

All species were identified, and their percent cover visually estimated for the entire plot area, as well as bare soil and rock cover for all three treatments (Barbour et al. 1998). A training session before assessments was conducted to standardize estimates among individuals. CERO seedlings were counted, and leaf number and height assessed, and a 1.5 cm long roofing nail marker was placed 1-2 cm next to each seedling. We returned in October

2019 and assessed CERO survival, i.e., seedlings next to a roofing nail, and additional germination, i.e., seedlings without a corresponding nail, and the leaf number, plant width and height of the survivors.

Wildlife surveys.—We sampled 12 sites (three unburned areas [controls] and nine areas within the firebreaks [treatment]) using motion-activated trail cameras (Model HC500; RECONYX Inc., Holmen, Wisconsin, USA). The cameras were placed on tree trunks and directed towards open areas; some vegetation was removed to avoid wind triggering the cameras. The camera data started on 19 March 2018 for five cameras and December 2018−February 2019 for the other 7 cameras. The data for analysis was subsampled (29 Jan 2019−11 Apr 2019, 12 Jun 2019−30 Jul 2019, 12 Sep 2019−10 Dec 2019; exceptions– camera 21: 12 Dec 2018−11 Apr 2019, 24: 11 Apr 2019−30 Jul 2019, 26: excluded 29 Jan 2019−11 Apr 2019 due to change in camera placement). The data reported here ends on 10 December 2019; however, data gathering is ongoing. We checked camera trap' batteries and replaced memory cards monthly.

Statistical analyses

All statistical analyses were completed using the program R (v.3.5.1, www.r-project. org, accessed 05 Mar 2020). To determine whether the vegetation data were distributed normally, we used the Shapiro-Wilks test (Stats v.3.6.2, www.rdocumentation.org/pack-ages/stats/versions/3.6.2, accessed 05 Mar 2020). We also used Levene's test to determine whether the variances between the plot treatment groups were homogenous (Car v.3.0-6, www.rdocumentation.org/packages/car/versions/3.0-6, accessed 05 Mar 2020). Due to the nonparametric and heteroskedastic format of most of our data, we used the robust ANOVA tests from the R package WRS2, which used 20% trimmed means and Welch's F-statistic to reduce biases due to nonparametric and heteroskedastic data (Mair and Wilcox 2019). For all CERO seedling data (other than number of seedlings per m^2), we used two-way robust ANOVAs to analyze the difference in measurement variables between data collected on different dates and treatments, modeling treatments and dates as interaction effects. For all other vegetation measurements, we used one-way robust ANOVAs to analyze the difference in measurement variables between treatment types. For ANOVA tests that showed significant differences between groups, we used pairwise Welch's t-tests with Bonferroni's correction for multiple *P*-values to further analyze which groups were significantly different from each other (Stats v.3.6.2, www.rdocumentation.org/packages/stats/versions/3.6.2, accessed 05 Mar 2020).

Community coefficients to determine similarity/difference in plant species composition between treatments (cleared and burned compared to cleared only) and between treatments and intact chaparral (cleared and burned compared to intact chaparral; cleared only compared to intact chaparral) were calculated using the Jaccard equation (Barbour et al. 1998). This measure illustrates whether the species of two sampled areas of vegetation are of the same or different communities and can be based on either or both numbers of shared species and percent cover of shared species. Both were calculated for the plants of the treatments/intact chaparral. A Jaccard index < 50 indicates that two sampled areas of vegetation represent different communities.

Diversity was determined for each treatment (cleared and burned 2017; cleared and burned 2018; cleared only) and for intact chaparral using Shannon indices H', H'$_{max}$, and J', where H' is a measure of the species richness and the distribution of the species within the

area sampled (e.g. across plots) combined; H'$_{max}$ in which H' for a community is compared with the maximum possible, if all species are equally represented; and J' the ratio of H'/H'$_{max}$, how closely H' for the community approaches the maximum possible (Zar 1984; Legendre and Legendre 1998).

We tested for positive correlation between CERO seedling growth measurements (number of leaves, height, and diameter) using Spearman's correlation coefficient (ρ) (HMisc: Harrell Miscellaneous v.4.3-1, https://cran.r-project.org/web/packages/Hmisc/index.html, accessed 05 Mar 2020). Due to the high positive correlation (ρ > 0.7, P < 0.05) between seedling height and the other growth measurements, we only used seedling height as a measure of growth in our analyses.

Wildlife analyses. —To limit the biases created by having multiple detections of the same wildlife individuals, we created a second dataset (hereafter unduplicated dataset) with consecutive detections of the similar individuals (determined by species, sex, and appearance when possible) at the same camera within 30 minutes of the first detection removed (Ridout and Linkie 2009). Within the unduplicated dataset, we also removed consecutive detections of the same species within an hour of the first detection at cameras located along the firebreaks and at the two adjacent control cameras in the southern portion of the property. We used the more conservative one-hour cutoff for adjacent cameras rather than 30 minutes because individuals traveling the perimeter of the property may reach the furthest cameras in more than 30 minutes due to the distances between the firebreak cameras (0.168 km – 1.45 km). We removed these consecutive detections due to the proximity of the cameras and photo evidence of individuals being detected by multiple adjacent cameras within one hour.

To analyze whether the presence of firebreaks, other camera site location variables, and species interaction variables affected wildlife movement, we used single-species occupancy models using the methods of MacKenzie et al. (2002), and the R package unmarked (Fiske and Chandler 2011) to estimate the detection probabilities of the most abundant species (mule deer, rabbits, western grey squirrels, coyotes, grey foxes, bobcats, pumas, and black bears) at camera sites. We only measured detection probabilities because the camera sites were too close to assume spatial independence for occupancy estimates (Legendre 1993; MacKenzie et al. 2002; Lazenby and Dickman 2013). We did not document or include species' population sizes in our occupancy models because the camera sites were close together (within 1.5 km), within the same vegetation community types, and sampled at the same time (Royle and Nichols 2003). Therefore, we assumed that the population dynamics of species at each camera site were the same and would not bias the results (Caldwell and Klip 2020).

We created three groups of similar species used in the models: rabbits (*Sylvilagus* spp. and *Lepus* spp.), large carnivores (pumas and black bears), and meso carnivores (coyotes, grey foxes, and bobcats). The detections of both rabbits and large carnivores were both used as single species in the occupancy models due to the similarities between rabbit species and the low detections of large carnivore species. The detection covariates we used in the occupancy models are shown in Table 1. We calculated species detection rate covariates by dividing the number of occurrences of a species at a camera site by the number of days camera data was collected at that site. To accurately estimate the total site usage by species, we used the species detection data without duplicates removed to calculate species detection rates. When fitting models, we only included species detection rates with likely predator-prey or competition interactions with the modeled species. Prior to fitting models, we calculated Spearman's correlation coefficients for all the covariates to ensure collinearity was not an

issue (Spearman's ρ>0.70, P<0.05). Rabbit and grey fox detection rates were correlated (ρ=0.74, P<0.05) and grey squirrel and grey fox detection rates were correlated (ρ=0.75, P<0.05). Therefor, we did not use grey squirrel and rabbit detection rates in species models that also had grey fox detection rates as a covariate.

We used the second-order Akaike's Information Criterion (AICc) (AICcmodavg: model selection and multi-model inference based on (Q)AIC(c) v. 2.2-2, cran.r-project.

Table 1. Summary of detection covariates used in single-species occupancy models for mule deer, grey squirrel, rabbits, grey fox, coyote, bobcat, black bear, and puma from 12 camera sites at the Pine Hill unit of the Pine Hill Ecological Reserve, El Dorado county, California from 2018−2019.

Variable	$\bar{x}$	SE	Description
Bobcat detection rate	0.011	0.018	Number of bobcats detected per camera per day.
Coyote detection rate	0.01	0.005	Number of coyotes detected per camera per day.
Human detection rate	0.056	0.085	Number of humans detected per camera per day.
Grey fox detection rate	0.024	0.039	Number of grey foxes detected per camera per day.
Grey squirrel detection rate	0.031	0.044	Number of grey squirrels detected per camera per day.
Large carnivore detection rate	0.007	0.012	Sum of number of pumas and black bears detected per camera per day.
Meso carnivore detection rate	0.046	0.054	Sum of number of grey foxes, coyotes, and bobcats detected per camera per day.
Mule deer detection rate	0.449	0.315	Number of mule deer detected per camera per day.
Rabbit detection rate	0.042	0.049	Number of rabbits (cottontail and jackrabbits) detected per camera per day.
Camera location			Defined by location of camera in the firebreak (burned) areas or unburned areas.
Property side			Defined by location of the camera relative to the closest side of the property (north, south, east, or west side).
Ordinal day			Ordinal date of each camera day. Range of 1–365.
Season			Season of each camera day (summer, fall, winter, spring).

org/package=AICcmodavg, accessed 05 Mar 2020) to compare models and considered models with differences in AICc < 4.0 as the best approximations for the data (Burnham and Anderson 2002; Anderson 2008). We also considered models with only camera location as a covariate to further investigate control versus firebreak area usage by species. We calculated the predicted detection probabilities, regression coefficients (β), standard error, and P-values for the top models' covariates using the unmarked package in R (Fiske and Chandler 2011). The following equation depicts the format of the models we used to predict detection probabilities:

$$logit(p_{ij}) = \beta 0_i + \beta 1_i \ (covariate \ 1)_j + \beta 1_i \ (covariate \ 2)_j + \cdots + \beta n_i \ (covariate \ n)_j \ ,$$

where *logit* is the logarithm of the odds, p_{ij} is the detection probability of species i at site j and covariates 1 through n are the values of each covariate used in the model at site j.

RESULTS

Plant surveys

As the perimeter of Pine Hill had never been comprehensively botanically surveyed, many of our findings were novel. A total of 120 rare plant locations on public land were recorded; 65 of these points were individual plants of FRDE, and patches of CERO, GACAS, PALA, and WYRE that had not previously been reported to the California Natural Diversity Database (CNDDB) or CalFlora.

Except for GACAS, all species were present or reported from chaparral communities on the sunnier aspects, and were mostly absent from the north aspect and under oak woodland; the exceptions being GACAS which was found only under the east side oak woodland canopy, three FRDE plants on the north side, and WYRE which grew under every aspect and condition (Table 2).

Table 2. Summary of rare plant species distributions on the perimeter of the Pine Hill unit of Pine Hill Ecological Reserve, El Dorado County, California from March 2017 to April 2019. All species were located with GPS and mapped except CHGR which was too numerous to map. Species are as follows: CERO (*Ceanothus roderickii*), CHGR (*Chlorogalum grandiflorum*), FRDE (*Fremontodendron decumbens*), GACAS (*Galium californicum ssp. sierrae*), PALA (*Packera layneae*), WYRE (*Wyethia reticulata*). FRDE was reported on private property on the east but was not found by the survey teams.

Species	New locations	Aspect				
		East-chaparral	South	West	North	East-oak woodland
CERO	10	Present	Present	Present	Absent	Absent
FRDE	6	Reported	Present	Present	Present	Absent
GACAS	16	Absent	Absent	Absent	Absent	Present
PALA	15	Present	Present	Present	Absent	Absent
WYRE	18	Present	Present	Present	Present	Present

Vegetation recovery, weed invasion, and recruitment by Ceanothus roderickii. —A total of 72 species were recorded across all treatments; 51 were native and 21 were exotic. All shrubs and trees were native. Jaccard community coefficient between intact chaparral and the burned and cleared treatment illustrated different communities, reflecting the low cover and number of shared species between them. Jaccard between the burned and cleared treatment and the cleared only treatment also showed different communities especially based on cover of shared species, reflecting the difference in treatment effects on establishment and growth (Table 3).

Highest Shannon diversity was found in the cleared and burned treatment - where burning occurred in 2017 - and in the cleared only treatment, reflecting the high species richness of the two treatments (39 and 32 species, respectively) and relatively even distribution of species across sampled plots. The lowest Shannon diversity was found in the intact chaparral, due to its lower species number (18), and the differences in species composition in each plot along the transect (8 of the 18 species were recorded in only 1 of the 4 plots of the transect; Table 4).

Table 3. Jaccard community coefficients of vegetation of paired treatments (burned and cleared, cleared only) and intact chaparral, calculated based on percent cover of shared species and on number of shared species (spp. #). Coefficients less than 50 indicate different communities between pairs. Data collected at the Pine Hill unit of the Pine Hill Ecological Reserve, El Dorado County, California in May and October 2019.

Community coefficients	By % cover	By spp. #
Jaccard intact chaparral with burned and cleared	5	25
Jaccard intact chaparral with cleared only	20	28
Jaccard burned and cleared with cleared only	20	46

Table 4. Diversity indices (Shannon) for each treatment (cleared and burned 2017, cleared and burned 2018, cleared only) and for intact chaparral. Higher H' and J' indicate higher species richness and evenness of species distribution across plots combined. H'_{max} indicates highest H' possible. Data collected at the Pine Hill unit of the Pine Hill Ecological Reserve, El Dorado County, California in May and October 2019.

Treatment	H'	H'_{max}	J' (H'/ H'_{max})
Cleared and burned 2017	1.49	1.59	0.94
Cleared and Burned 2018	1.30	1.36	0.95
Cleared only	1.39	1.50	0.92
Intact chaparral	1.20	1.26	0.95

Vegetation assessment showed that intact chaparral had higher cover but lower species richness of both native and exotic species than all disturbed treatments (Figure 2) (cover: ANOVA: $F = 6.239$; df = 3, 6.36; $P = 0.026$) (number of species per m^2: Welch's t-test burned 2018 and intact: df = 2.386, $P = 0.029$; Welch's t-test cleared and intact: df = 9.665, $P = 0.029$). The density of non-native species was significantly higher in the burned 2017 treatment (Welch's t-test: df = 4.482, $P = 0.009$) and the cleared treatment (Welch's t-test: df = 9.346, $P < 0.001$) than in the intact treatment (ANOVA: $F = 15.927$; df = 3, 4.48; $P = 0.008$). The native cover in the intact treatment was higher than in all the disturbed treatments (burned 2017 [Welch's t-test: df = 5.779, $P = 0.056$], burned 2018 [Welch's t-test: df = 4.037, $P = 0.056$]), cleared treatment [Welch's t-test: df = 4.436, $P = 0.084$]).
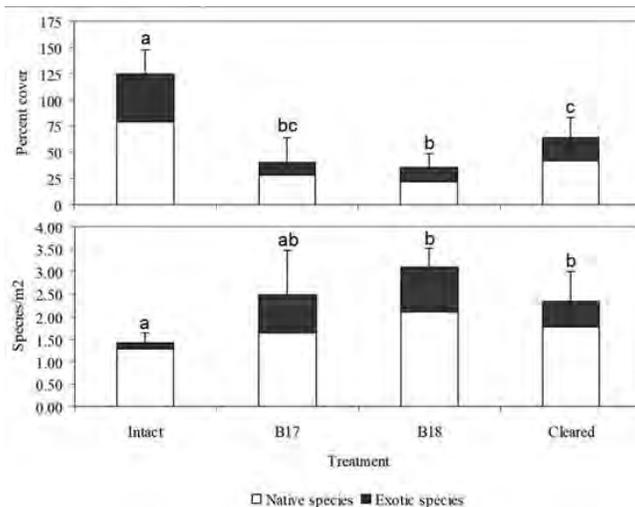
Figure 2. Upper chart: average percent cover; lower chart: average number of species per square m, with standard deviation of total cover and total species number; bars topped by a different letter are significantly different at $P < 0.05$. Bar segments show the contributions of native (clear) and exotic (black) species to the total for each of the four treatments (intact chaparral [Intact, 4 plots]), burned 2017 [B17, 5 plots], burned 2018 [B18, 3 plots], cleared only [Cleared, 8 plots], sampled at the Pine Hill unit of the Pine Hill Ecological Reserve, El Dorado County, California in May 2019.

Unvegetated bare ground, covered by soil, ash, or boulders accounted for an average of $61.76 \pm 17.83\%$ of the area for the burned treatments, while $36.10 \pm 19.6\%$ bare ground was found in the cleared treatments; intact chaparral had little bare ground ($1.1 \pm 2.2\%$) and over 100% total cover (average $124.48 \pm 20.20\%$) by vegetation due to layers of low and high growing species (Table 5).

Examining cumulative percent cover by all exotic grasses (*Aira caryophyllea*, *Brachypodium distachyon*, *Bromus hordeaceus*, *Bromus madritensis rubens*, *Cynosurus echinatus*, *Festuca myuros*, *Gastridium phleoides*, *Hordeum murinum leporinum*), the cleared treatments had almost three times the cover by exotic grasses (22% cover) as the burned treatments (8% cover) and intact chaparral had 45% cover (Table 5). *Festuca myuros* and *B. distachyon* accounted for most of the exotic species cover in disturbed plots. There was but a single dominant exotic species in the chaparral, the grass *Brachypodium distachyon*. In only a single cleared treatment plot did this species reach a comparable cover of 60% but it was present in almost all disturbed treatment plots, cleared and burned.

Native and exotic annuals had generally low cover, bulbs had low but uniform cover throughout all treatments, and herbaceous perennials, like *Salvia sonomensis*, that were likely to be killed by fire had five times the cover in unburned treatments (cleared and intact) as in the fire treatments (2017 and 2018) (Table 5). Intact chaparral was dominated by a few native species with high cover; seeder shrubs *Arctostaphylos viscida* (17% cover) and CERO (8%), resprouting *Rhamnus ilicifolia* (8%), and *Frangula californica tomentella* (5%), and herbaceous *Salvia sonomensis* (14%) and *Carex xerophila* (14%). The cover of resprouting species increased 5-fold from earlier (2017) to later fire (2018) treatments primarily due to *Eriodictyon californicum*, but resprouters were low in cleared treatments. C*rocanthemum scoparium* was the dominant seeder in burned treatments, while mature CERO which by design escaped hand clearing, but is killed by fire, was the dominant seeder species in cleared treatments. *Arctostaphylos viscida*, cut down during clearing, did not resprout in the cleared treatment, and few seedlings were observed in the burned treatments.

There are two common species in the Lamiaceae family whose regeneration method following fire is little known. *Lepechinia calycina* has been reported to root-resprout following fire (Conrad 1987), but in our plant surveys elsewhere along the Pine Hill perimeter we saw resprouting only outside the fire's edge, with seedlings emerging from the ash within the burned areas. The regeneration strategy of *Salvia sonomensis* has not been reported. We found neither resprouts nor seedlings within burns; the low cover in fire treatments (2.5%) was entirely due to lateral stem expansion from outside the fire's edge. In contrast, the cleared treatment averaged 20% cover by this single species. Neither species is palatable to vertebrate herbivores (Conrad 1987) due to highly aromatic foliage.

The density of CERO seedlings was far lower in the cleared, unburned treatment (0.06 seedlings/m^2) than in either of the burned treatments (Welch's t-test, burned 2017 and cleared treatments: df = 9.182, $P < 0.001$; Welch's t-test, burned 2018 and cleared treatments: df = 5.018, $P = 0.038$) resulting in an overall significant treatment effect (ANOVA: $F = 81.41$; df = 2, 5.04; $P < 0.001$). There was no difference in seedling density between the 2017 (3.10/m^2) and 2018 (4.67/m^2) burned treatments assessed in either May (above) or October (October 2017: 4.44/m^2; 2018: 2.08/m^2). The increase in density in October 2019, in 2017 treatments was due to additional seedling germination after May 1, while the decrease in 2018 treatments was likely due to seedling mortality (2017: average of $24.11 \pm 31.41\%$ mortality versus 2018: average of $47 \pm 44.83\%$, ns). Seedlings in the 2017 burned treatment grew taller during the 2019 growing season (May to October) than seedlings from the later 2018 burns (ANOVA: $F = 84.396$; df = 1, 203.55; $P < 0.001$).

Wildlife surveys

With the cameras, we collected an average of 343 ± 24 (SD) days of data per site. The cameras captured 2,872 unduplicated wildlife and human detections, with the most common species being mule deer, humans, rabbits, western grey squirrels, and grey foxes (Table 6).

Table 5. Cumulative percent cover of plants sorted into functional groups reflecting native or exotic status, life form, and method of recovery after fire (resprouting versus seeding) (averaged over treatments: burned 2017 [B17, 5 plots], burned 2018 [B18, 3 plots], cleared [8 plots], and intact [4 plots]).These data were collected from the Pine Hill unit of the Pine Hill Ecological Reserve, El Dorado County, California in May 2019.

Functional group	Cumulative percent cover (average [SD]) by treatment			
	2017	2018	Cleared	Intact
Exotic grass	7.8 (4.9)	8.8 (3.1)	21.9 (22.5)	45.1 (13.0)
Exotic annuals	5.1 (3.1)	5.1 (4.2)	2.3 (3.3)	0.0 (0)
Native grass	0.0 (0)	0.0 (0)	0.1 (0.4)	1.3 (2.5)
Native annuals	0.3 (0.4)	0.7 (0.6)	0.9 (1.1)	0.0 (0)
Bulbs	3.5 (4.0)	2.0 (1.0)	1.9 (1.5)	2.4 (1.6)
Herb perennials	3.2 (2.9)	7.1 (10.4)	23.0 (17.2)	30.3 (8.7)
Resprouters	14.5 (20.1)	3.4 (1.5)	4.0 (4.4)	16.3 (6.9)
Seeders	5.8 (2.9)	8.0 (10.4)	9.8 (7.9)	26.6 (24.0)
Unvegetated	59.9 (23.1)	64.9 (13.5)	36.1 (19.6)	1.1 (2.2)

Table 6. Species detected at 12 (nine treated and three control) camera sites in the Pine Hill unit of Pine Hill Ecological Reserve, El Dorado County, California from years 2018−2019. The average detection rates (DR, number individuals detected per camera per day) at control and treated camera sites is also shown.

Common name	Number detected	$\bar{x} \pm$ SE DR control sites	$\bar{x} \pm$ SE DR treated sites
Birds[a]	34	0.003 ± 0.003	0.008 ± 0.008
Opossum	4	0 ± 0	0.002 ± 0.004
Rabbits[b]	154	0.009 ± 0.012	0.052 ± 0.052
Grey squirrel	124	0.013 ± 0.016	0.037 ± 0.050
Human	360	0.008 ± 0	0.072 ± 0.094
Raccoon	8	0 ± 0	0.003 ± 0.004
Striped skunk	2	0 ± 0	0.001 ± 0.001
Black bear	12	0.003 ± 0.003	0.003 ± 0.004
Coyote	45	0.004 ± 0.002	0.012 ± 0.004
Domestic dog	13	0.001 ± 0.002	0.004 ± 0.004
Grey fox	96	0.008 ± 0.007	0.030 ± 0.044
Bobcat	46	0.005 ± 0.008	0.014 ± 0.020
Domestic cat	2	0 ± 0	0.001 ± 0.002
Puma	17	0.001 ± 0.002	0.005 ± 0.011
Mule deer	1,955	0.164 ± 0.143	0.544 ± 0.301
Total	2,872		

[a]All birds detected including California scrub jay, California towhee, western bluebird, wild turkey, and other species of the order Passeriformes.
[b]All rabbit species detected including cottontail rabbits and jackrabbits.

For western grey squirrel, rabbits, mule deer, grey fox, coyote, bobcat, and large carnivores (combined detections of black bears and pumas), we used single species occupancy models to analyze species' detection probabilities at each camera site.

Western grey squirrels' predicted detection probabilities at camera sites from the supported model (out of 25 tested) (Table 7) ranged from 0–0.297. Detection probabilities decreased in the spring ($p=0$–0.086; $\beta=-0.708$, $P = 0.028$) and summer ($p=0$–0.067; $\beta=-0.970$, $P<0.01$) and increased in the winter ($p=0$–0.297; $\beta=0.808$, $P<0.01$) compared to the fall. Further, their detection probabilities were positively correlated with detection rates of meso carnivores ($p=0$–0.297; $\beta=31.032$, $P<0.001$) and negatively correlated with detection rates of large carnivores ($p=0$–0.297; $\beta=-235.520$, $P<0.001$). In the model with camera location as the only covariate, grey squirrel detection probabilities decreased at control camera sites compared to treated (burned and cleared) camera sites ($p=0.022$; $\beta=-0.945$, $P = 0.001$) (Figure 3).

Table 7. Top-ranked single-species occupancy models and models with camera location tested to estimate the detection probabilities (p) of western grey squirrel, rabbits (cottontail and jackrabbits), mule deer, grey fox, coyote, bobcat, and large carnivores (pumas and black bears) at 12 camera sites in the Pine Hill unit of Pine Hill Ecological Reserve, El Dorado County, California from 2018−2019. We ranked models by the second order Akaike's Information Criterion (AIC$_c$) and considered models with a difference in AIC$_c$ (ΔAIC$_c$) < 4 to be supported. We did not evaluate covariate effects on the occupancy (Ψ) of the sites by species. We also show the models with no covariates (.) as comparison, the number of model parameters (K), and the model weights (w_i).

Models by species[a]	K	AIC^{cb}	ΔAIC^c	w_i
Grey squirrel				
Ψ(.) p(season + camera location + meso carnivore DR + large carnivore DR)	8	835.04	0.00	1.00
Ψ(.) p(camera location)	3	909.70	74.66	0.00
Ψ(.) p(.)	2	919.19	84.14	0.00
Rabbits				
Ψ(.) p(property side + camera location + human DR)	7	948.34	0.00	0.92
Ψ(.) p(camera location)	3	1000.13	51.80	0.00
Ψ(.) p(.)	2	1023.45	75.11	0.00
Mule deer				
Ψ(.) p(camera location + property side)	6	3499.12	0.00	0.99
Ψ(.) p(camera location)	3	3546.90	47.78	0.00
Ψ(.) p(.)	2	3696.22	197.10	0.00
Grey fox				
Ψ(.) p(season + camera location + grey squirrel DR)	7	683.08	0.00	0.98
Ψ(.) p(camera location)	3	748.41	65.33	0.00
Ψ(.) p(.)	2	769.58	86.50	0.00
Coyote				
Ψ(.) p(ordinal day + camera location)	4	391.75	0.00	1.00
Ψ(.) p(camera location)	3	DNC		
Ψ(.) p(.)	2	DNC		

Models by species[a]	K	AIC[cb]	ΔAIC[c]	w_i
Bobcat				
Ψ(.) p(property side + grey squirrel DR)	7	444.82	0.00	1.00
Ψ(.) p(camera location)	3	480.14	35.33	0.00
Ψ(.) p(.)	2	482.91	38.10	0.00
Large carnivore				
Ψ(.) p(ordinal day + human DR)	4	225.49	0.00	0.39
Ψ(.) p(ordinal day + meso carnivore DR)	4	228.31	2.82	0.09
Ψ(.) p(ordinal day + camera location + human DR + mule deer DR)	5	228.93	3.44	0.07
Ψ(.) p(ordinal day + human DR + mule deer DR)	5	228.93	3.44	0.07
Ψ(.) p(ordinal day + camera location + human DR + meso carnivore DR)	5	229.20	3.71	0.06
Ψ(.) p(ordinal day + human DR + meso carnivore DR)	5	229.20	3.71	0.06
Ψ(.) p(ordinal day + camera location + human DR)	5	229.24	3.75	0.06
Ψ(.) p(ordinal day + mule deer DR)	4	229.40	3.91	0.05
Ψ(.) p(camera location)	3	DNC		
Ψ(.) p(.)	2	DNC		

[a]DR = detection rate (defined as number of species detections at each camera divided by the number of total camera days), meso carnivores = combined detections of coyotes, bobcats, and grey foxes.

[b]DNC = the model did not converge.

Rabbit predicted detection probabilities at camera sites from the best supported model (out of 25; Table 7) ranged from 0–0.099. Compared to the eastern side, detection probabilities increased at camera sites located near the northern ($p=0.01$–0.083; $\beta=1.569$, $P<0.01$) and western ($p=0.035$–0.099; $\beta=1.786$, $P<0.001$) side of the property. Their detection rates were also negatively correlated with human detection rates ($p=0$–0.099; $\beta=-19.586$, $P<0.001$) and decreased at camera sites in unburned areas compared to treated areas ($p=0.004$–0.019; $\beta=-1.604$, $P<0.001$) (Figure 3).

Mule deer predicted detection probabilities from the top model (out of 19 tested) (Table 7) ranged from 0.066–0.361. Compared to the eastern side, detection probabilities decreased at camera sites near the northern ($p=0.093$–0.298; $\beta=-0.283$, $P=0.041$), southern ($p=0.066$–0.227; $\beta=-0.0634$, $P<0.001$), and western ($p=0.17$; $\beta=-1.014$, $P<0.001$) aspects of the property. Their detection rates also decreased at control camera sites compared to treated camera sites ($p=0.066$–0.093; $\beta=-1.424$, $P<0.001$) (Figure 3).

Grey fox predicted detection probabilities from the top model (out of 40) (Table 7) ranged from 0.003–0.188. Compared to fall, detection probabilities decreased in the spring ($p=0.003$–0.057; $\beta=-1.336$, $P<0.001$) and summer ($p=0.003$–0.066; $\beta=-1.185$, $P<0.001$). Their detection probabilities were positively correlated with western grey squirrel detection rates ($p=0.003$–0.188; $\beta=20.713$, $P<0.001$) (Figure 4). Grey fox detection rates also decreased in control camera sites compared to treated; this effect was not significant in the top model ($p=0.003$–0.02; $\beta=-0.24$, $P=0.561$), but it was significant when tested with no other covariates (Model with camera location only: $p=0.008$; $\beta=-1.326$, $P<0.001$) (Figure. 4).

Coyote predicted detection probabilities from the top model (Table 7) ranged from 0.002–0.018. Their detection probabilities decreased at camera sites located in control areas
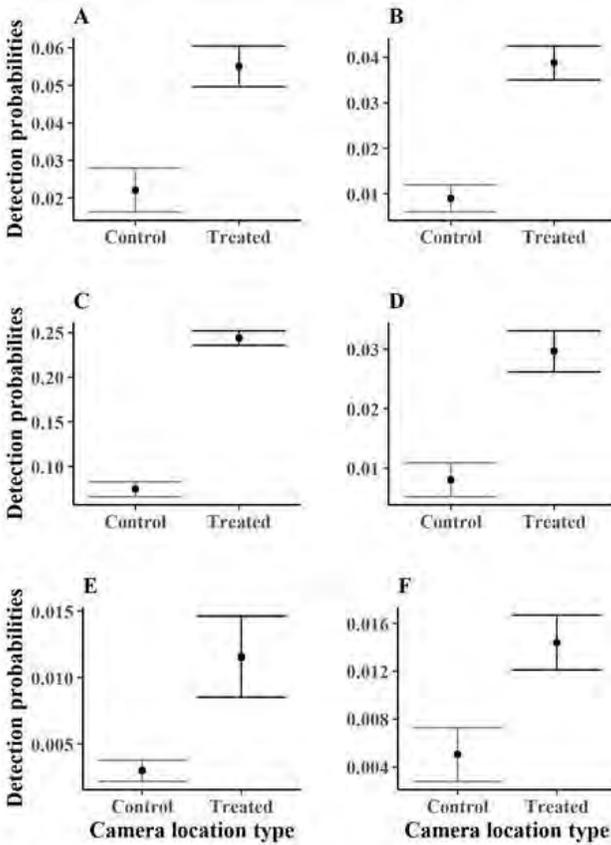
Figure 3. The effects of camera location in control (unburned and uncleared) areas and treated (burned and cleared) areas on predicted detection probabilities for grey squirrel (A), rabbits (cottontail and jackrabbits, B), mule deer (C), grey fox (D), coyote (E), and bobcat (F) from species' occupancy models with camera location as the only covariate for detection probabilities. The data was collected from 12 camera sites at the Pine Hill unit of the Pine Hill Ecological Reserve, El Dorado County, California from 2018−2019.
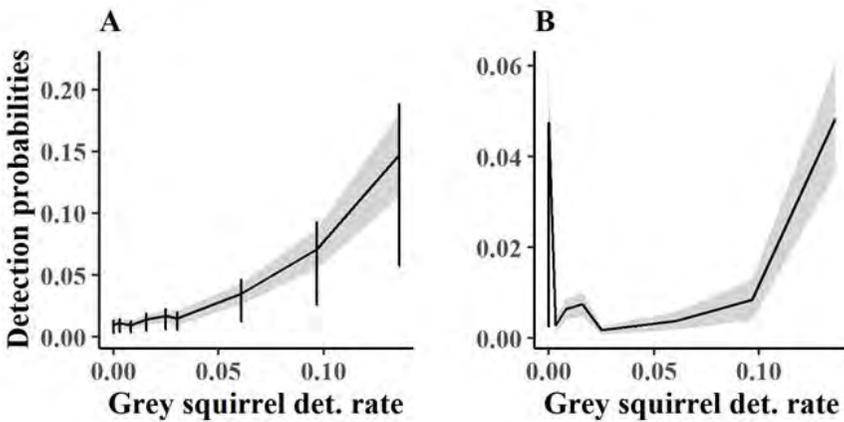
Figure 4. The effects of western grey squirrel detection (det.) rates on predicted detection probabilities from top occupancy models for grey fox (A; model with covariates season, camera location, and grey squirrel detection rate) and bobcat (B; model with covariates property side and grey squirrel detection rate). The data was collected from 12 camera sites at the Pine Hill unit of the Pine Hill Ecological Reserve, El Dorado County, California from 2018−2019.

compared to treated areas ($p=0.003$–0.02; $\beta=-1.36$, $P = 0.024$) (Figure 3). We compared a total of eight models with only temporal and location covariates (ordinal day, season, camera location, and property side) because all coyote occupancy models with species detection rates did not converge, likely due to the small sample size.

Bobcat predicted detection probabilities from the top model (out of 39 tested) ranged from 0.002–0.048. Compared to the eastern side, detection probabilities decreased at camera sites on the northern ($p=0.002$–0.008; $\beta=-3.853$, $P < 0.001$), southern ($p=0.005$–0.008; $\beta=-2.227$, $P < 0.001$), and western ($p=0.023$–0.048; $\beta=-2.92$, $P < 0.001$) sides of the property. Their detection probabilities were positively correlated with western grey squirrel detection rates ($p=0.002$–0.048; $\beta=21.633$, $P<0.001$) (Fig. 4B). In the model with camera location as the only covariate, bobcat detection rates decreased at camera sites in control areas compared to treated areas ($p=0.005$; $\beta=-1.061$, $P = 0.026$) (Fig. 3F).

For large carnivores we compared a total of 47 models. Their predicted detection probabilities from the top models (Table 4) ranged from 0–0.018. Likely due to small sample sizes, large carnivore detection probabilities did not significantly correlate with any of the top covariates with a P-value < 0.05; however, there were some covariate effects in the top models that had a P-value < 0.1 reported here. Large carnivore detection probabilities were positively correlated with meso carnivore detection rates (model with ordinal day and meso carnivore detection rate: $p=0.003$–0.013; $\beta=5.6$, $P = 0.093$) and mule deer detection rates (model with ordinal day, human detection rate, and mule deer detection rate: $p=0$–0.018; $\beta=1.268$, $P = 0.089$). Large carnivore detection probabilities were negatively correlated with human detection rates (model with ordinal day, camera location, human detection rate, and mule deer detection rate: $p=0$–0.017; $\beta=-21.704$, $P = 0.094$). We also found that all tested models with camera location showed a decrease in large carnivore detection probabilities at camera sites located in control areas compared to treated areas; however, this effect was not significant (model with ordinal day, camera location, and human detection rate: $p=0.003$–0.005; $\beta=-0.714$, $P = 0.141$). The large carnivore occupancy model with camera location as the only covariate did not converge, likely due to the small sample size.

DISCUSSION

The establishment of a firebreak along the perimeter of Pine Hill presented an opportunity for collaboration between botanists from the California Native Plant Society and biologists from the California Department of Fish and Wildlife to study the effects of hand clearing and pile burning on vegetation growth and composition, and wildlife response to the disturbances. We found burning of many cleared vegetation piles may be a suitable substitute to allow fire cued seeds to germinate even if man-made fires may not follow natural burn regimes (Steel et al. 2015). Generally, we found that wildlife responded by using treated areas more than the control sites.

Plant survey

The distributions of the rare species on the Pine Hill perimeter were in accord with the vegetation community classification proposed by Wilson et al. (2009) and supported by extensive sampling by Gogol-Prokurat (2014). The three communities on the perimeter were oak woodland, where only GACAS and WYRE were found, and xeric to mesic chaparral, where all rare species except GACAS were found. Grassland was uncommon. The most

mesic and shady northern aspect only contained the rare species FRDE and WYRE in a mixed chaparral-woodland community (Table 3).

Vegetation recovery and weed invasion. —Disturbance due to clearing only or clearing and burning resulted in the establishment of differing communities as measured by the Jaccard community coefficient, especially when determined using percent cover of shared species. This is an expected result, as such disturbances cause a niche opening for germination and growth of plants present in the seed bank, from vegetative structures, and of seeds dispersed into the opening. However, community difference was also found between treatment types, which suggested that the two treatments are not equal in terms of niche opening for different species. A concern is that a substantial proportion of plants differing between pairs of communities were exotic species, including species rated as moderately or highly invasive (California Invasive Plant Council 2020). Continued monitoring of the cleared perimeter of Pine Hill will be necessary to determine how colonization by invasive exotic species affects native community types.

Similarly, the high Shannon diversity found in the cleared and burned and cleared only treatments reflects the opening of niches for plants suppressed or barred from establishment in intact chaparral, which had the lowest Shannon diversity. Both establishment of native species and exotic species contributed to the high diversity of the treatments, with exotic species comprising 30% or more average cover in plots of the treatments. The historical fire disturbance in chaparral in California has allowed for successional communities that increase habitat variability; however, the high degree of invasion by exotic species may result in conversion of community type and lower native species diversity with changes in fire regime from historical patterns (Keeley and Davis 2007). The higher exotic species cover in the cleared treatment versus the cleared and burned treatment contributes to a different community type and to Shannon diversity, suggesting that continued clearing may cause conversion to a community type not historically found, with substantial cover by exotic species.

Disturbance (either clearing and burning or clearing only) resulted in colonization by a diversity of non-native plants. Further, there was higher cover by exotic grasses and native herbaceous perennials, species killed by fire, in the cleared than the burned treatments. However, intact, dense chaparral was no guarantee that weed invasion would not occur as the intact chaparral treatment contained high cover of *Brachypodium distachyon*, an exotic, fall germinating, shade tolerant grass. These last two traits mean that the grass germinates, grows up to 40 cm tall, and leaves dry, dead stalks under the shrub canopy after flowering in the spring (Piep 2012; CABI 2020). It is noted by CABI (2020) that this species can modify fire regimes, alter habitat, modify successional patterns, and form monocultures that smother native species resulting in reduced native biodiversity, including loss of rare species. Grasses provide the fuel to light the shrubs on fire (Brooks et al. 2004), and thus this one species may alter the natural fire dynamics of the chaparral by making invaded mature chaparral more vulnerable to fire. More generally, repeat fires, fueled by invasion of annual grasses, can lead to the conversion of deep-rooted shrub communities to shallow rooted grasslands and eliminate both resprouting and seeding native species (Keeley and Brennan 2012).

As well, *Brachypodium distachyon* was almost ubiquitous in the disturbed treatments, meaning clearing and fire were no impediment to its establishment. As the Pine Hill perimeter borders private property with a long history of disturbance and weed invasion (most homes were built before 1993, "Zillow" 2020), and the west perimeter contained a bulldozed fuel

break wherein weed populations flourished (Merriam et al. 2006), seed sources are close by. In contrast, there was an almost complete lack of weeds 12 years after the Pondo 50-Palmer fire (pers. obs. Ayres and Meyer); this site borders areas that were little disturbed and/or lacked abundant weed populations to spread into this preserve. Whether our limited data, based on a single western aspect site, will hold true for other aspects and sites on Pine Hill is unknown, but we argue that invasion by *B. distachyon* is an unreported vulnerability for the gabbro chaparral, and by extension, other chaparral where it occurs.

In northern California chaparral, Potts and Stephens (2009) examined short term (three year) vegetation responses to fire and clearing (mastication) and found that mastication treatments had the highest number of exotic invasive species with 34% higher exotic annual grass abundance than the fire treatments, similar to what we found two years after clearing (39% higher grass cover in cleared relative to burned treatments). Comparisons of longer term outcomes (13 years post treatment) of fuel hazard reduction treatments suggest that mechanical removal (mastication) can result in higher numbers of non-native species, including grasses, than fire treatments, and that the chaparral becomes once more vulnerable to fire after only 10 years (Wilkin et al. 2017). Perchemlides et al. (2008) compared mastication to hand clearing plus pile burning in chaparral in southern Oregon 4–7 years after clearing and found no difference in the herbaceous community composition between the two types of clearing; further they posit that retention of shrub cover may retard invasion by exotic grasses even though the effectiveness of the fuel break may be diminished by leaving shrub cover. Merriam et al. (2006) found that proximity to fuel breaks, especially old ones constructed with bulldozers, was associated with non-native invasion as the fuel breaks were readily colonized by non-native species that then moved into nearby undisturbed vegetation. In addition to fuel break creation that minimizes bare ground, they recommend retaining some overstory canopy and ground cover to retard invasion by non-native plants. Our method of fuel break construction minimized bare ground, soil disturbance, and left low cover by CERO and *Salvia sonomensis* in place - all of which may retard erosion and deter the long-term establishment of non-native plants. In the cleared treatment, combined cover by these two species averaged 28% while in the burned treatments it was <4% indicating hand clearing was successful in retaining low cover. Whether this low cover results in a reduction of non-native species in the future is not known. Short and long-term monitoring of the Pine Hill perimeter will determine the fate of these fuel reduction treatments on vegetation recovery, weed invasion and CERO.

Ceanothus roderickii seedling germination and survival.—CERO is an obligate seeder (Boyd 2007); obligate seeders are killed by fire and persist as seeds in the soil until cued to germinate by the fire's heat or charred leachate; only the treatments that burned contained abundant seedlings. About 50% of the seedlings that germinated the first spring following fire died during the growing season. Seedling densities and survivorship range are in accord with that reported by Ayres(2011). In second-year treatments, about 25% of the crop of spring-marked seedlings, a mixture of new and 1-year old seedlings, died during the growing season but we observed new seedlings in the fall after our spring counts which indicated the window of germination extended beyond early spring and is greater than one year post-fire. Therefore, the assumption that most seeds cued to germinate by fire do so in the year following fire should be assessed for each species of concern. The taller stature of seedlings in the earlier 2017 burn treatment is consistent with these plants being one year older than those following the recent fires in 2018. Cleared treatments retained mature CERO plants that escaped hand clearing while there were no mature plants within the burned treatments.

We conclude that land managers in the short-term may consider that burn piles that promote fire cued seeds to germinate may be a viable substitute for widespread fires to establish fuel breaks where the risk to local homes and air quality concerns preclude large fires.

Wildlife survey

Our occupancy models for western grey squirrel, rabbits (cottontail and jackrabbits), mule deer, grey fox, coyote, and bobcat showed that these species all had a higher probability of being detected at cameras in treated areas (cleared and burned) compared to control areas (not cleared or burned). While this effect was not significant for large carnivores (black bears and pumas), likely due to a small sample size, large carnivores also showed higher detection probabilities overall at cameras placed in treated areas. We saw higher wildlife usage at the cleared perimeter of the property compared to the dense interior, suggesting that hand clearing and pile burning may contribute to higher wildlife activity. We hypothesize that this may be due to two main reasons. First, the unburned and uncleared areas were so dense that large bodied mammals such as pumas, black bears, and deer were not physically able to traverse them. Clearing the perimeter of Pine Hill allowed animals to travel the perimeter more easily. The habitat also likely became more attractive to species like mule deer and rabbits that prefer ecotones (Kufeld et al. 1988; Lombardi et al. 2003), since limited clearing created more habitat patchiness, which is supported by other studies in Arizona and California (Bock and Bock 1990). Second, openings in the canopy and reduced competition from shrubs allowed new vegetation to sprout, offering increased forage for herbivores along the fuel breaks. A seven-year study in Glenn and Colusa counties, California, demonstrated an increase in deer forage and consequently more usage and increased populations as a result of managed fire (Thornton 1982). Despite its high cover, intact chaparral mostly consisted of unpalatable native shrubs and *Salvia sonomensis* (Conrad 1987); in this study, we found that cleared and burned patches had 30-60% cover by soft, presumably palatable vegetation (Conrad 1987). Small-bodied herbivores, such as rabbits and squirrels which were not as limited by dense vegetation as larger mammals, had higher detection rates in treated areas and likely used increased food resources in these areas. Increased fuel break usage by herbivores may have contributed to higher detection rates of predators in treated areas, such as grey fox, which were also positively associated with higher detection rates of western grey squirrels. These findings are supported by camera detections of grey foxes carrying small prey species. Additionally, large carnivores appear to use the fuel breaks frequently, and mule deer detections had a positive association with large carnivore detection probabilities. Previous research in Southern California also reported that pumas used burned areas in response to prey availability (Jennings et al. 2016). Even though black bears were present in the study area, due to small sample sizes we could not identify whether they preferred treated areas; detection rates were the same in treated and control areas. Researchers in Florida did not report higher usage of burned habitats by black bears either (Stratman and Pelton 2007) and researchers in Arizona showed black bears avoided burned areas (Cunningham et al. 2003). Overall, generalizable responses of predators to burned areas appear to be lacking (Geary et al. 2019). Since we only evaluated one year of data in this study, it might be possible that effects were delayed due to generational lag time to produce foods for species such as bears (Young and Beecham 1986; Costello and Sage 1994). Further, comparing results to the general fire ecology literature base is complex because most studies focus on fire events at a much larger scale than in this study.

The property side where the cameras were placed was also an important covariate in the occupancy models. The east side of Pine Hill borders larger private properties and some include ponds which likely attract wildlife; both mule deer and bobcats had higher detection rates on the east side. On the south, west, and north sides more development is present, and mule deer and bobcats had lower detection rates in these areas.

Hand clearing and pile burning around the perimeter of Pine Hill appeared to have a positive effect on wildlife usage, and this could result in increased human-wildlife conflict in the housing developments surrounding the property. While we did not assess population sizes due to the limitations of the study area size and camera locations, we did observe an abundance of mule deer in the area and recorded higher detection rates in the fuel breaks. Previous research reported that burned areas may generate higher deer populations (Florence and Florence 1988), and even though burning has been utilized to improve deer habitat since at least the 1970s, responses might be more varied in other situations (Kie 1984; Klinger et al. 1989). While further study is needed to determine if the deer population is increasing at Pine Hill, higher deer activity at the perimeter of the property, adjacent to residential areas, as shown in our results could contribute to closer interactions between deer and humans than deer activity within the interior of Pine Hill. High mule deer activity near housing developments may result in higher rates of prized garden plant consumption, which can generate human-wildlife conflict in the area (McCullough et al. 1997; Rondeau and Conrad 2003). Anthropogenically created openings may persist as mule deer preferentially browse in these areas (Velamazán et al. 2018). Future research should focus on whether openings around the perimeter persist due to herbivory and may have positive effects on wildlife and special status plants.

Additionally, multiple pumas used the area, which will likely perpetuate and further generate conflict with hobby livestock such as goats and sheep in the area (Orlando 2008; Dellinger et al. 2020). From nearby property owner reports, we were previously aware of pumas predating on alpacas in the area and black bears damaging private property. Overall, even though Pine Hill is entirely landlocked by private properties, it appeared to support a wide assemblage of wildlife species including multiple carnivores and herbivores. This was contrary to our expectations as environments impacted by development are often considered as inadequate habitat to sustain large predators (Beier et al. 2008).

While Pine Hill is not open to public usage, our cameras detected significant usage of the fuel break by people due to increased connectivity around the property's perimeter; prior to hand clearing and pile burning it was not possible to walk the perimeter of the area because of dense shrubs. Increased public usage of Pine Hill could be detrimental to wildlife activity as human presence was negatively associated with usage by large carnivores (George and Crooks 2006; Wang et al. 2017). The area is not posted or signed indicating closure to the public, primarily because the area is difficult to access; however, we recommend signage be installed to deter public usage. People that used the area may all be neighboring property owners, but additional effort to understand who used the area is needed.

Epilogue

Pine Hill Flannelbush, *Fremontodendron decumbens*, is the rarest and most endangered plant in El Dorado County, only occurring on Pine Hill and in the immediate vicinity. Seedlings were last observed in December 1983 to April 1984 immediately following a 1 ha experimental fire on the top on Pine Hill in October of 1983 that burned down 38 mature

flannelbush shrubs (Boyd 2001). Boyd (2001) marked and followed over 1100 seedlings for 13 months post-fire; 93% were killed by rodents, drought, or shading from flannelbush shrubs that resprouted from roots after the fire. Survival of seedlings was 2.4 times higher in the gaps between the former shrubs than under their canopies (11.5% vs 4.7) indicating the importance of dispersal away from mature shrubs.

On 4 May 2020, we found 4 seedlings within three fire scars from shrub piles that burned in March 2019 on the south perimeter. Shriveled seed leaves, cotyledons, were present on each seedling plant. The closest flannelbush shrubs were at least 6 m away. No seedlings were found in cleared and regrowing chaparral vegetation that was not burned as the seeds are cued to germinate by fire's heat (Boyd 2001). Ant dispersal is likely how the seeds got to the burn scars (Boyd 1996, 2001). The seeds have protein-rich elaiosomes attached to the tough-walled seed coat; native harvester ants, *Veromessor andrei*, can carry these seeds up to 12 m from the mature plant to their nests where they eat the elaiosomes and then deposit the seeds on their midden piles. The seedlings were large; spreading up to 13 cm, growing up to 8 cm tall, and with many true leaves suggesting they germinated with the 2019–2020 fall-winter rains and grew rapidly during the spring. There were likely many more seedlings that were eaten by rodents at the cotyledon stage (Boyd 2001). Will these new seedlings survive the summer drought and herbivores? We will see as we continue to monitor their survival and growth. Pile burning within 12 m of flannelbush shrubs may be an effective strategy to ensure the long-term survival of the species as its survival will depend on the establishment of new plants due to the eventual mortality of the mature shrubs (as yet unknown).

ACKNOWLEDMENTS

Author Contributions
Conceived and designed the study: all authors
Collected the data: all authors
Performed the analysis of the data: MRC
Authored the manuscript: MK, MRC, DA
Provided critical revision of the manuscript: MK, MRC, DA, VM

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ORIGINAL RESEARCH

Survival of the rare *Packera layneae* (Asteraceae), under chaparral and after fire

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Conservation of rare plants requires an understanding of how the species responds to natural and artificial disturbance dynamics. For chaparral species this includes the natural disturbances of fire and shrub canopy closure during the interfire period, and the effect of shrub clearing for fuel reduction. *Packera layneae* is a federally listed rare herbaceous perennial subject to all these disturbances; its center of distribution is upon the gabbro soils surrounding Pine Hill in western El Dorado County, CA an area known as a hotspot of botanical diversity. Combining genetic data with mapping following a 2007 wildfire in Shingle Springs, we found that the species survives fire and chaparral overgrowth due to underground rhizomes and caudices that resprout after fire and enable its persistence under dense chaparral canopies; as well, seed recruitment of new genetic individuals occurred within discrete patches. Seedlings were not found the spring following the 2007 fire, suggesting fire killed the soft-walled seeds. Surveys across the Pine Hill area from 2005-2007 found populations flowering and producing seed in recently burned and cleared areas as well as under mature chaparral; however, the proportion of plants flowering decreased as shrub density increased. From our 2019 surveys of a new 4.25 km fuel break around the perimeter of Pine Hill in Rescue, CA (0.983 km^2) we found the species resprouted from plants growing under the dense chaparral canopy on the southern, eastern, and western aspects but did not occur on the northern exposure or under dense oak canopy. As the seedling regeneration niche is unknown, preservation of established populations is vital to the long-term persistence of the species.

Key words: El Dorado County, fire ecology, gabbro soil, *Packera layneae*, Pine Hill

Packera layneae (Greene) W.A. Weber & A. Love (Asteraceae), Layne's ragwort, is a federally listed threatened and state listed rare plant that occurs in the Sierra Nevada foothills of central California. It is a perennial herb that dies back in the winter and emerges from the soil in mid-March. It reportedly resprouts from a tap-rooted caudex, grows 4-7+ dm tall, and flowers from April to June (Trock, 2012). The center of its distribution is upon the gabbro-derived soil intrusion around Pine Hill in western El Dorado County (see Klip et al. 2020, this issue for additional description) where the species is found flowering in openings within and adjacent to chaparral. It also has limited occurrence on serpentine soils in Tuolumne and gabbro and serpentine soils in Yuba County (Williams 2014). The species is primarily outcrossing, and has the ability to disperse its seeds on the wind (Marsh and Ayres 2002); however, Williams (2014) found most seeds dispersed within 1 m of the maternal plant. Genetic analyses revealed pronounced genetic differences among the populations in the three geographically distant counties, and between two El Dorado County populations separated by 5.5 km (Marsh and Ayres 2002).

Chaparral is a shrub-dominated community that periodically burns and re-establishes after fire. Species adapted to these dynamics must survive fire by re-sprouting or arising from seeds in the soil, and survive the subsequent closure of the shrub canopy lasting several decades. Early reports (Baad and Hanna 1987) speculated that *P. layneae* was an early successional species occupying temporary openings in the chaparral that was eliminated as the chaparral regrew after fire. On the other hand, from 2005 to 2007, we found *P. layneae* in both undisturbed, mature chaparral, as well as in previously burned or mechanically cleared areas, suggesting it can persist under varying disturbance regimes. The questions of whether and how the species survives fire, clearing, and a long interfire period (90+ years) under a dense chaparral canopy are questions addressed in this paper.

METHODS

We evaluated population size, flowering, and seed output in plots representing varying levels of disturbance from 2005–2007. Plant survival and occurrence were evaluated following a 2007 wildfire in Shingle Springs, CA and 2017–2019 shrub clearing to create a fuel break around the perimeter of Pine Hill, Rescue, CA; the two sites are separated by approximately 8 km (Figure 1).

Disturbance study

We collected data at 33 plots where *P. layneae* was present from 2005–2007, including burned, mechanically cleared, and undisturbed mature chaparral. Data collected at each plot included shrub cover estimates, number of *P. layneae* plants, metrics of plant size and flowering, and seed output. For a full description of methods, see Gogol-Prokurat (2009).

Post-fire study

On 7 June 2007, the 12 ha (30 acre) Palmer wildfire broke out on the Ponderosa 50 parcel of the Pine Hill Preserve in Shingle Springs, a 20 ha preserve, due north of Highway 50 and 400 m west of Ponderosa Road (hereafter Pondo), a site dominated by *Arctostaphylos viscida* /*Adenstoma facsicularis* chaparral. Tree ring counts of a *Quercus kelloggii* individual
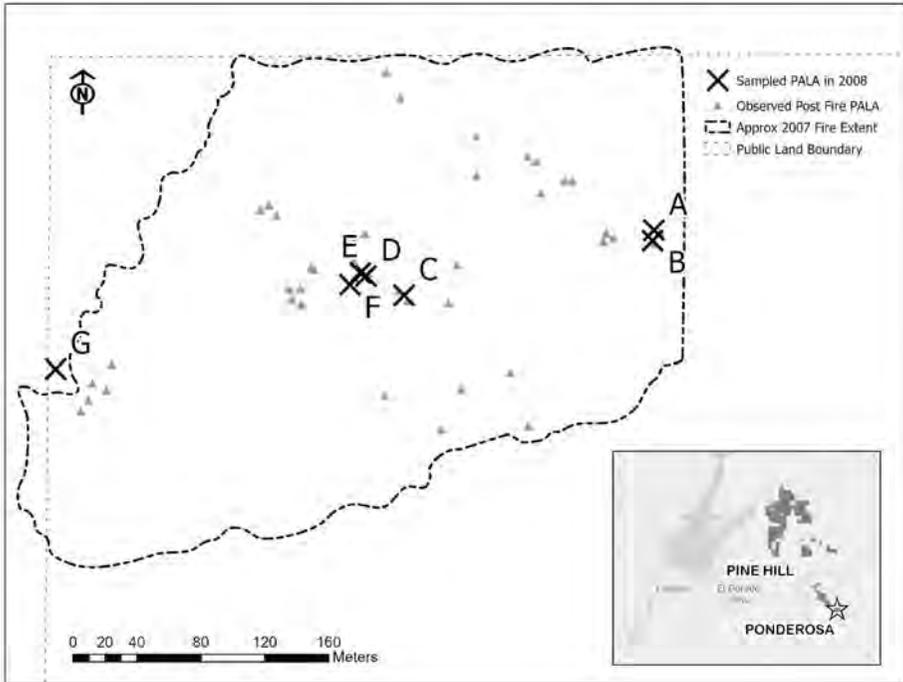
Figure 1. Map of *Packera layneae* within the Ponderosa-Palmer Fire in Shingle Springs, CA. Inset locality map shows the Pondo and Pine Hill study sites; the dark multi-square areas are the units of the Pine Hill Preserve on the gabbro soil intrusion.

killed in the fire indicated the tree was over 90 years old at time of death, suggesting the chaparral had last burned in 1917 or earlier. We surveyed the burned area 14 April 2008. *Packera layneae* rosettes were aggregated into 42 discrete patches, that were mapped, scattered throughout the burned area (Figure 1). The number of rosettes was counted in 16 patches. Seven patches were chosen for genetic analysis, 6 of which were within the burned area (patches A-F); patch G was outside the fire's perimeter and was densely flowering; the number of flower heads on 10 flowering stems, haphazardly chosen, were counted; heads per stem ranged from 2 to 13 (average = 5). None of the rosettes in the burned area flowered. The *P. layneae* rosettes were clearly resprouts, not seedlings, as the rosettes were robust, with many leaves, and lacked cotyledons.

Genetic analyses

In May 2008, we collected newly emerged leaves, one per rosette, from the 7 mapped patches, sampling 4–10 rosettes per patch (n = 39) for genetic fingerprinting. The burned patches were haphazardly chosen along a line through the center of the population (Figure 1). We sampled rosettes at the north-south and east-west limits of each chosen patch, as well as in the patch center, and counted the rosettes included in the patch. Each sample's location was determined and documented by GPS. Samples were placed on ice and taken to the lab at UC Davis. DNA extraction and PCR reactions were performed according to the protocols of Marsh and Ayres (2002). Due to limited funding, PCR was performed using only 2 ISSR

primers, 807 and 823 that had each produced 3 polymorphic bands in previous work (6 bands total) (Marsh and Ayres 2002). We ran reactions twice to verify band reproducibility.

To facilitate identification of genets (genetic individuals) and ramets (multiple rosettes from a single genet), we analyzed the presence/absence (1/0) matrix of the 6 polymorphic bands for genetic distance using the Euclidean distance coefficient and the resulting distance matrix was then used to construct a dendrogram using NTSYS-pc, version 2.01d (Rohlf 1993). Those rosettes within a patch that had identical or different genetic fingerprints were readily identified.

Mapping distribution on Pine Hill

From 2016 to 2019, the El Dorado Chapter of the California Native Plant Society (CNPS) collaborated with the California Department of Fish and Wildlife (CDFW) and the California Department of Forestry and Fire Protection (CalFire) to establish a 21-m firebreak along the 4.25 km perimeter (area surveyed = 8.9 ha) of Pine Hill to prevent fire from moving onto the Pine Hill Preserve from private land and vice versa (see Figure 1, Klip et al. 2020, this issue). The fire break was created by hand crews with chainsaws who cut down all shrubs taller than 30 cm followed by pile burning of the debris. The CNPS's goal was to survey for rare plants, map their distribution along the perimeter (see Klip et al. 2020, this issue) and locate areas free of rare plants to place the burn piles. There is no record of when the perimeter last burned in a wildfire, although there is some evidence for fuel break burning in 1975 and 1983 (Mario Klip, CDFW, personal communication).

We conducted botanical surveys in 2017 along created pathways before general clearing and after clearing was completed in 2019. The CNPS waited to begin the surveys until leaves of *Wyethia reticulata* and *P. layneae* emerged in the spring and became identifiable; this occurred in mid-March. A cadre of volunteers was formed, team leaders were trained by experienced botanists, and 12 survey days were held from 16 March through 11 April 2017. After the perimeter had been cleared, botanists from the El Dorado Chapter of the CNPS returned and completely surveyed and mapped the perimeter for all rare plant species in spring 2019.

RESULTS

Disturbance study

P. layneae populations were identified in areas with a history of recent burning and clearing as well as in undisturbed chaparral. There was no significant difference in the number of plants found in populations regardless of disturbance history (Table 1; Gogol-Prokurat 2009); however, the proportion of plants flowering decreased as shrub density increased (Figure 2).

Post-fire study

In 2008, small rosettes of *P. layneae* were found in 42 discrete patches; the total area occupied by patches (0.02 ha) was 0.17% of the total burned area of 12 ha. Each rosette in a patch was separated by 0.5–4 m (Figure 1). The number of rosettes per patch ranged from 8 to 173, with an average of 42.4 small rosettes/patch, for a total of 1,782 rosettes. Rosette
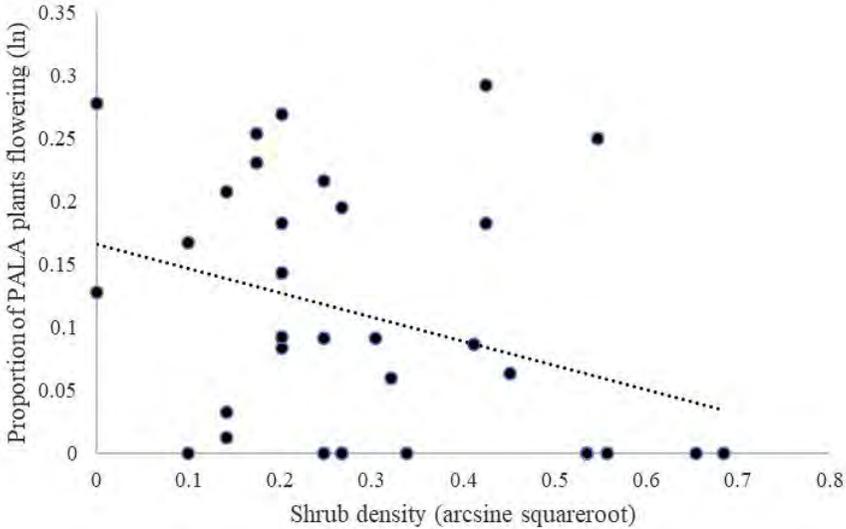
Figure 2. Relationship between chaparral shrub density and the proportion of *P. layneae* plants flowering per population, 2005–2007 surveys of populations throughout the gabbro soil, El Dorado County, CA.

Table 1. Summary of plant density and flowering in 33 occupied plots, 2005–2007 surveys of populations throughout the gabbro soil, El Dorado County, CA.

Disturbance type	# of Plots	Average (SE) % shrub cover	Range of shrub cover	Average (SE) number of plants/m²	Range of plants/m²	% of plants flowering	Average (SE) plant height (cm)	Seed output (SE) per plant
Undisturbed	10	22 (3.6)	7–42	0.15 (0.05)	0.005–0.52	17	54 (2.5)	520 (59)
Cleared	15	12 (2.4)	2–29	0.49 (0.21)	0.03–2.46	21	48 (3.8)	600 (90)
Burned	8	6 (0.7)	2–8	0.32 (0.16)	0.04–1.25	16	50 (2.0)	580 (65)

density over the entire burned area was 0.015 rosettes/m² while density within patches was 14 rosettes/m². The six patches chosen for genetic analysis had an average of 63 rosettes/patch, within an average area of 4.6 m² (Table 2). No seedlings were found in the spring immediately following fire. None of the rosettes in the burned area flowered in the year following fire; 2 years after fire flowering was abundant (personal observation).

Genetic analyses

Plants arising from a single sexually produced seed are genetic individuals that are termed "genets." If the plant expands clonally, then the clonal offshoots from a genet will have the identical genotype and are termed "ramets." We indentified 19 unique genotypes in 39 samples. Twenty-nine samples with either a unique genotype or that occurred in different patches were considered to be genets that arose from separate seed establishment events

Table 2. Summary of 2008 genetic analyses, mapping, and rosette densities of 7 *Packera layneae* patches at Ponderosa Preserve, Shingle Springs, CA following a 2017 wildfire.

Patch	Patch size (m^2) burned plots	# of Samples per Plot	# of genets per plot	Max distance between ramets (m)	# of rosettes/ m^2 burned patches	# of Genets/ m^2 burned patches
A	5.70	5	1	3.3	4.6	4.56
B	5.84	5	4	2	4.1	3.29
C	7.74	6	6	No ramets	22.3	22.34
D	1.00	4	3	0.36	20.9	15.67
E	1.75	5	5	No ramets	12.0	12.03
F	5.61	5	2	1.8	20.5	10.26
G (unburned)	N/A	10	8	N/A	N/A	N/A
Average (SE) for burned patches	4.61 (1.08)	5.00 (0.26)	4.14 (0.76)	1.86 (0.60)	14.10 (3.42)	11.36 (3.26)

(Table 2). All samples in patches C and E were genetically different and therefore were genets. Genetically identical samples from within a patch could have resulted by chance or due to clonal expansion of a single genet, i.e. ramets. The odds of obtaining 2 genetically identical samples by chance, as in patches B, D, and G were 0.23 (19/39)*(18/38); the odds of 4 identical samples as in patch F were 0.047 (19/39)*(18/38)*(17/37)*(16/36); and the odds of 5 identical samples as in patch A were 0.020. The distances separating presumed ramets were 2m to 3.3m in patch A and 0.80m to 2m for patch F. As 74% (29/39) of the samples were genets the population size is estimated to be 1,324 genets (0.74*1,782).

Mapping distribution on Pine Hill

Packera layneae was found resprouting along the cleared perimeter on the sunnier exposures, South-, East-, and West-facing slopes previously covered by dense chaparral; there were no occurrences on the shady northern perimeter or in the oak woodland on the eastern exposure. In 2019, two years after clearing, seedlings were observed in the cleared SE corner (pers. obs.). As we did not record the presence of seedlings in the 2017 survey, it is unknown yet whether the species recruits by seed under the dense chaparral canopy.

DISCUSSION

Packera layneae survives both fire and clearing due to underground structures protected by the insulation of 3 to several cm of soil. Clonal expanse up to 3 m, based on genetically identical ramets occurring in the same patch, indicates that the species is capable of rhizomatous growth. However, clonal growth within patches does not explain the extremely patchy distribution we found after wildfire as we also found genetic evidence of multiple recruitment events by seed within patches (Table 1). Local seed dispersal of <1 m was found by Williams (2014) perhaps explaining the patchy distribution. Rhizomes and caudices likely allow the plants to survive long periods of canopy closure between fires, perhaps longer than 90 years. Clearly, *P. layneae* is not a successional species that dies out under chaparral as once posited. However, conclusions on clonal spread based on only 6 markers should be regarded as preliminary awaiting robust genetic studies using more markers and samples

as the 6 genetic markers were not adequate to resolve all samples. The species either does not have a seed bank, or seeds are killed by fire. Williams (2014) found seeds germinated 3 weeks following cold-moist stratification without a longer dormancy period.

In extensive surveying throughout the gabbro soil intrusion the species was found to occur more or less equally in undisturbed, cleared, and previously burned sites; the effect of disturbance was to increase plant density 2- to 3-fold, but not plant occupancy (Gogol-Prokurat 2009). The higher abundance in disturbed sites suggests vegetative growth or recruitment by seedlings was favored once the site was cleared or burned; however, the time when the disturbance occurred was not known. Across all surveys, there s great variation in rosette density, which may be influenced by both plot placement and disturbance history. Intriguingly, while the Pondo plants did not flower the first spring following fire, our broader disturbance surveys found that *P. layneae* flowered under all conditions. However, the disturbance surveys found the proportion of plants flowering was lower in recently burned plots, possibly also reflecting a delay in flowering after burn events (Table 2).

We found that the proportion of plants flowering declined as total shrub cover increased (Figure 2); therefore, as chaparral matures and shrub cover increases, the proportion of *P. layneae* plants flowering declines. Gogol-Prokurat (2009; Figure 3.1) found a strong correlation between *P. layneae* flower density per population and overall seed output; therefore, as chaparral matures and shrub density increases, the density of flowering *P. layneae* and in turn the overall reproductive output may be expected to decline until the next disturbance event. Plants in undisturbed plots were also taller than those in disturbed areas (Table 2), and it is possible that the increased resource use to compete for light could explain the depressed reproductive output.

Estimating population size in clonal plant species is particularly difficult without the insight provided by genetic analysis. Even so, our estimate of a population size of 1,324 genets exceeds what has been previously reported for this species; population size records for the species vary from 10 to over 1,000 individuals (California Natural Diversity Data Base 1998 reported in USFWS 2002). The distinction between ramets and genets is critical for the conservation of rare clonal plants as genets are the evolutionarily important units while ramets are genetic replicates (Tepedino 2012) that in self-incompatible species, such as *P. layneae*, cannot effect pollination. Tepedino (2012) suggests the population size of clonal plants be estimated downward at least 25% - an estimate in accord with our genetic study.

An important consideration of long-term plant species survival is the nature of the regeneration niche (Grubb 1977). This concept posits if environmental conditions only favor adult plant growth and survival, but not seed production, dispersal, germination, and/or seedling establishment, then the species cannot endure over evolutionary time intervals. Many chaparral species are killed by fire and only persist by seedling establishment following fire-stimulated germination of seed in the soil seed bank. Therefore, for obligate seeder species such as *Ceanothus roderickii*, fire is an integral component of the regeneration niche. We do not know the dimensions of the seedling regeneration niche for re-sprouting *P. layneae*; seedlings do not appear in the year after fire, and flowering is delayed until the second spring after fire. Flowering did occur in 70% of undisturbed sites, a frequency comparable to the disturbed sites, with equally high seed output per plant (520–600 seeds/plant) under all conditions (Table 2). Whether seed output resulted in seedling establishment is not known.

On the other hand, Keeley (1991) points out that germination and seedling establishment of resprouting species do not necessarily require fire; rather they regenerate under the

shaded and mesic conditions found under the canopy of existing shrubs. As seedling occurrence has not been studied, this aspect of the regeneration niche is unknown. However, we found genetic evidence that multiple local recruitment events occurred to form patches at the Pondo fire site; data and our observations suggest seedling appearance and establishment in naturally open rocky areas, and proximate to an established plant following hand clearing. Further study focusing on the location and survivorship of seedlings is needed to describe the regeneration niche of *P. layneae* to identify the key components for long-term species persistence and to aid in human augmentation and/or introductions of *P. layneae* populations.

Wilson et al. (2009) analyzed the distribution of plant species on the gabbro intrusion in western El Dorado County and determined that there were two variants of the chaparral community, termed mesic resprouting and xeric seeding, based on degree of insolation and plant regeneration strategies. *Packera layneae* was associated with mesic chaparral with resprouting shrubs Toyon (*Heteromeles arbutifolia*), Coffeeberry (*Frangula californica ssp. tomentella*), and Redbud (*Cercis occidentalis*), resprouting perennial *Wyethia reticulata*, and chaparral sedge *Carex xerophila*, and the species was not associated with the most xeric chaparral on the southern exposures or oak woodland on the northern exposures. This is consistent with our surveys on Pine Hill and observations at the Pondo site; *P. layneae* was mostly absent on the north side and under the canopy of oaks on the east side, but was present under the chaparral on the east, south and west sides. These species associations were supported by Gogol-Prokurat (2009, 2014); in addition, proximity to disturbance such as roads or clearing was a strong predictor of *P. layneae* occurrence (Gogol-Prokurat 2009). Also of note, Wilson et al. (2009) found the complete absence of any of the rare species on exotic-grass dominated grassland suggesting that naturally occurring grasslands are not suitable habitat for the rare species and/or frequent disturbance that results in conversion of chaparral to grassland will eliminate both rare and common chaparral species.

Conservation implications

Plants survive, persist, and spread under chaparral disturbance dynamics by underground rhizomes up to 3.3 m in length in addition to individual caudices.

Estimates of population size should be reduced by at least 25% to take into account rhizomatous spread by ramets.

There is pronounced genetic structure (Marsh and Ayres 2002) meaning that many populations should be preserved and linked through corridors to allow gene flow.

Evidence indicates that both sexual and asexual reproduction are reduced as chaparral matures and total shrub cover increases. Although the species is adapted to survive and persist through these intervals between disturbance events, a regular disturbance regime is important to ensure the continued reproduction and persistence of this species.

Preservation of suitable habitat, using shrub dominants as indicator species, may be the correct approach to the conservation of this and the other listed species (Gogal-Prokurat 2014). These indicator species may also signal where artificial seeding may be most successful. As local scale genetic structure was also found (March and Ayres 2002) only local seed sources should be used in artificial seeding efforts.

Investigations into the regeneration niche are needed to determine whether clearing by hand is as effective as fire in species regeneration. This knowledge can be used to aid in population growth and augmentation by human-seeding efforts.

ACKNOWLEDGMENTS

Author Contributions
Conceived and designed the study: All authors
Collected the data: All authors
Performed analyses of the data: DA,VM, MG-P
Authored the manuscript: DA
Provided critical revision of the manuscript: VM, MG-P

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RESEARCH NOTE

Post-wildfire response of Shasta snow-wreath

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Key words: Hirz fire, *Neviusia cliftonii*, post-wildfire response, Shasta snow-wreath, vegetative reproduction

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Shasta snow-wreath (*Neviusia cliftonii*) is a rare shrub of the Rosaceae: tribe Kerrieae endemic to the southeastern Klamath Mountains in the general vicinity of Shasta Lake, Shasta County, California. The species was discovered less than 30 years ago (Shevock et al. 1992; Taylor 1993) and initially considered a limestone obligate. Subsequent occurrences have also been found on various non-limestone substrates (Lindstrand and Nelson 2005a, b, 2006; DeWoody et al. 2012; Jules et al. 2017). The only congener, Alabama snow-wreath (*Neviusia alabamensis*), also has a limited range restricted to several disjunct populations in the southeastern United States and occurs on limestone and non-limestone sedimentary substrates (Long 1989; Freiley 1994).

Shasta snow-wreath is deciduous and produces flowers with showy white stamens, five toothed green sepals, and rarely, one to three narrow white petals. Based on our observations since its discovery, the species reproduces vegetatively, forming thickets of stems from the root system. Despite observations of developing achenes, no viable seed nor seedlings have been collected or observed. We are not aware of any pollinators and the blooms lack detectable scent. Genetic sampling at 21 Shasta snow-wreath populations conducted during 2011 revealed low genetic diversity within populations, high variation between populations, and low overall genetic diversity, supporting the theory that sexual reproduction is less common than vegetative reproduction and that there is, at best, low gene flow within and between populations (DeWoody et al. 2012). Alabama snow-wreath is also only known to reproduce vegetatively, in the wild (Freiley 1994).

Shasta snow-wreath currently holds a California Rare Plant Rank of 1B.2 (CDFW 2020) and also is considered a Sensitive species by the Region 5 U.S. Department of Agriculture Forest Service and the California Region of U.S. Department of Interior Bureau of Land Management. Recent petitions have been submitted to the U.S. Fish and Wildlife Service and California Fish and Game Commission seeking species protection under the Federal Endangered Species Act and California Endangered Species Act, respectively (CFGC 2019; Roche 2019; USFWS 2019).

Little is known about the species response to natural disturbances or land management activities. Based on our observations, four populations occur in habitat subject to historic logging; and a hiking trail, which receives occasional maintenance, was constructed through another. Shasta snow-wreath plants along the trail were also grubbed or cut for a prescribed burn in the 1990s and plants resprouted in the disturbed area. Several shrubs occupying a limited portion of a small population at another location were burned during a low-intensity prescribed fire in 2011, and these plants also showed vegetative resprouting. Additionally, two populations were disturbed by historic dirt road construction and Shasta snow-wreath plants have since reoccupied some of the former road surfaces. The Klamath Mountains historically experienced frequent wildfires (Taylor and Skinner 2003; Fry and Stephens 2006; Safford and Van de Water 2014), including within the species range, and burn scars occur on trees among several Shasta snow-wreath populations. While existing in a historically fire-prone landscape, no known Shasta snow-wreath populations had been subject to wildfire since its 1992 discovery, until 2018.

Several large wildfires occurred in Shasta County, California, during 2018, including the Hirz Fire. This human-caused fire started 9 August and was contained 15 September 2018. The fire footprint encompassed approximately 18,676 ha and included a burned and unburned mosaic, with burn areas characterized by low, medium, and high burn severity classes as classified using Parsons et al. (2010), depending on location. Two known Shasta snow-wreath populations occur in the Hirz Fire footprint; one located near the Ellery Creek confluence with the McCloud River Arm of Shasta Lake (40.9148, -122.2473) (Figure 1), and a second located in an unnamed creek drainage approximately 0.59 km south of Ellery Creek. The fire burned portions of the "south of Ellery Creek" population and the entire Ellery Creek population, providing opportunity to observe post-wildfire response of Shasta snow-wreath at a large scale. We determined the Ellery Creek population best suited for post-wildfire monitoring and planned a monitoring effort at the site.
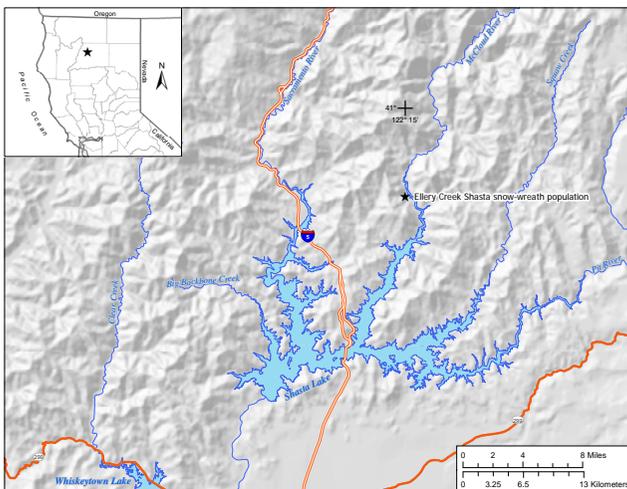
Figure 1. General location map, Ellery Creek Shasta snow-wreath population, Shasta County, California, USA.

The Ellery Creek Shasta snow-wreath population encompasses approximately 11.5 ha and occurs on a northerly aspect slope in a steep canyon characterized by numerous limestone outcroppings. Overall habitats are dominated by hardwood-conifer forest with chaparral inclusions surrounding the limestone outcroppings. The Ellery Creek population occurs in three habitats: hardwood-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), canyon live oak (*Quercus chrysolepis*) and California black oak (*Quercus kelloggii*); hardwood forest dominated by California black oak; and chaparral habitat dominated by Brewer oak (*Quercus garryana* var. *breweri*).

We initiated post-fire monitoring at the Ellery Creek Shasta snow-wreath population during October 2018 by conducting a site visit to determine the extent of fire damage and overall condition of the population. During the visit we established an informal transect used to conduct monitoring observations. We designed the transect to meander through the entire population, including all three habitats and elevational gradient, and generally walked the same transect during each visit. The entire Ellery Creek population burned in the fire, with moderate and high burn severity classes (Figure 2). Most of the Shasta snow-wreath population occurring in the hardwood-conifer forest habitat burned at moderate severity, while those portions occurring in the hardwood and chaparral habitats burned at high severity. The fire top-killed all above ground Shasta snow-wreath stems, most of which burned to the ground leaving small root crowns, or charred skeletons remaining. Examination of the below ground stem segments suggested they remained viable, as the stems appeared "green" and otherwise normal, including at high severity burn areas. During the October visit, we

Figure 2. Portion of the Ellery Creek Shasta snow-wreath population during October 2018 burned in the 2018 Hirz Fire, Shasta County, California, USA. Photo by Len Lindstrand III.

observed numerous associated species crown-sprouting shortly following the fire, including big-leaf maple (*Acer macrophyllum*), California black oak, Brewer oak, canyon live oak, California snowdrop bush (*Styrax redivivus*), western redbud (*Cercis occidentalis*), deer brush (*Ceanothus integerrimus*), poison oak (*Toxicodendron diversilobum*), mock orange (*Philadelphus lewisii*), spicebush (*Calycanthus occidentalis*) and hazelnut (*Corylus cornuta*). However, we did not observe resprouting Shasta snow-wreath at that time.

Following the initial assessment, we conducted monthly site visits from March through July and October 2019. During each visit we made observations of Shasta snow-wreath response to the fire, including presence or absence of vegetative sprouting, seedlings, plant health and vigor, and other ecological factors such as sign of herbivory and associated species.

We observed resprouting Shasta snow-wreath at the beginning of the first growing season following the fire on a site visit conducted 30 March 2019. The newly emerged growth ranged from 0.6 and 1.9 cm tall and was observed throughout the population sprouting from woody rhizomes and burned root crowns (Figures 3, 4). We observed continual vigorous and dense resprouting from April through July (Figure 5), with the new growth reaching 0.9 m tall. The October 2019 visit showed the new growth reaching 1.1 m tall (Figure 6), likely the upper height limit for the 2019 growing season. By this time several rain events

Figure 3. Shasta snow-wreath resprouting from burned root crown during March 2019, Ellery Creek, Shasta County, California, USA. Photo by Len Lindstrand III.

Figure 4. Shasta snow-wreath resprouting from woody rhizome during March 2019, Ellery Creek, Shasta County, California, USA. Photo by Len Lindstrand III.

Figure 5. Dense Shasta snow-wreath resprouting during October 2019 following the 2018 Hirz Fire, Ellery Creek, Shasta County, California, USA. Photo by Len Lindstrand III.

had occurred and cooler fall temperatures arrived. Many of the Shasta snow-wreath plants showed new leaf growth and some additional new rhizome and root crown sprouting. New leaf growth during the fall is a regular response of "normal" Shasta snow-wreath populations and many other local shrub species, suggesting this resprouting population is following a typical growth pattern.

The Ellery Creek Shasta snow-wreath population is extant and in good overall condition. The resprouted plants did not flower during 2019, and monitoring will be continued to determine the duration until the shrubs bloom again. We observed occasional deer (*Odocoileus hemionus*) browsing among the re-sprouting Shasta snow-wreath; however, the browsing appeared limited to those plants located on and adjacent to game trails, and not throughout the entire population. No evidence of plant disease was observed.

The 2019 post-wildfire monitoring observations confirmed our belief that Shasta snow-wreath responds well to wildfire by vegetative reproduction. We speculated that Shasta snow-wreath seed might have been stimulated by this fire event and that seedlings would appear; however, none were observed during our monitoring. Our confirmation of reproduction exclusively by resprouting is consistent with known genetic relationships within and among Shasta snow-wreath populations (i.e., DeWoody et al. 2012) and is consistent with previous observations regarding seedling observations and seed viability. Considering wildfire is by far the most common historical and current natural disturbance within the species range, our observations suggest that Shasta snow-wreath reproduction may be restricted to only vegetative reproduction.
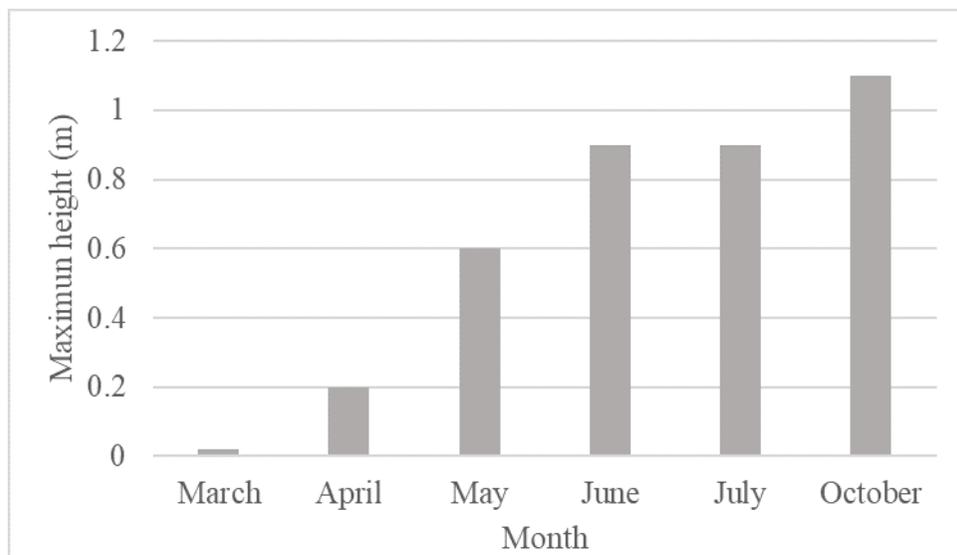
Figure 6. Shasta snow-wreath resprouting stem heights during 2019 following the 2018 Hirz Fire, Ellery Creek, Shasta County, California, USA.

Authors Note: During a site visit to Ellery Creek on 28 April 2020, the first Author documented portions of the Shasta snow-wreath population in flower, demonstrating the species is capable of flowering two years post-fire. Several of the flowers observed included a single petal, a rare species trait, as most flowers and populations are typically apetalous.

ACKNOWLEDGMENTS

Author Contributions
Conceived and designed the study: LL
Collected the data: LL, JK
Performed analyses of the data: LL, JK, DWT
Authored the manuscript: LL
Provided critical revision of the manuscript: JK, DWT

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SECTION 3.
Fire Impacts on Wildlife and Water

Top: Gray fox (*Urocyon cinereoargenteus*) from a camera trap placed in Pine Hill Ecological Reserve, El Dorado County, CA after fuel break vegetation treatments. Photo Credit: Mario Klip, CDFW.

Left: Sooty hand holding a yellow-eyed salamander (*Ensatina eschscholtzii*) and California newt (*Taricha torosa*). Photo Credit: Veronica Davison, USFWS.

Below: A stream in a high severity burn area in Wallace Canyon, Eldorado National Forest, CA one year after the 2014 King Fire. Photo Credit: Cristin Walters, CDFW.

ORIGINAL RESEARCH

Elk forage response to prescribed fire in Boyes meadow, Prairie Creek Redwoods State Park, California

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Prescribed fire should increase plant and forage biomass for herbivores in meadows, but the response is likely to be influenced by environmental conditions. Across 15 years prescribed fires occurred every two to four years in September in Boyes meadow, Humboldt County, California. We measured the presence or absence of prescribed fires in September, climatic conditions one month later, Roosevelt elk (*Cervus elaphus roosevelti*) abundance, and the biomass of elk forage in January. From analysis of a linear mixed effects model we found that prescribed fires increased forage biomass the first January post-burn and even more so a year after the burn. Forage biomass two years post-burn decreased but was still more than three to four years post-burn. October precipitation had a positive effect on forage biomass but we detected no influence from low temperature in October or elk abundance. Given that prescribed fire increased elk forage biomass two years later, continuing to burn Boyes meadow on a three to four year rotation is suggested.

Key Words: California, forage biomass, herbivory, precipitation, temperature

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Prescribed fire is becoming a widely used habitat management tool (Long et al. 2008; Starns et al. 2019). Fires facilitate nutrient cycling via the deposition of labile, burned plant material (Ojima et al. 1994), reduce coverage of senescent vegetation which increases sunlight that reaches new growth (Knapp et al. 2012), and can drive plant community composition towards species that respond favorably to disturbance (Collins et al. 1995). These changes influenced by prescribed fires can increase forage for herbivores (McNaughton 1979; Stewart et al. 2006; Long et al. 2008; Spitz et al. 2018). The rate at which fire increases forage biomass for herbivores, however, depends on the ability of the plants to compensate for loss of above-ground material. The capacity for plants to increase forage varies a great deal between ecosystems and is largely dependent on the condition and morphology of the plants, local weather following a burn, and nutrient availability in the soil (McNaughton 1979; Noy-Meir 1993; Baker 2009).

Despite the role of environmental heterogeneity on plant response to burning, many investigations of the effects of prescribed burns on forage biomass for herbivores examine one to two burns (e.g., Heisler et al. 2004; Sachro et al. 2005). Studies that track one or two burns are limited in their ability to examine the effects of weather conditions and herbivore abundance on forage biomass following a burn. Such a limited scope also makes it difficult to determine how often prescribed burns should occur to stimulate forage production.

We measured elk forage biomass in January across 15 consecutive years where prescribed fires occurred every two to four years in all or parts of Boyes meadow in Prairie Creek Redwood State Park, Humboldt County, California. We estimated change in elk forage biomass up to three to four years post-burn and examined if elk abundance, precipitation, and low temperature influenced forage biomass. Precipitation and temperature are climatic variables that have been shown to influence plant production after burns (McNaughton 1979; Stewart et al. 2006). January is shortly after burns and is also early in the plant growing season (Starns et al. 2015). Measuring forage biomass in January should reveal how quickly plants respond to fire.

Boyes meadow has a history with fire and elk. The meadow was seasonally occupied by Native American tribes, and was probably burned by Native Americans (Veirs 1987). By 1862, Boyes meadow was occupied by Europeans. The meadow was plowed, used for farmland, and also grazed by domestic livestock until it was purchased by the Save the Redwoods League in 1932 and gifted to California State Parks (Veirs 1987). Prescribed fire began in the mid-1980s by State Park personnel (Kristan 1992). Since 1994, Floyd W. Weckerly has observed when prescribed burns occurred and noted if all of Boyes meadow was burned or the part of the meadow that was burned. Elk persisted in the area after unregulated market hunting and subsistence hunting was abolished in the late 19th and early 20th century. Several elk were first documented in Boyes meadow in 1937 by State Park personnel (Harn 1958; Weckerly 2017). The elk population then appeared to increase rapidly to 100–200 in the 1940s. Thereafter, elk abundance in and around Boyes meadow seemed to range between 3 to 50 elk.

METHODS

Study area

Boyes meadow is 50-ha in size. In the mild, maritime climate there is a distinct wet season from October to early May and a dry season for the rest of the year. During the wet season, the area experiences temperatures from 10–16 C and typically receives 1500 mm of precipitation. During the dry season, temperatures range from 16–21 C and there is little precipitation. The Newton P. Drury parkway bisects the meadow into an eastern two-thirds part and western one-third area (Figure 1). Vegetation in the meadow is dominated by annual and perennial grasses, with bracken fern (*Pteridium*), some forbs, and blackberry (*Rubus*) in more well-drained areas which are prevalent west of the parkway and sedges (*Carex*) in more mesic and poorly drained areas that are evident east of the parkway (Figure 1). Since 1994, Boyes Meadow or a part of the meadow has been burned in September every 2 to 4 years.

Vegetation surveys

Every January from 2005–2019, we estimated forage biomass in 240 quarter-m^2 plots. Plots were spaced 10 meters apart on two randomly placed transects in each of three sectors delineating the south, middle, and north parts of Boyes meadow (Figure 1). Each transect had 40 plots. The sectors were delineated ensure that all parts of Boyes meadow were surveyed. In each plot, we used Daubenmire coverage classes to measure the cover of grasses, forbs, and shrubs palatable to elk. Elk palatability of plant species was determined
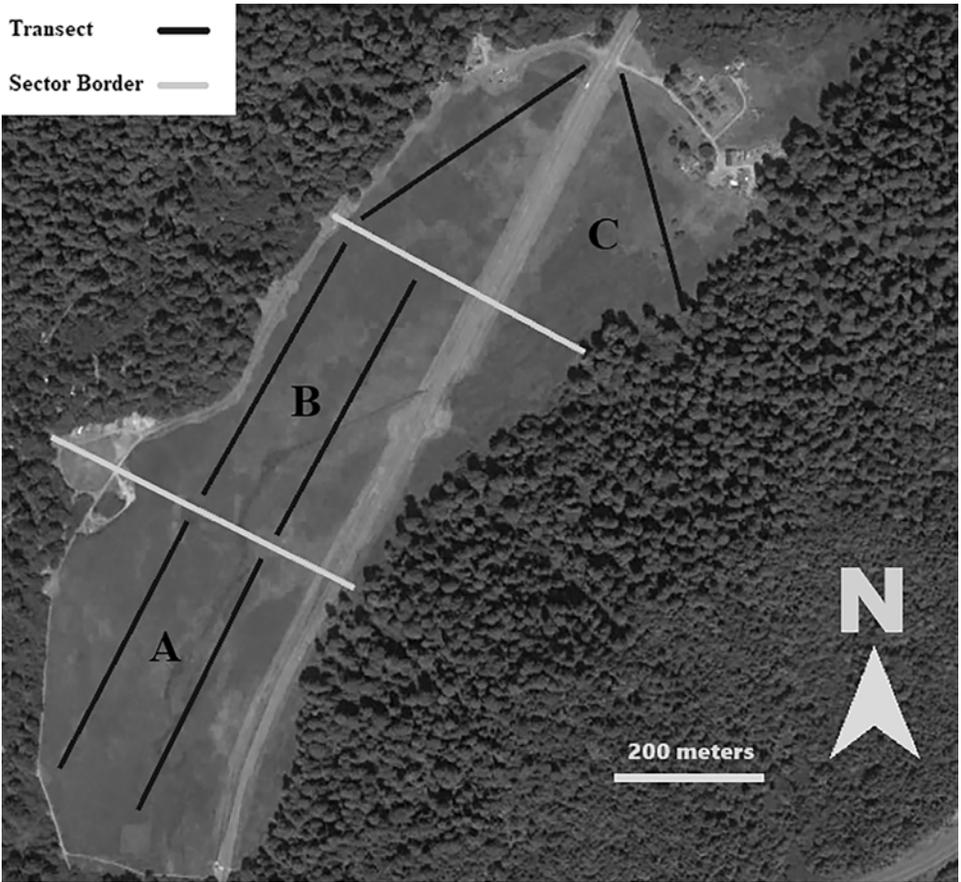
Figure 1. Aerial photograph of Boyes prairie, Prairie Creek Redwoods State Park, CA. Transects where plots were spaced 10 m apart in the three sectors (A, B, C) are delineated with black lines.

from a prior food habit study of elk conducted, in part, in Boyes meadow (Harper et al. 1967). After recording coverage, we measured the height of the vegetation to the nearest centimeter at eight different points within each plot. From the coverage and height measurements, we estimated forage biomass from calibration regressions. Calibration regressions were estimated from data collected in a different set of 129 randomly placed plots. In these plots the same coverage and plant height was measured, afterwards forage was clipped to ground level, sorted into palatable grasses, forbs, and shrubs, dried at 60 C for 48 hours, and weighed. We then estimated a multiple regression models or calibration regressions that predicted dried biomass of grasses ($r^2 = 0.84$, $F_{7, 122} = 97.1$, $P < 0.001$) and forbs and shrubs ($r^2 = 0.33$, $F_{2, 93} = 24.9$, $P < 0.001$; Peterson and Weckerly 2017). Estimated forage biomass in plots was the sum of predicted grass and forb – shrub biomasses.

Elk abundance

Each January from 2005–2019, we performed 10 surveys to count elk. Each survey began at sunrise and lasted 1.75 hours. The elk in Prairie Creek State Park were habituated to people, and this allowed us to collect our observations within 200 m of the elk using either the naked eye or binoculars. We took the highest count across the 10 surveys as our index of elk abundance in Boyes meadow.

Weather data

We measured mean monthly low temperature and total precipitation each October. After prescribed fires in September, October precipitation and low temperature should influence the rate that plants regrow (Williams and Biddiscombe 1964). Weather data was acquired from National Oceanic and Atmospheric Administration land-based weather stations. The Boyes station (station # 046498) was in Boyes meadow. There were many missing values, however. Consequently, we estimated the missing values using a regression that utilized data from a weather station 48km to the north near Crescent City (station # 042147). Data from the Crescent City station predicted monthly precipitation and low temperature in October ($r^2 = 0.70 – 0.71$) in Boyes meadow (Starns et al. 2014, Starns et al. 2015).

Statistical analyses

We analyzed a linear mixed-effect model using R (v. 3.5.2) to estimate forage biomass. Fixed factors were the January post-burn, the January one year post-burn, the January two years post-burn, the Januarys three to four years post-burn, elk abundance, and October precipitation and low temperature. Three to four years post-burn was the longest time between burns. Also, three to four years post-burn was the reference category. The Januarys after burns were coded as dummy variables. As recommended by Bates et al. (2015), we scaled elk abundance, October precipitation, and low temperature to have a mean of zero and standard deviation of one. Our random factors were year and sector. To meet the assumption of homoscedasticity, we took the natural log transformation of forage biomass after adding one. We added one because there was no vegetation in about one percent of plots.

RESULTS

There were four years when all of Boyes meadow was burned between 2005 and 2019. Burns in only the area west of the Newton P. Drury parkway occurred in three years and one burn occurred in only the area east of the parkway. Elk abundance ranged from 3 – 10, precipitation in October ranged from 0.45–26.5 cm, and mean low temperature in October ranged from 4.28–9.76 C. Across all 15 years the ratio of forbs-shrubs to grass elk forage was 0.15 (95% CI: 0.14 – 0.16). Post-burn estimates of forage biomass (grass, forbs, and shrubs) taken from our linear mixed-effects model were greater the January immediately after, one year later, and two years later compared to estimates of forage biomass 3–4 years post-burn (Table 1). We also found that precipitation positively impacted forage biomass, but low temperature and elk abundance were uninfluential (Table 1). The random effects of year that the survey took place and sector were similar as the 95 percent confidence

Table 1. Estimates and 95% confidence intervals (lower bound LB, upper confidence bound UB) of the fixed and random effects from analysis of a linear mixed-effects model with forage biomass as the response variable. Our fixed factors were post-burn predictors, October low temperature and precipitation, and elk abundance. The post-burn reference category was 3–4 years post-burn. The random effects (Sd – standard deviation, lower and upper 95% confidence bounds) were sector in Boyes meadow and year of survey. Data was collected in Boyes Meadow of Prairie Creek Redwood State Park, Humboldt County, CA, USA, from 2005–2018.

Fixed effects			
Predictor	Estimate	LB	UB
Three – four years post-burn	1.282	1.070	1.478
Three months post-burn	0.126	0.024	0.235
One year post-burn	0.438	0.338	0.539
Two years post-burn	0.177	0.057	0.295
Low temperature	0.039	-0.072	0.151
Precipitation	0.126	0.007	0.260
Elk abundance	-0.063	-0.181	0.058

Random effects and residuals			
Attribute	Sd	LB	UB
Year of survey	0.255	0.129	0.315
Sector	0.133	0.008	0.258
Residual	0.587	0.572	0.601

intervals overlapped. But the amount of variation in each random effect was less than the residual standard deviation.

After back-transforming forage biomass, we estimated mean forage biomass the January after the burn, one year, two years, and three to four years post-burn from the fixed effects. We controlled for precipitation, low temperature, and elk abundance by using mean values for each of these predictors. Relative to three to four years post-burn, forage biomass increased slightly the January immediately after the burn, peaked one year post-burn, and then declined two years post-burn to a value that was still marginally higher than the estimate of forage biomass three to four years post-burn (Figure 2).

DISCUSSION

Forage response three months following burns and the amount of growth in that short time in the Boyes meadow was noteworthy. Most of the forage in Boyes meadow was grass (>85 percent) with forbs making up most of the remaining 15 percent (Weckerly 2017). Most other studies measuring grass and forb production after burns were conducted in areas of continental climates. Burns were usually initiated shortly before or during the growing season (spring, summer) and forage biomass was often measured at the conclusion of growing seasons one or more years later. The amount of growth we observed in three months took one to two years at higher elevation sites exposed to winter weather that was cold with much
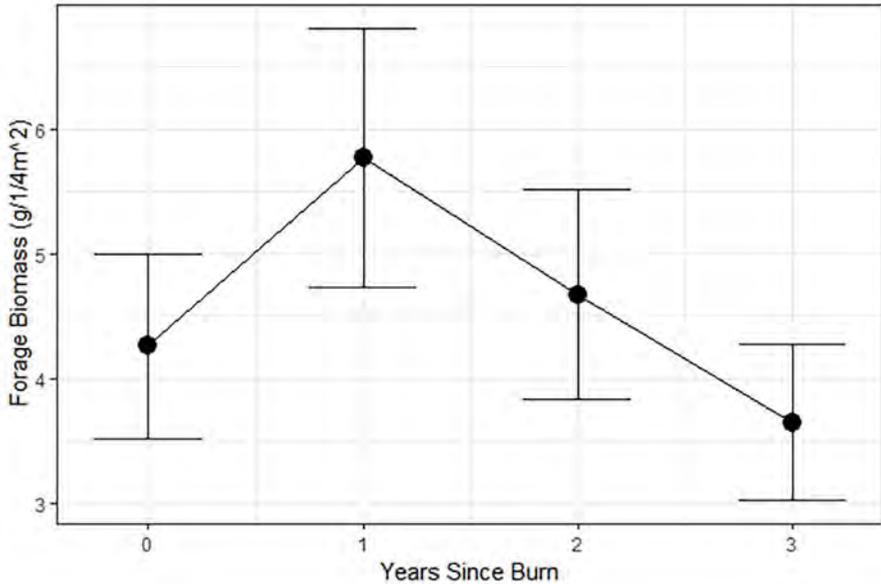
Figure 2. Predicted mean biomass of forage (g/quarter-m²), and 95% confidence intervals, in Boyes meadow of Prairie Creek Redwood State Park, Humboldt County, CA, USA. Data was collected in January 2005–2018. Year zero is the January three months post-burn.

snow (Cook et al. 1994, Sittler et al. 2019). At the scale of years our estimates indicated that prescribed burns in Boyes meadow can increase forage biomass for elk in January up to two years post-burn. Again in areas with continental climates, grass and forb biomass invariably increased one to three years following a controlled burn (Hobbs & Swift 1985, Briggs et al. 1994, Cook et al. 1994, Heisler et al. 2004, Long et al. 2008, Sittler et al. 2019). At a Montana study site, elevated grass and forb productivity was detected up to nine years after a fire (Van Dyke & Darragh 2005). In Boyes meadow, elevated grass and forb production appears to be quick. Grasses and forbs respond in a matter of months to autumn fires, but the effect to burns was undetectable three to four years after a fire.

Forage plants appeared to respond similarly across sectors to prescribed fire over the 15 years of the study. Relative to the residual standard deviation, which measures variation within a sector of Boyes meadow in a year, the random effects (i.e., standard deviations) of sector and years were smaller. There was variation in grass and forb production within sectors in each year that was noticeably greater than across sectors and years. Heterogeneity in grass and forb production that occurred even though prescribed fires are purposefully done at the end of the dry season when soil moisture is low and meadow vegetation is more likely to be senesced and dry (Underwood et al. 2003). Spatial variation in severity of burns from a fire can be considerable (Sittler et al. 2019). Across the 50 ha Boyes meadow, heterogeneity among plots within sectors in grass and forb production might be due to variation in burn severity, soil moisture, plant species, and amount of shading.

For herbivores such as elk, fire usually results in young growing plants that are nutritious because the growing plant tissue is high in protein and low in fibers that are either indigestible or take days to ferment (Van Soest 1994). After a burn forage quality for elk

has been documented to range from somewhat more nutritious to noticeably more nutritious (Barker et al. 2019, Sittler et al. 2019). During rapid plant growth in late winter and early spring forage quality might indeed be high following a September burn in Boyes meadow (Weckerly 2017). In January, however, when grass and forb growth is low there might not be a noticeable increase in forage nutrition. Increased use of burned areas by elk has been noted the January after a fire however (Weckerly 2017). The increased use might be from the removal of senesced plants by burning which, in turn, should increase elk foraging efficiency on green grasses and forbs (Hobbs and Swift 1985; Peterson and Weckerly 2018; Sittler et al. 2019).

We found a positive correlation between October precipitation and forage biomass the following January. It has been established that moisture availability is an important factor in determining how plant communities respond to prescribed burns (McNaughton 1979; Frank et al. 2016). Presently, there are few published studies that directly measure the effects precipitation has on plant forage biomass production after a prescribed fire (Anderson et al. 2007). Robichaud (2000) found that prescribed burns can affect water infiltration rate through soil compaction and that the rate of water infiltration declines as temperature and duration of the burn increase. In the mild, maritime climate in the Boyes meadow it is unlikely that prescribed fires burn hot enough to create hydrophobic soil conditions that would negatively affect the ability of the soils to take in moisture.

We did not detect an influence from elk abundance on forage biomass the January after a burn. These results are atypical given that studies indicate that herbivore abundance correlates positively (Stewart et al. 2006) or negatively (Painter and Belsky 1993) with forage biomass. Our findings are similar to Sittler et al. (2019) in that no effect from elk or Stone's sheep (*Ovis dalli stonei*) was detected after burns. Both our study and that by Sittler et al. (2019) had low herbivore abundances. It is well-established that herbivores affect a myriad of factors in plant communities (McNaughton 1979; Kuijper et al. 2006; Stewart et al. 2006; Frank et al. 2016). It is likely that an effect of elk abundance on forage biomass would have been detected if elk abundance had been higher than the 3–10 elk estimated to occur in Boyes meadow during the time of our study.

We also found no correlation between low temperatures in October and forage biomass the following January. This is likely because October low temperature only ranged from 1.9 C to 5.9 C. Multiple studies have found that growth-rate of grasses and forbs varies with temperature, even when temperatures only vary from 3–4 C (Williams and Biddiscombe 1964; Peacock 1976; Durand et al. 1999). The former two studies found, however, that the strength of the relationship between temperature and plant growth rate varied based on the temperature itself and growth-phase of the plants. Williams and Biddiscombe (1964) found that plants sensitivity to changes in temperature decreased as temperature decreased, and Peacock (1976) found that grass species are more sensitive to changes in temperature during the reproductive growth stage than during the vegetative growth stage. It is possible that between October and January, which is early in the growing season when temperatures are generally low and plants are in their vegetative stage of growth, plant growth is not substantially affected by temperature. Nonetheless, there might be other metrics that we did not measure that could affect plant response in the Boyes meadow. In the cool, moist climate at Boyes meadow daily solar radiation might have a detectable influence.

Boyes meadow is a visitor attraction and is likely to be maintained in perpetuity by California State Parks (Veirs 1987). How to manage Boyes meadow to maintain produc-

tive plant communities and, in turn, food supplies for Roosevelt elk will require long-term monitoring and research. Further research is needed because of the climatic changes that are presently occurring in north coastal California (Johnstone & Dawson 2010). Our findings indicate that prescribed fires at three to four-year rotations promote forage production because plant growth is stimulated for up to two years after a burn. Nonetheless, across our 15 yearlong study there were only eight burns. Monitoring of elk and their food supplies in Boyes meadow should continue. But more detailed work is needed into ecosystem processes such as nutrient cycling, processes that impact how Boyes meadow plant communities respond to fire.

ACKNOWLEDGMENTS

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ORIGINAL RESEARCH

Post-fire species composition and abundance of a lentic-breeding amphibian assemblage: case study of Ledson Marsh

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Amphibians frequently inhabit wildfire-prone environments, but little is known how amphibians respond to fire. This study assessed the post-wildfire species composition and abundance of an amphibian assemblage in an 11.8-ha seasonal marsh. Pre-fire, four native amphibians occupied Ledson Marsh, including: California red-legged frog (*Rana draytonii*), Pacific treefrog (*Pseudacris regilla*), California newt (*Taricha torosa*), and roughskin newt (*Taricha granulosa*), in addition to the exotic American bullfrog (*Rana* [*Lithobates*] *catesbeiana*). Qualitative data revealed the California newt and Pacific treefrog were abundant species. In 2017, the Nuns Wildfire burned the majority of ground cover within the watershed. Nearly all marsh vegetation burned to charred and desiccated stubble. Renewal of substantial marsh vegetation occurred after one growing season, indicating a protected rootstock in a majority of perennial wetland plants. Post-fire, the same four native amphibians were still present. In addition, western toad (*Anaxyrus boreas*), a species previously undetected, also appeared. Appearance of western toad is consistent with its positive short-term response to fire, as described in other studies. The California newt and Pacific treefrog remained the two most abundant species post-fire. Over the short-term, the amphibian assemblage appeared resilient, or potentially benefitted, due to the temporary disturbance of wildfire within their lentic breeding habitat. The conclusion is based on the persistence of all pre-fire species, colonization by the western toad, and the return to an earlier successional stage, which may extend the longevity of the marsh. Since the rapid seasonal drying of habitat can increase the likelihood of fire under the current climate trajectory, we need a better understanding of the mechanisms that enable amphibians to cope with fire. This is particularly important over longer timelines and within wetland habitats that have the potential to burn.

Key words: amphibians, fire, frog, Ledson Marsh, newt, northern California, survival, toad, wetlands

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Until recently, little was known about the effects of fire on amphibian ecology even though amphibians frequently inhabit wildfire-prone environments (Bury et al. 2002; Pilliod et al. 2003; Bury 2004). Fire can cause direct mortality, changes in diversity, and alterations in habitat, contributing to both immediate and long-term consequences (Pilliod et al. 2003;

Rochester et al. 2010). However, a series of fire–amphibian studies over the last 25 years has begun to alter this view. Most of these studies have evaluated wildfire or prescribed fire on primarily stream or terrestrial taxa (Kirkland et al. 1996; Keyser et al. 2004; Hossack et al. 2006; Greenberg and Waldrop 2008; Cano and Leynaud 2009; Sutton et al. 2013). The research does not emphasize lentic-breeding amphibian use of wetlands. Until recently, wetlands were less likely to burn because conditions were less conducive to fire (Jolly et al. 2015). Since the risk and severity of drought due to climate change (Allen et al. 2010) has increased the likelihood of large fires (Perry et al. 2011), there is greater potential to impact more wetland habitat not typically prone to fire. This phenomenon has led researchers to examine fire response among lentic-breeding amphibians using wetlands (Hossack and Corn 2007, 2008; Hossack et al. 2013).

Hossack and Pilliod (2011) reviewed amphibian responses to wildfire in the western United States, which have provided some perspectives on the response of lentic-breeding amphibians. The authors suggested wetlands would experience the smallest fire-related changes, in contrast to the stream and terrestrial habitats amphibians utilize that are the most likely to benefit amphibian larvae. The authors further opined that amphibians in larger lentic habitats would be less vulnerable than those in smaller lentic habitats because the larger habitats typically maintain longer hydroperiods and thus, are less likely to burn. Hossack and Pilliod (2011) also stated the high perimeter-to-surface ratio of small wetlands, which conjoins them more tightly to the terrestrial landscape, may make the amphibian populations more vulnerable. Hence, the type and degree of fire impacts on lentic-breeding amphibians will likely depend on the size of the aquatic habitat as well as the relative impact of the fire on the aquatic habitat versus the juxtaposed terrestrial habitat.

On 8 October 2017 and the days following, several wildfires ignited in eastern Sonoma County, California. These fires, collectively named the Nuns Wildfire, burned a combined 22,887 ha before they were contained on 30 October 2017 (Gabbert 2018). The Nuns Wildfire burned through Ledson Marsh, where David G. Cook (DGC) had been examining the amphibian assemblage since 1996. Although some of the pre- and post-fire surveys differed, the Nuns Wildfire afforded a rare opportunity to examine the changes in amphibian composition, abundance, and specific habitats. In this case study, the authors describe the following changes in Ledson Marsh prior to and following the Nuns Wildfire: 1) amphibian species composition; 2) adult amphibian breeding populations and reproductive effort; and 3) marsh vegetation and aquatic habitats. The authors provide data on herpetofauna survival within the post-fire watershed of Ledson Marsh to provide context on the survival of species that are similar ecologically to the Ledson-breeding amphibians in terms of terrestrial habitat use and mobility. The patterns illustrated by this case study, including the precipitation patterns, correspond with the suggestions made by Hossack and Pilliod (2011) regarding short-term lentic-amphibian response to fire and long-term changes due to climate conditions.

METHODS

Study area

Ledson Marsh is located on a hilly plateau in Trione-Annadel State Park, Sonoma County, California, USA (38.40°N, 122.60°W; WGS84; 476 m elevation). Every winter, rains fill the marsh in January or February and it typically dries in late summer. The current aquatic footprint of Ledson Marsh is approximately 11.8 ha at full inundation, and it maintains a maximum depth of approximately 1.3 m. The marsh was created in 1930 via construc-

tion of a small earthen and rock dam (Furtini 1976). Prior to 1930, aquatic habitat existed at the site, though its size was likely much smaller (P. Northen, personal communication). The >2000-ha Trione-Annadel State Park encompasses approximately 95% of the 84.8-ha Ledson Marsh watershed, and all of Ledson Marsh proper. The State Park encompasses six habitat types, including: oak (*Quercus* spp.) woodland, Douglas-fir (*Pseudotsuga menziesii*) forest, chaparral, grassland, meadow, and marsh (Cook and Jennings 2007). The primary habitats and related vegetation classifications (Klein et al. 2015) within the Ledson Marsh watershed include: freshwater marsh (*Schoenoplectus californicus* Alliance), Douglas-fir forest (*Pseudotsuga menziesii* Alliance), and oak woodland (*Quercus* spp. Alliance) with an understory dominated by California fescue (*Festuca californica*). The Ledson Marsh watershed is largely undeveloped. However, in the early 1900s, basalt for street cobble was quarried on a small scale (Whatford 1995); a few shallow pits and tailing mounds up to 2 m high that collectively cover approximately 0.09 ha attest to this historic activity.

Life history of Ledson Marsh amphibians

Nomenclature for the amphibians discussed follows Crother et al. (2017). Five amphibian species regularly breed at Ledson Marsh, including: the California red-legged frog (*Rana draytonii*; a California Species of Special Concern and listed as threatened by the Federal Endangered Species Act), Pacific treefrog (*Pseudacris regilla*), California newt (*Taricha torosa*; California Species of Special Concern), and roughskin newt (*Taricha granulosa*), in addition to the invasive American bullfrog (*Rana [Lithobates] catesbeiana*; Cook and Jennings 2007; Stokes et al. 2011; DGC, personal observation).

The native amphibian assemblage that breeds in Ledson Marsh is adapted to the summer drought imposed by California's Mediterranean climate (Storer 1925; Keeley and Swift 1995; CDFG 2003; Cook and Jennings 2007). Larvae of members of this assemblage typically metamorphose by mid-summer prior to the marsh drying. The dominant amphibians breed in winter and deposit eggs in shallows < 40 cm deep along the shoreline (Cook and Jennings 2007; DGC, personal observation). In this case study, the authors refer to egg cluster for species that typically deposit several groupings of eggs during oviposition (California newt, roughskin newt, Pacific treefrog) and egg mass for species that typically deposit a single group (California red-legged frog and American bullfrog). Winter breeders consist of the California red-legged frog, California newt, and Pacific treefrog (Table 1). Though the Pacific treefrog breeds primarily in winter, its breeding can extend from late-fall to spring. Prior to the Nuns Wildfire, the only spring-breeding amphibian in Ledson Marsh was the roughskin newt. A second spring-breeder, western toad (*Anaxyrus boreas*), was known within Trione-Annadel State Park. Prior to the wildfire, individual western toads had been observed at non-breeding sites near the Ledson Marsh watershed (DGC, personal observation). In addition to the native assemblage, the non-native American bullfrog, which breeds late spring into summer, is also present in Ledson Marsh (Cook and Jennings 2007). American bullfrog tadpoles frequently overwinter at least once before metamorphosis (Bury and Whelan 1984). However, at Ledson Marsh, metamorphosis has occurred within the same year tadpoles develop from eggs (Cook and Jennings 2007). This has been observed during wetter years and the longest hydroperiods (DGC, unpublished data). Except for the Pacific treefrog, all amphibian species at Ledson Marsh require at least two years to reach sexual maturity (Table 1).

Table 1. Breeding characteristics of amphibians at Ledson Marsh.

Species	Sexual Maturity (yr)[a]	Local Breeding Period (peak)[b]	Egg Mass or Clusters Produced[c]	Egg Clutch Size[c]
American bullfrog	2-3	Apr-Jul (May-Jun)	1	20,000
California newt	3	Jan-Feb	3-6	130-160
California red-legged frog	2-3	Jan-Apr (Feb)	1	2,100
Pacific treefrog	1-2	Nov-Jul (Feb-Mar)	9-80	400-750
Roughskin newt	4-5	Apr-Jul	200-300	No Data[d]
Western toad	4-6	Jan-Jul (Mar-Apr)	1	12,000

[a] Lannoo (2005)

[b] Cook and Jennings (2007); Stokes et al. 2011; Petranka 1998; DGC, personal observation

[c] Lannoo 2005; Cook 1997; Stokes et al. 2011

[d] Roughskin newts deposit single eggs (Jones et al. 2005) in widely scattered patterns in soft aquatic vegetation (MPH, unpublished data)

Pre-fire surveys

The first author (DGC) conducted more than 250 Visual Encounter Surveys (VES) at Ledson Marsh, with the assistance of several others, following Heyer et al. (1994) since 1996 (Cook and Jennings 2007; DGC, unpublished data). Annual VES focused on enumerating California red-legged frogs in the egg, post-metamorphic, and adult life stages. We conducted the minimum number of seasonal site visits according to Heyer et al. (1994) between 1996 and 2016, as follows: three surveys in winter, three surveys in spring, and two surveys in summer. Since 2017, only the winter site visits were completed. Researchers recorded qualitative observations of California newt and Pacific treefrog breeding and the abundance of egg clusters. Researchers recorded maximum water depth during each site visit using a permanent gauge located in the deepest area of the marsh, near the dam.

Satellite imagery (2013) and Geographic Information System maps were used to delineate and quantify vegetation and habitat types present at Ledson Marsh prior to the 2017 Nuns Wildfire (Sonoma County 2019a). We estimated the dominant vegetation types according to surface area of the marsh and percentage of shoreline. Researchers confirmed pre-fire vegetation types based on field observations, recorded annually since 1996, and noted changes in plant species and mapped vegetation patterns.

Post-fire surveys

On 7 November 2017, one week after the Nuns Wildfire was contained, DGC investigated the severity and extent of damage in the watershed. This investigation consisted of a walk-through and visual inspection of the dry marsh and surrounding woodland and forest habitats. DGC also searched for unburned areas or areas that may have served as refuge for wildlife during the fire. The field observations confirmed the patterns illustrated on burn severity maps produced from satellite imagery (Sonoma County 2019b).

Researchers estimated wetland habitat and egg cluster/mass production of winter-breeding amphibians at Ledson Marsh in 2018 and 2019. The surveys were similar to the pre-fire surveys for CRLF, with an added stratified random approach (Heyer et al. 1994). The post-fire surveys served to effectively sample other lentic-breeding amphibians, particularly California newts that lay numerous egg clusters as conducting a total count can be unfeasible. Prior to the wildfire, we collected only qualitative estimates. To add the stratified random approach to surveys, researchers established 36 sample plots in 2018 along the 1604-m full-pool shoreline, where most amphibian oviposition occurs (DGC, personal observation). The number of plots were stratified based on the percent of pre-fire dominant vegetation types: 18% common spikerush (*Eleocharis palustris*), 67% broad-leaved cattail (*Typha latifolia*), 5% mixed spikerush/cattail, and 10% mixed cattail/California bulrush (*Schoenoplectus californicus*). These vegetation types occurred in 10 areas along the shoreline in 2013 (Sonoma County 2019a). Plot size was 3×5 m with the shorter side positioned approximately parallel to the shoreline. The longer sides were oriented into the marsh to accommodate fluctuating water levels. We marked plot borders with wooden stakes and string. Plots covered 6.7% of the shoreline perimeter length.

We sampled plots twice monthly during the winter (January to March). During one of the field visits, two investigators conducted a VES of each plot. All amphibian egg clusters/masses were identified to species and the developmental interval recorded using a four-category scale. The Gosner system (1960) was used to identify three categories between Gosner stages 1 and 22, described as follows: 1) spherical (1-12); 2) bean-shaped (13-18); or 3) banana-shaped (19-22). Hatching was the fourth category. Gosner stages (1960) are best applied to anurans (frogs and toads). However, the coarse categories made it useful for staging salamanders as well based on the similarity to salamander developmental stages proposed by Harrison (1969). Researchers recorded the maximum depth at each plot and the maximum depth of the marsh during each site visit. We conducted VES between plots to determine if a species was breeding but not detected within the sample plots. To estimate post-fire changes in habitat, DGC visually scored the percent cover of dominant wetland plants and open water habitat to the nearest 5% within each plot during the last site visit each winter. Open water habitat was categorized as either barren open water (if the substrate appeared burnt) or vegetated open water (if unburnt vegetation or organic material covered the substrate). Winter surveys ended when no newly deposited eggs since the last visit were observed. This equated to no eggs younger than Gosner (1960) stage 13 (i.e., no bean-shaped eggs), which requires approximately two weeks to develop at Ledson Marsh (DGC, unpublished data).

After completing the 2018 winter aquatic plot surveys, we conducted terrestrial VES within the marsh watershed to characterize the amphibian and reptile fauna that survived the wildfire. These surveys included visual inspection beneath rocks and logs that were not completely burned in the wildfire. Anecdotal observations of amphibians at Ledson Marsh's dam were obtained from a biological monitor during a dam repair project over a three-week period in August 2018.

On 10 May 2019, we conducted timed dipnet surveys to determine the larval amphibian composition at Ledson Marsh (Heyer et al. 1994). The surveys were designed to detect larvae produced from both winter and spring breeding as it was unlikely to detect spring-breeding amphibians during the winter plot sampling. A crew of six conducted dipnet surveys and sampled for six minutes in each of the ten vegetation areas. We identified all larval amphib-

ians to species and counted. These surveys allowed the researchers to determine the complete assemblage of amphibians breeding at Ledson Marsh.

Water quality and climatic data

Water-quality monitoring was conducted during the post-fire winter of 2018. On 19 January 2018, we used a YSI 85 digital meter to assess water samples from the 10 vegetation patches. A YSI Series 6600 data sonde was installed in the deepest area of the marsh near the dam and suspended approximately 30 cm above the bottom. The data sonde recorded at one-hour intervals from 22 January to 9 March 2018. Both instruments recorded temperature (°C), dissolved oxygen (DO in mg/L), and pH.

Precipitation data was obtained from the California Department of Water Resources, California Data Exchange Center weather station (SRO) located in Santa Rosa, California, approximately 14 km northwest of Ledson Marsh. We summarized data by water year (1 October through 30 September) for the 24-year period from 1996 to 2019.

Data analysis

The numbers of egg masses or clusters and adult breeding amphibians were estimated from winter plot data by multiplying the mean plot densities and shoreline area. Shoreline area was determined by the shoreline length (1,604 m) and plot length. We used the typical number or range of egg masses or clusters produced by females (Table 1) and a 1:1 sex ratio was assumed to estimate the adult breeding populations in Ledson Marsh.

Standard descriptive statistics (mean [$\bar{x}$], standard deviation [$\pm$ SD]) were used to describe the variation within selected variables. We completed a regression of precipitation data per water year (October through September) using a general linear model. To assess long-term precipitation patterns, we determined whether the regressions had a non-zero slope. A two-tailed t-test was used to compare the annual (water year) data, the halves of the 24-year timeline, and the water depths along sample plots between two post-fire study years. In all cases, variables approximated normal distributions and were homoscedastic, so t-tests for equal variances were employed. We conducted all analyses using JMP™ version 13.0.

RESULTS

Pre-fire species composition and abundance

Pre-fire observations of amphibians at Ledson Marsh revealed four native species (California red-legged frog, Pacific treefrog, California newt, and roughskin newt) and one exotic species (American bullfrog) occupied the marsh every year for 22 water years leading up to the Nuns Wildfire (1996-2017; DGC, unpublished data). Evidence of recruitment, based on some individuals reaching metamorphosis, has been observed every year throughout the course of the study for all species except for the American bullfrog. In contrast, American bullfrog annual recruitment has been irregular with a 50% frequency between 1996 and 2016. These numbers reflect the combination of onset timing of annual breeding and the duration of aquatic habitat available for egg and tadpole development before marsh drying.

Pre-fire timeline observations of amphibians at Ledson Marsh provide qualitative data on abundance for most species and quantitative data for the California red-legged frog. Field observations revealed California newts and Pacific treefrogs were abundant (numbers in the tens of thousands), roughskin newts were common (in the hundreds), and American bullfrogs were relatively few. In 1996, Cook (1997) estimated the presence of 39 adult American bullfrogs in Ledson Marsh. Quantitative data on California red-legged frogs over the interval 1996 to 2017 estimate the adult breeding population ranged between 8 and 234 ($\bar{x} = 60.2 \pm 27.1$; Cook 1997; DGC, unpublished data). The California red-legged frog adult breeding population falls between the range of roughskin newts and American bullfrogs.

In 1996, approximately half of the Ledson Marsh vegetation consisted of large, dense, tall, and emergent (> 2 m) stands of California bulrush and broad-leaved cattail, particularly within the center. The remaining half was interspersed with open water and low-emergent (< 0.5 m) common spikerush, particularly along the shoreline (Cook and Currylow 2014; Figure 1). Primary changes in vegetation since 1996 demonstrate an increase in tall-emergent vegetation, mainly broad-leaved cattails invading open water and common spikerush areas. Additionally, the aquatic fern (*Azolla filiculoides*), first observed in 2005, covered much of the open water and large portions of the shoreline prior to the Nuns Wildfire. The small floating fern created dense mats, particularly on the downwind (eastern) side of Ledson Marsh. In 2013, Ledson Marsh was composed of 81% tall-emergent (bulrush/cattail) and 19% common spikerush, interspersed with other low-emergent plants, open water, and aquatic fern. Moist microhabitats, available during the dry season prior to the wildfire, consisted of dense thatch within stands of California bulrush, broad-leaved cattail, and thick mats of aquatic fern.

Figure 1. Pre-fire landscape of Ledson Marsh on 18 February 2010 looking northwest. Dormant broad-leaved cattail and California bulrush are in the background and new growth of common spikerush is in the foreground. The position and direction of the photograph are similar to the images in Figure 3.

Nuns wildfire effects on habitat

When the approximately 23,000 ha Nuns Wildfire burned through Sonoma Valley in October 2017, fire swept through all of southern Trione-Annadel State Park, encompassing a radius > 1 km around Ledson Marsh (Figure 2; Sonoma County 2019b). Nearly all of the Ledson Marsh watershed (> 95%) sustained low to moderate severity fire. Visual inspection of the watershed in November 2017 indicated nearly all ground cover burned, including herbaceous material, shrubs, and downed trees. The exception to this were large logs (> 45 cm diameter) that did not burn entirely; these logs were rare in the watershed. In some areas, the fire burned below the soil surface as indicated by large voids at the base of once standing trees. Some tree trunks burned to nearly a meter below the soil surface, and lateral roots burned for several meters leaving hollow openings below ground (DGC, personal observation). These subsurface fires smoldered for days after the initial fire. In contrast, with few exceptions, the canopy of the oak woodland and Douglas-fir forest did not burn.
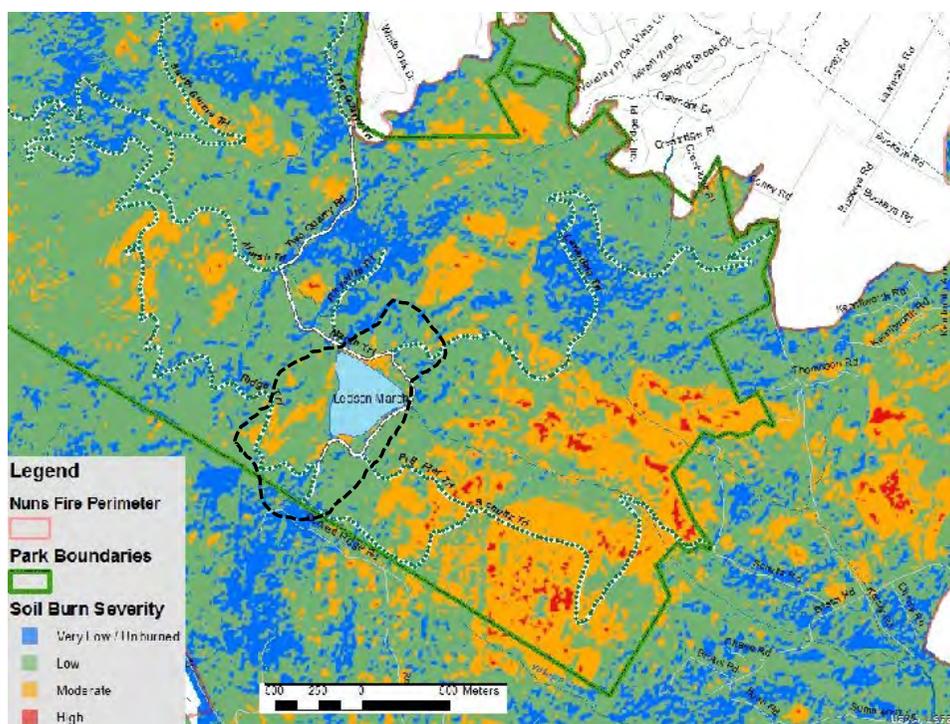
Figure 2. Nuns Wildlife soil burn severity map for southern Trione-Annadel State Park (Sonoma County 2019b). The black dashed line is the Ledson Marsh watershed boundary.

During the wildfire, Ledson Marsh was lacking any standing water and nearly all marsh vegetation burned to charred and desiccated stubble (Figure 3A). All the common spikerush and aquatic fern, and most stands of California bulrush and broad-leaved cattail, were dry enough to burn. The exception to this included three small patches of California bulrush and broad-leaved cattail collectively covering 0.14 ha in the central marsh and consisting of 1.2% of the surface area of the marsh.

Figure 3. Post-fire landscape of Ledson Marsh looking northwest: A) immediately post-burn (7 November 2017); and B) roughly 18 months post-burn (10 May 2019).

Weather patterns and amphibian breeding habitat

Over the 24-year study interval, the region has experienced generally declining precipitation with what appears to be an increase in variability (Figure 4). Annual (water year) precipitation levels reflect severe drought conditions to very wet conditions. The wettest year observed during the study (1998) maintained precipitation levels over 3.5 times compared to the driest year (2014). Over the first 12 water years (1996–2007), annual precipitation averaged 14 cm greater than the next 12 water years (2008–2019). Regressing precipitation for the entire time series revealed a significant (non-zero) negative slope for annual precipitation ($\beta = 0.70$; $P = 0.007$; Figure 4).
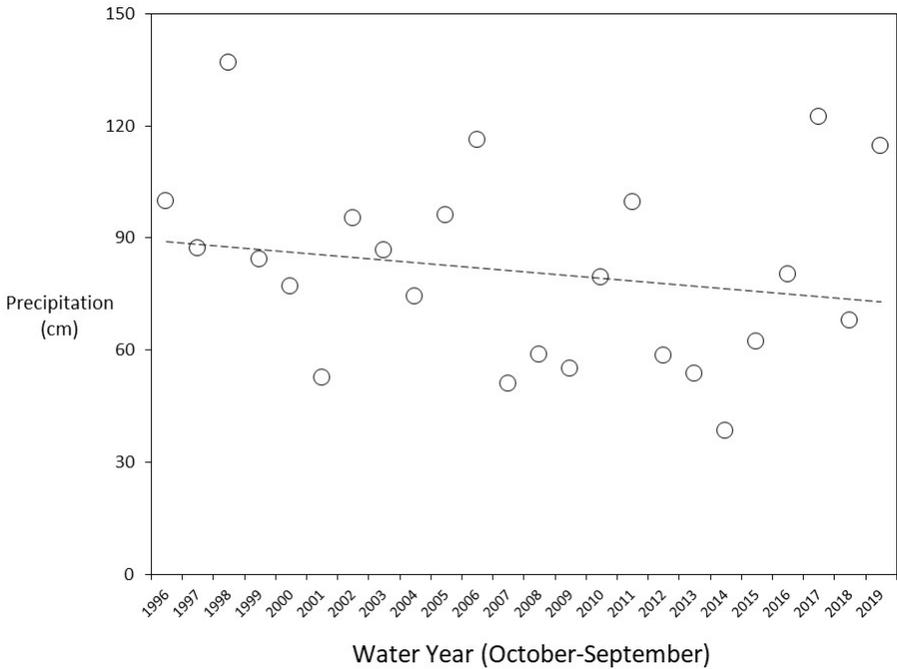
Figure 4. Variation in annual (water year) precipitation, 1996-2019. Precipitation data are from the California Data Exchange Center weather station located in Santa Rosa, CA. The trend line has a significant negative non-zero slope. See text for details.

The two years after the Nuns Wildfire were climatically and hydrologically very different. Severe drought characterized the 2018 winter (December to March) as compared to the wet 2019 winter. In particular, precipitation during winter 2018 was 36.0 cm or 64% of the 24-yr mean (56.0 cm). In contrast, 2019 winter precipitation was 83.3 cm or 149% of the 24-yr mean. Researchers recorded a 2.3-fold increase in winter precipitation and a 1.7-fold increase in water-year precipitation between 2018 and 2019. In 2018, amphibian breeding habitat was only partly inundated. For example, sample plot water depths in 2018 ($\bar{x} = 15.8$ cm $\pm$ 14.1) averaged less than half the depths in 2019 ($\bar{x} = 35.7$ cm $\pm$ 15.5), an unambiguous difference (t-test: $t = -18.368$, df $= 34$, $P < 0.001$).

Post-fire species composition and abundance

All five amphibian species known to occur at Ledson Marsh were detected after the Nuns Wildfire (Table 2). We also detected the western toad for the first time at Ledson Marsh after the wildfire. Post-fire, terrestrial surveys in the watershed found adult California newt, roughskin newt, and Pacific treefrog using the very sparse downed wood and rock cover available (Table 3). Two terrestrial salamander species (California slender salamander [*Batrachoseps attenuatus*], yellow-eyed salamander [*Ensatina eschscholtzii xanthoptica*]), and four reptile species (western fence lizard [*Sceloporus occidentalis*], ring-neck snake [*Diadophis punctatus*], common gartersnake [*Thamnophis sirtalis*], and western pond turtle [*Actinemys marmorata*]) were also observed in the uplands surrounding Ledson Marsh.

Table 2. Estimates of amphibian egg production and adults at Ledson Marsh, 2018–2019. Estimates of egg clusters and masses are based on shoreline plots. Estimates of adults assume a one-to-one sex ratio.

Species	2018		2019	
	Egg Masses	**Adults**	**Egg Masses**	**Adults**
American bullfrog				1[a]
California newt	3,089	1,030–2,059	29,585	9,862–19,723
California red-legged frog	3[b]	6	2[b]	4
Pacific treefrog	178	4-40	371	9-83
Roughskin newt				
Western toad		1[c]		

[a] Adult male heard vocalizing during spring dipnet survey.
[b] Egg masses observed during winter VES between sample plots.
[c] Adult male detected during winter VES between sample plots.

Table 3. Terrestrial herpetofauna observations in the Ledson Marsh watershed. Data are summarized observations from five single-pass Visual Encounter Surveys conducted between 19 January and 9 March 2018.

Species	Count
Amphibians	
California newt (*Taricha torosa*)	18
California slender salamander (*Batrachoseps attenuatus*)	436
Pacific treefrog (*Pseudacris regilla*)	66
Roughskin newt (*Taricha granulosa*)	2
Yellow-eyed salamander (*Ensatina eschscholtzii xanthoptica*)	5
Reptiles	
Common garter snake (*Thamnophis sirtalis*)	1
Ring-neck snake (*Diadophis punctatus*)	1
Western fence lizard (*Sceloporus occidentalis*)	18
Western pond turtle (*Actinemys marmorata*)	1

For most species, amphibian egg clusters and masses were higher in 2019 when above-normal rainfall occurred, except for the California red-legged frog (Table 2). In winter 2019, California newt maintained the highest estimate of abundance with 29,585 egg clusters, reflecting an estimated 9,862 to 19,723 breeding adults. Pacific treefrogs ranked second in abundance with an estimated 371 egg clusters, reflecting 9 to 83 breeding adults. One adult male western toad was observed in Ledson Marsh during a winter 2019 survey.

California red-legged frog egg masses were not detected within the survey plots. However, we observed three egg masses in 2018 and two egg masses were observed in 2019 outside of the plots, indicating four to six breeding adult California red-legged frogs. More California red-legged frogs are known to have survived the fire than detected during winter surveys. During the Ledson Marsh dam repair from 22 August to 11 October 2018, C. Shafer (personal communication) made observations of 49 juvenile and 15 adult California red-legged frogs over 20 different days. The highest single-day observation of California red-legged frogs during this period was 13 juveniles and 1 adult.

Spring larval surveys detected four native amphibians, including: California newt, roughskin newt, Pacific treefrog, and western toad (Table 4). Pacific treefrogs maintained the largest complement of larvae at 58.9%, larger than the California newt (39.3%), though California newt egg clusters and adult estimates were much greater than Pacific treefrog estimates in winter (Table 2). A small proportion of larval amphibians from the spring surveys were roughskin newt (0.5%) and western toad (1.3%). California red-legged frog and American bullfrog tadpoles were not detected during the 2019 spring surveys. One male American bullfrog was heard calling during spring dipnet sampling and served as the only detection of this species during the post-fire surveys.

Table 4. Relative percentages of 4,468 observations of larval amphibians at Ledson Marsh, spring 2019 based on dipnet surveys conducted in May 2019.

Species	Percentage
American bullfrog	0
California newt	39.3
California red-legged frog	0
Pacific treefrog	58.9
Roughskin newt	0.5
Western toad	1.3

Habitat response to fire

Loss of marsh vegetation at Ledson Marsh resulting from the Nuns Wildfire was near complete (Figure 3A), though its regeneration was rapid (Figure 3B). In winter 2018, breeding areas were either dry (44.0%) or consisted of open water over charred substrate (46.5%) (Figure 5). After only one growing season (2019), substantial increases in broad-leaved cattail (44.1%) and to a lesser extent common spikerush (4.6%) were observed (Figure 5). Despite the increases, cover levels were lower than pre-fire conditions in 2013 (67% broad-leaved cattail and 18% common spikerush) based on 2013 shoreline vegetation types (Sonoma County 2019a).
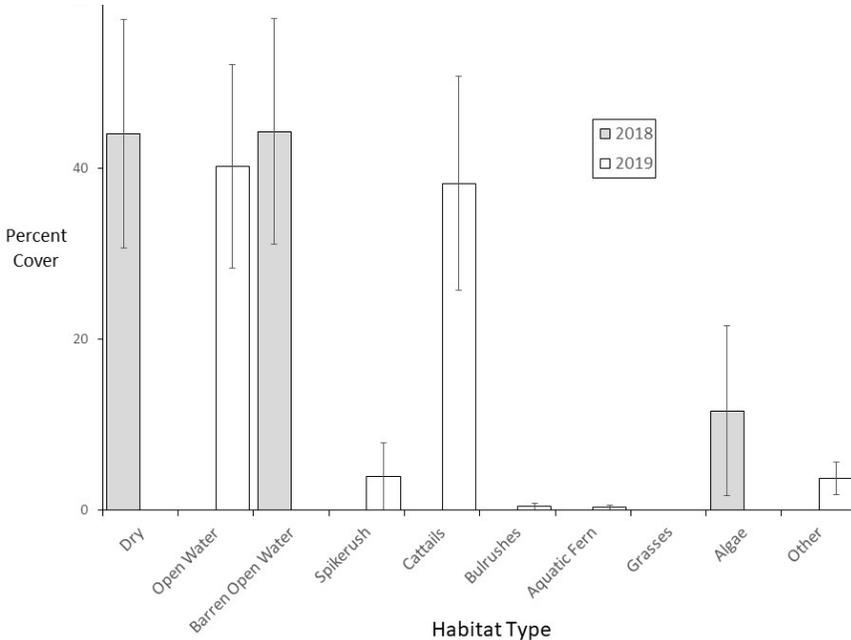
Figure 5. Habitat change in shoreline plots, Ledson Marsh, 2018 and 2019. Columns indicate mean values; whiskers are standard deviations. Barren open water is open water over charred ground.

Although the ranges in water quality parameters tolerated by amphibians in Ledson Marsh are not known, post-fire water quality revealed no unusual conditions that would likely effect the normal development of larval amphibians. Water on 19 January 2018 was cool (9.0 ± 0.8°C), near neutral pH (6.9 ± 0.5), and high in dissolved oxygen (9.4 ± 1.5 mg/L). Continuous winter monitoring near the dam in 2019 found similar temperature (9.2 ± 2.15°C) and pH (6.2 ± 0.1) conditions, and somewhat lower dissolved oxygen (5.6 ± 3.3 mg/L).

DISCUSSION

This case study contributes to our limited but growing understanding of amphibian response to the effects of wildfire, a condition that Hossack and Pilliod (2011) underscored. Overall, the amphibian assemblage at Ledson Marsh appeared resilient to or benefitted from the temporary disturbance caused by the Nuns Wildfire, at least through two years post-fire. This was demonstrated by the persistence of species detected prior to the wildfire, colonization by the western toad, and a return to an earlier successional stage that may prolong the marsh. The apparent relative constancy in species composition post-fire can be attributed to a combination of factors, including: 1) a short-term fire disturbance, 2) rapid vegetation regeneration, 3) affected amphibians with adult longevities longer than one year (assuming they could evade the fire), and/or 4) affected amphibians having a refuge from the fire. There is some data to support the first three points. However, the fourth point is speculative. Nevertheless, each merits a brief comment.

The Nuns Wildfire was clearly large in magnitude (Gabbert 2018) and fire movement was frequently fast and short in duration (Nauslar et al. 2018). Observations at Ledson Marsh and within the vicinity correspond with this perspective. Ground fire rapidly eliminated herbaceous and shrubby vegetation, crowning was rare, and pockets of more substantial fuel (large wood) were extremely dry due to preceding climate conditions (Nauslar et al. 2018), resulting in longer-term burning only locally. The authors speculate this pattern reduces the likelihood that fire, or the conditions resulting from a fire such as local temperatures and other air quality conditions, affected herpetofauna present in concealed refuges within the Ledson Marsh watershed. The terrestrial survey results correspond with little evidence of a fire effect. In addition, renewal of substantial vegetation in Ledson Marsh occurred after one growing season reflecting the protected rootstock of the perennial emergent plants (broad-leaved cattail, California bulrush, common spikerush) and their fire responsiveness (Rivard and Woodard 1989; Bowles et al. 1996). This rapidly re-established some vegetation structure, providing amphibian oviposition anchorage and refuge for larvae and post-metamorphic life stages during their rearing period.

Except for the Pacific treefrog, all native amphibian species that use Ledson Marsh typically live at least two years as reproductive adults and some live longer (Pimentel 1960; Watters and Kats 2006; Marc P. Hayes [MPH], unpublished data). Assuming they did not colonize from elsewhere, most adults that bred during the 2018-2019 survey period had to survive the Nuns Wildfire. Given the large footprint of the Nuns Wildfire, which encompassed the entire drainage basin around Ledson Marsh (Figure 2), and the known species range of movement in this amphibian assemblage (Pimentel 1960; Bulger et al. 2003; Smith and Green 2005; Fellers and Kleeman 2007), colonization from outside the fire area seems unlikely.

If Ledson Marsh amphibians did not colonize from elsewhere, a basic unknown is what refuges were used when the fire passed through the area. Native amphibian larvae within the marsh typically metamorphose by mid-summer (DGC, unpublished data) and two to three months prior to the marsh drying, so all life stages would have needed to find terrestrial refuge before the fire. Since most near-surface refugia (patches of unburned California bulrushes [rare], downed wood [rare], rock tailings from pit mining [limited]) had either burned or were likely too dry to provide refuge (the latter a basic reason for the rapid successful movement of this fire across the landscape), the authors suspect that refugia were largely not near the surface and/or concentrated in small areas. Understanding the refugia that amphibians and other herpetofauna might use to evade fire clearly merit study.

The exception to the lack of change in the species composition pattern, western toad, merits particular comment because the western toad had not been recorded at Ledson Marsh since monitoring began in 1996. Pre-fire, western toad had been observed outside the Ledson Marsh watershed but within the footprint of the 2017 wildfire. Western toad adults and tadpoles were detected post-fire, indicating successful breeding within Ledson Marsh. In Glacier National Park, Hossack and Corn (2007) found western toad colonized nine burned wetlands within two years post-fire in an area where no breeding had been detected and adults were rarely seen. Following the eruption of Mt. St. Helens in Washington State in 1980, western toad was the first amphibian colonizer of newly created ponds on the pumice plain (Crisafulli et al. 2005). Conditions that influenced western toad breeding habitat in these circumstances differ markedly (fire versus volcanic eruption), but both returned vegetation to an earlier successional stage. The Nuns Wildfire resetting of vegetation succession likely represents a parallel pattern for the response of western toad at Ledson Marsh. In addition,

the fire may have prolonged the natural conversion of the marsh to a wet meadow by returning the plant community to an earlier successional stage.

Larval California red-legged frogs were not detected during the spring of 2019, although egg masses were detected the previous winter. The cause may be due to one or more of the following: 1) dipnet sampling intensity, 2) low reproductive effort, and/or 3) low larval survival. The latter two reasons may not be an indication of decline of this threatened frog. The post-fire adult estimates were low, but similar to the range recorded since 1996. Also, the main habitat used for oviposition is common spikerush (Cook and Jennings 2007), which had a slower recovery post-fire as compared to the broad-leaved cattail (Figure 5). Adults may have been present and forgone breeding due to poor habitat conditions.

Climate projections indicate that temperatures across California will rise substantially (1 to 3°C) by 2050 (Cayan et al. 2008; Cayan et al. 2009). Increased evapotranspiration associated with higher temperatures is expected to exacerbate drier conditions (Matthews 2010) and the likelihood of drought (Mastrandrea and Luers 2012) may result in an increase in fire activity, including severity, area burned, ignitions, and season (Flannigan et al. 2000; Flannigan et al. 2005; Perry et al. 2011). The authors believe the Nuns Wildfire reflects this ascending trajectory. Though it may be tempting to speculate that maintenance of an early successional stage represents a benefit for western toad, increasing fire frequency may have complex interactive effects that include shifts in marsh vegetation seedbed, alteration of amphibian refuges to fire, and synergistic adverse impacts from environmental stress (e.g., reproductive and larval failure from prolonged and severe drought). This kind of complexity creates high uncertainty in terms of outcomes, not only for western toad but for the entire amphibian community within sites such as Ledson Marsh. The authors regard unambiguous understanding of species-specific refuges as among the most important data gaps needed to unravel potentially complex effects of fire on amphibians.

ACKNOWLEDGMENTS

Author Contributions
Conceived and designed the study: DGC
Collected the data: DGC
Performed the analysis of the data: MPH and DGC
Authored the manuscript: DGC and MPH
Provided critical revision of the manuscript: MPH and DGC

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ORIGINAL RESEARCH

Analysis of the impacts of the Soberanes Wildfire on stream ecosystems

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Wildfires within the western United States are expected to increase in frequency and magnitude but our understanding of how they impact coastal streams is limited. The 2016 Soberanes Wildfire provided an opportunity to determine which biotic and abiotic factors were most impacted by the fire occurring on the California Central Coast. Water quality, benthic macroinvertebrate samples and habitat measurements were taken both before and after the fire. We observed an increase in the levels of phosphorus 4 months and 8 months post-fire which may have contributed to observed increases in microalgae growth. There was a complete loss of shredders in the benthic macroinvertebrate community which could be caused by the loss of vegetation in stream-adjacent riparian areas. These post-fire results were expected based on previous research, however organic material inputs to the stream unexpectedly did not change between pre- and post-fire conditions, which may be due to a delayed increase in inputs from riparian vegetation which short-term monitoring is unable to capture. A long-term monitoring program effort is critical for understanding the recovery of these coastal watersheds from fire.

Key words: abiotic, benthic macroinvertebrates, biotic, coastal watersheds, water quality, wildfire

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Areas burned by wildfires are expected to increase dramatically due to the changing climate. Specifically, fire frequency and burned areas are predicted to increase in the western United States due to predicted warmer summers and reduced levels of precipitation (Sankey et al. 2017; Westerling et al. 2011). Brown et al. (2008) estimated that about 65% of the water supply in the western United States originates in watersheds that contain fire-prone vegetation, making these watersheds even more important to understand (Sankey et al. 2017). The burning of watersheds is known to impact downstream aquatic ecosystem, infrastructure, recreational use, water supply and water quality (Marina et al. 2019; Hallema et al. 2018; Sankey et al. 2017; Gresswell 1999).

In general, our understanding of how coastal streams recover from wildfires in Mediterranean climates is limited. These coastal watershed experience additional factors that in-land watersheds may not such as greater salt deposition, greater fog influence and greater

numbers of biologically isolated organisms. Wildfires are known to impact all aspects of a stream (i.e., hydrological, geochemical, and biological) so understanding the holistic picture of these watershed ecosystems post-wildfire is critical for managing both water resources and biodiversity in California. Although recent work has provided a better understanding of particular impacts of fire on stream ecosystems (summarized by Bixby et al. 2015), more holistic examinations of the effects of fires in Mediterranean systems are still needed.

In 2016, the Soberanes Wildfire burned large areas within Monterey County and Los Padres National Forest, but it also provided a natural, large-scale experiment on the effects of fire on coastal watershed streams and ecosystems. The availability of historical biological and chemical monitoring data from this area within the Central Coast allowed us to compare conditions pre and post-fire.

Our objective was to determine the extent to which abiotic factors (e.g., nutrients, sediments, and other physical aspects) and biotic factors (algae and benthic macroinvertebrates) were impacted by the Soberanes Wildfire. We predicted that nutrients such as a phosphate and nitrate will increase post-fire similarly to other research (Bixby et al. 2015; Diemer et al. 2015; Sherson et al. 2015). Additionally, previous studies indicated that there may be an increase erosion and sediment inputs, transport and deposition which we expect to see as an increase in finer sediments (Cooper et al. 2015). Finally, we expected benthic macroinvertebrates to decrease in abundance post-fire due to increases in sediment deposition, but algae might increase due to increased nutrients.

METHODS

Study area

The Soberanes Wildfire burned throughout the California Central Coast and within the Garrapata State Park and the Los Padres National Forest (Figure 1). Burn intensities varied considerably among the coastal and inland watersheds. For this study, we focused on a few specific coastal watersheds because of their importance to threatened west coast steelhead which rely on some of these coastal streams for reproduction and rearing habitat (NMFS and NOAA 2000). The coastal watersheds of Garrapata Creek (36.417°N, -121.914°W) and Soberanes Creek (36.455°N, -121.923°W) had most of their watershed areas burned in the fire and were the primary focus of this data analysis effort (Figure 1, Table 1). Geomorphological data from three other coastal watersheds are also presented (Table 1). Watersheds examined ranged in size with the Big Sur River Watershed having the largest area of approximately 60 square miles. However, the watersheds supporting Garrapata Creek and Soberanes Creek were more representative of the small watersheds typical of the Central Coast, with watershed areas of 27.7 and 8.0 km^2, respectively.

All watersheds in the study comprised mostly natural land cover with low amounts of agriculture. Prior to data collection, sites were selected based on the US Forest Service Burned Area Emergency Response Team soil burn severity (USFS BAER Team 2016) and low landscape variability (e.g., only small difference in elevation). We calculated the percent of high, medium, and low soil burn severity for all coastal watersheds in the study area that had published pre-fire chemical, physical, or biological data and sites were chosen from across this range of burn severity. For example, Garrapata Creek and Soberanes Creek were both burned to similar extents, with approximately 86 and 83 percent of each watershed burned, respectively. Other watersheds varied in the proportion burned such as Limekiln

Figure 1. Map representing sites where SWAMP surveys were completed as denoted by 'X' and where water chemistry samples were taken denoted by blue circles. Soberanes Creek Watershed and Garrapata Creek Watershed are symbolized on the map from North to South, respectively.

Table 1. Coastal watersheds analyzed by abiotic or biotic factors.

Watershed	Biological	Water Chemistry	Geomorphological
Soberanes Creek	X	X	X
Garrapata Creek		X	
Limekiln Creek			X
Big Sur River			X
Rocky Creek			X

Creek which was unburned and served as our control site. Verification of these watershed delineations were done using known watershed boundaries from the U.S. Geological Survey National Hydrography Dataset (USGS 2017) . Post-fire measurements were made in the vicinity (within 100 m) of the pre-fire data, which was downstream of the portion of the watershed burned in all cases.

Spatial watershed methods

To supplement field measurements taken at these coastal streams, we also delineated watersheds and used datasets acquired from the USEPA StreamCat for each of our sites using ESRI ArcGIS and R (Hill et al. 2016; Environmental Systems Research Institute, Inc., Redlands, CA, USA; R v.3.6.1, www.r-project.org, accessed Jun 2017; Appendix I). The StreamCat datasets are watershed summaries of natural variables that influence stream conditions (e.g., geology, topography, soils, vegetation, and climate; Hill et al. 2016). Watershed summaries not available in the USEPA StreamCat were created using various geospatial datasets such as Landfire's fuel models, USGS National Map and PRISM Climate Group and calculated their zonal statistics (Appendix I). Some of these predictor watershed summaries included identification of potentially high erosion areas, year since last wildfire, and estimated valley slopes (Appendix I). At burned sites, we also added the summarized severity and extent of the burn at the watershed scale calculated previously during site selection.

Abiotic methods

We collected water quality samples for analysis of nitrate and phosphate concentrations at Garrapata Creek and Soberanes Creek weekly from October 2016 until March 2017 (Figure 1, Table 1). At each site, we collected metadata such as time and water temperature. We placed all water quality samples on ice until they could be processed (within 24-hours of collection). In the laboratory, a Hach colorimeter (accuracy ±0.03 mg/L for nitrate, ±0.06 mg/L for phosphate) was used for all samples to measure phosphate and nitrate concentrations (mg/L). We obtained measurements of phosphate, nitrate, and water temperature collected by other regional research and monitoring efforts from California Environmental Data Exchange Network (CEDEN) (State Water Resources Control Board 2020.). Visualization and comparison of phosphate, nitrate and water temperature were done using R (R v.3.6.1, www.r-project.org). From CEDEN, Soberanes Creek had water chemistry data for two years (2000 and 2016) and Garrapata Creek had data for four years (2002, 2003, 2009 and 2015) before the fire.

Surface Water Ambient Monitoring Protocol (SWAMP) surveys were completed within four coastal watersheds post wildfire in the summer of 2017 (i.e., Soberanes Creek, Rocky Creek, Big Sur River and Limekiln Creek; Table 1) following the reach wide benthos protocol (Ode et al. 2016). We collected physical habitat measurements such as substrate size using the Wolman 'pebble count' technique which allows the collector to calculate the percentiles of particle size (Ode et al. 2016). We then compared our data to previous SWAMP data available through CEDEN.

We constructed generalized linear models (GLMs) in R (R v.3.6.1, www.r-project.org) to examine the influence of natural factors and fire on the size of river, and percent fine sediment (% of substrate less than 2 mm in diameter) were calculated from SWAMP field measurements. Predictor data were developed from the spatial watershed metrics mentioned previously (i.e., StreamCat datasets, supplemental zonal statistics). The natural factors we used as potential predictors of sediment size are detailed in Appendix I and include 9 geology/soil variables, 5 hydrology variables, 4 topography variables, and 26 vegetation variables. GLMs can suffer over fitting if too many predictors are used, so we used stepwise Akaike information criterion (AIC) regression methods to select the model with predictors that best fit the data (Pleog et al. 2014). These models were created from a dataset of other coastal streams that included Garrapata and Soberanes Creeks (n = 9).

Biotic methods

While physical habitat measurements were being taken at each transect following the SWAMP standard operation procedures (Ode et al. 2016), we recorded microalgae thickness class observations at each substrate size class measurement. Following Ode et al. (2016), classes are defined as: class 0- no microalgae present, class 1- present, but not visible (i.e., can be felt but not seen), class 2- < 1 mm, class 3- 1-5 mm, class 4- 5-20 mm, and class 5- > 20 mm.

At each SWAMP location, we collected benthic macroinvertebrates at 11 transects 15-m apart over a 150-m sampling reach. A 500-μm mesh D-frame net was used to collect benthic macroinvertebrates in the immediate 0.09 m^2 area in front of the net (Ode et al. 2016). Incidental vertebrates collected were immediately released, and collected invertebrates were stored in 70% ethanol for later identification in the lab (Ode et al. 2016).

These invertebrate samples were only processed in part for Soberanes Creek for two predominantly sensitive taxonomic orders, Ephemeroptera (Mayfly) and Plecoptera (Stonefly) due to available time and funding. Due to the diversity in life cycle traits and sensitivity to disturbance at the genus level, these two orders may provide sufficient information for understanding how diversity within genera and functional feeding groups may respond to fire disturbance (Merritt and Cummings 1996; Buss et al. 2007; Rosenberg et al. 1993). Both orders are known to be sensitive to changes in sediment or water quality and are therefore commonly used in the detection of water quality changes (Merritt and Cummins 1996; Buss et al. 2007; Rosenberg et al. 1993). Previous benthic macroinvertebrate samples were collected prior to the fire in 2010 and 2016 at Soberanes Creek which were available through CEDEN. Post-fire samples were collected by students at California State University, Monterey Bay (CSUMB) about four months post-fire (February 2017), and again eight months post-fire (June 2017) by members of the Watershed Environments and Ecology lab at CSUMB. These datasets provide the time series for analyses reported here. We compared the counts of individuals by order and by functional feeding groups, and diversity

calculated using the Shannon diversity index (Shannon 1948) from before and after the fire associated (Hughes 1978; Lydy et al. 2000).

RESULTS

Abiotic results

Phosphate increased after the wildfire at Soberanes Creek and Garrapata Creek, however nitrate and water temperature had minimal change or remained constant (Figure 2 and Figure 3). In addition, no change was observed for coarse particulate organic matter (CPOM) or wetted width measurements at these two sites.

At the four sites we sampled using the SWAMP protocol, the percent of fines are consistent but dramatically increased around June of 2017, and the D_{15} decreased over time
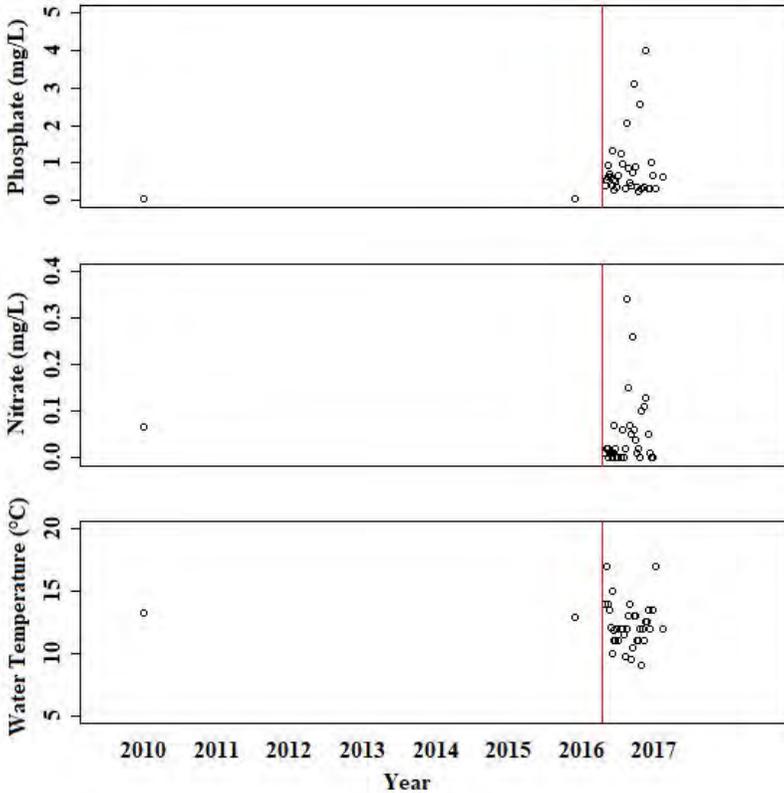

Figure 2. Data points represent water chemistry samples including water temperature, nitrate and phosphate from Soberanes Creek, pre-fire (before the event point in red) and post-fire. An outlier was removed from this figure which represented Soberanes Creek water quality data where on 20 January 2017, there was a phosphate measurement of 15.1 mg/L.
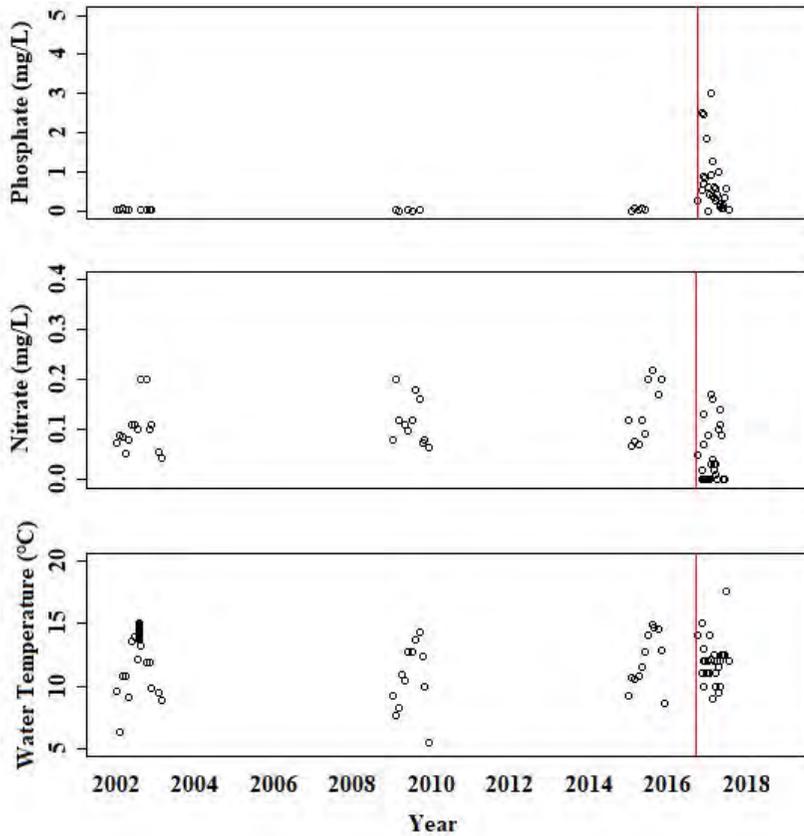
Figure 3. Data points represent water chemistry samples of water temperature, nitrate and phosphate taken at Garrapata Creek, pre-fire (before the event point in red) and post-fire.

(Figure 4). In addition, D_{50} and D_{84} remained constant then decreased in June of 2017 (Figure 4). All of the GLMs relating variation in sediment size distributions in coastal streams to environmental factors contained significant predictors and explained the majority of variation in sediment sizes (r^2 values 79%-90%; Table 2). The percent fine sediment model explained 90% of model variation, including the same factors as the other models, but also factors representing natural variation (i.e., average temperature change from 1981-2010, year since last fire, previous year's average precipitation and percentage of clay in the watershed). We examined the partial dependence plots to determine how each predictor variable influenced percent fines (Figure 5). Percent fines decreased as average temperature, percent of clay substrate in watershed, and years since last fire increased. The opposite pattern is seen for average precipitation for the year prior to SWAMP survey, as the precipitation increases the percent of fines increased.

Table 2. Results of GLM models for river sediments response data. Significance represented as <0.001:***, <0.01:**, <0.05:*

| Models	R^2	AIC
D15~Average Temperature (1981-2010)+Years Since Last Fire***	93%	56.7
D50~ Average Temperature (1981-2010) + Year Since Last Fire***	90%	79.0
D84~Average Precipitation (1981-2010) + Average Elevation* + Year Since Last Fire**	79%	100.8
Percent Fines~ Average Temperature (1981-2010)*+Year Since Last Fire**+Previous Years' Precipitation + Percent Clay in Watershed	90%	63.5
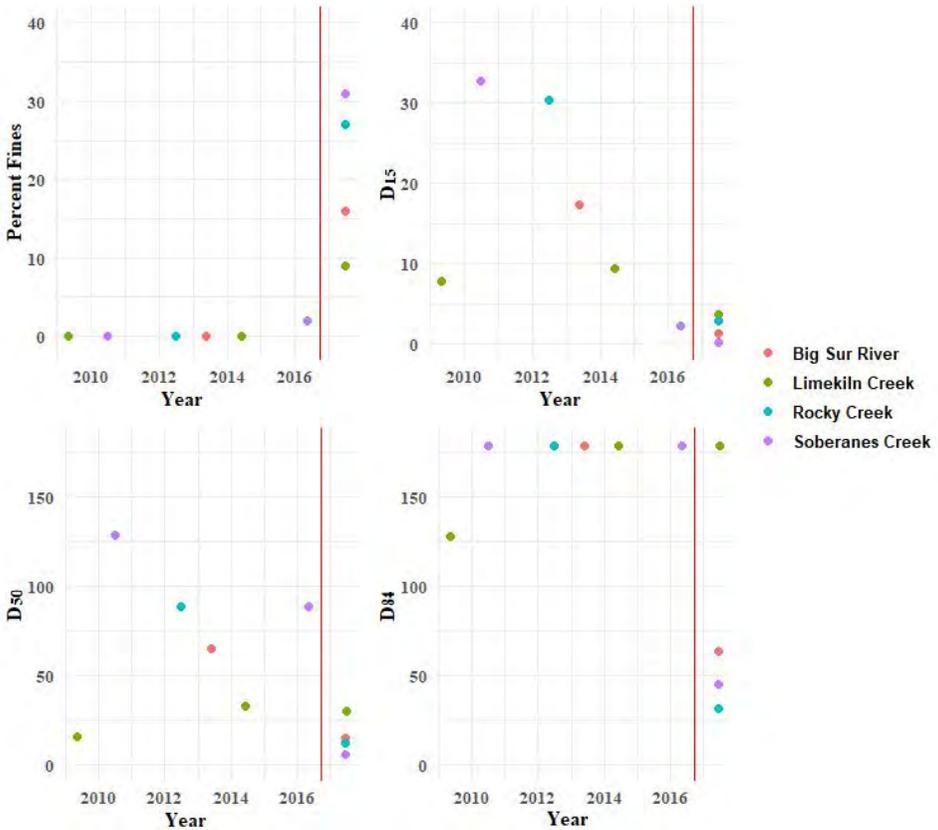
Figure 4. Changes in particle size D_{15} (where 15% of total sample is smaller than this size), D_{50} (where 50% of total sample is smaller than this size), D_{84} (where 84% of total sample is smaller than this size), and percent of fines at the four SWAMP survey locations.
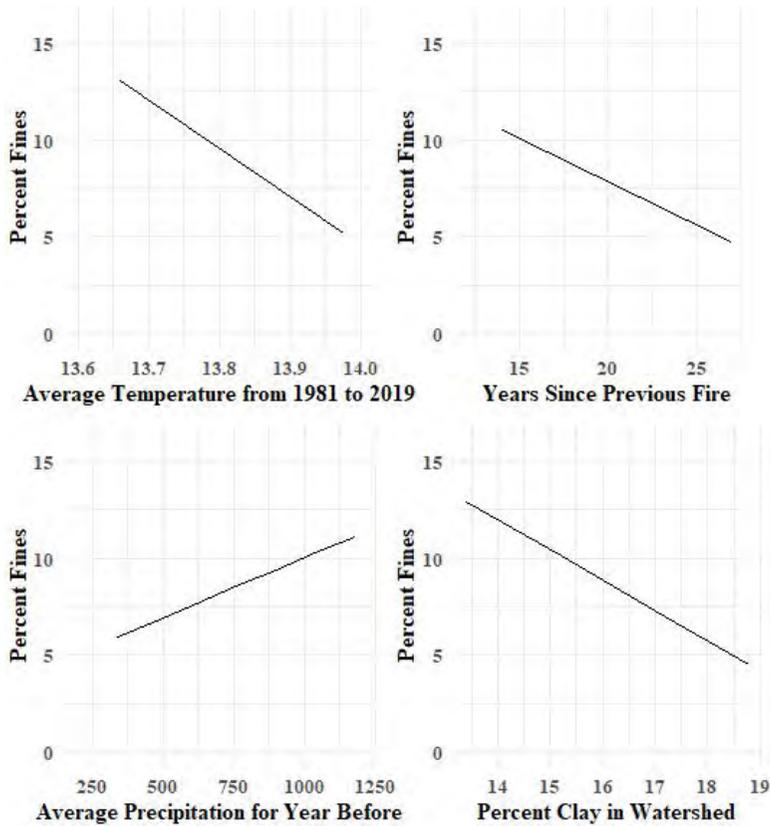
Figure 5. Partial dependence plots of the percent fine sediment generalized linear model predictors.

Biotic results

Microalgae thickness classes increased post-fire at Soberanes Creek, Big Sur River and Rocky Creek (Figure 6). Limekiln Creek (control site) had the greatest microalgae thickness before the wildfire but also showed increased thickness post-fire (Figure 6). There were greater abundances of Ephemeroptera and Plecoptera before the fire in 2010 and 2016 compared to four months and eight months post fire (269, 234, 36, 148 combined counts, respectively). An increasing trend is shown from four months to eight months post fire potentially indicating a recovery in abundance of Ephemeroptera (Figure 7).

Before the fire, functional feeding groups for these two orders mainly contained collectors, scrapers, shredders, and a small number of predators (Figure 8). However, four months post fire, where there was a noticeable loss in abundance of organisms (Figure 7), and a decline in counts for all functional feeding groups. At eight months post fire, there was an increase in abundance of collectors and predators, however no shredders have collected (Figure 8). From June of 2010 to June 2017, there was also a slight but continuous decrease in the scraper functional feeding group (16, 9, 6, 3 chronologically, Figure 8).
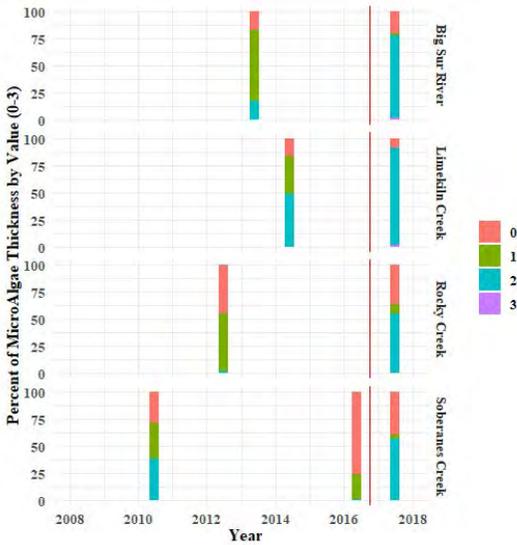
Figure 6. Pre and post fire thickness classes of microalgae on rocks at SWAMP survey sites. Microalgae thickness classes: 0- no microalgae present, 1-present, but not visible, 2-greater than 1 mm, and 3-1–5 mm.
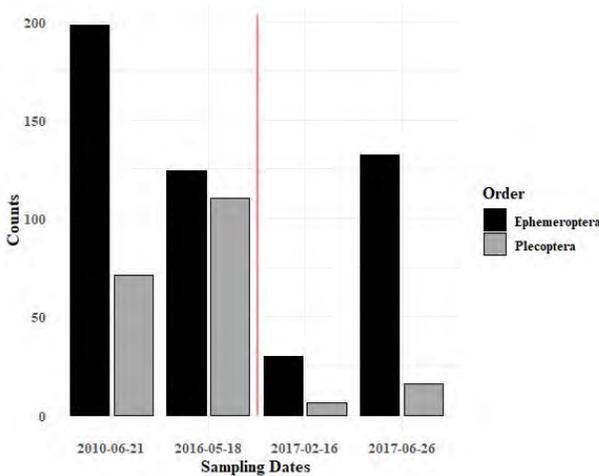
Figure 7. Pre and post abundance results for the two orders of concern. Red line represents the Soberanes Wildfire start event in October of 2016.

Genus level Shannon diversity index scores range from about 1.5–2 before the fire, to 0.9–2.1 after the fire (Figure 9). There was little change in diversity immediately after the fire, but later that year we observed a decrease.

DISCUSSION

We expected nutrient concentrations to increase, as nitrogen and phosphorus are often mobilized by fires (Bixby et al. 2015; Diemer et al. 2015; Sherson et al. 2015). We did not observe any change in nitrate concentrations post-fire but did see the expected increases in phosphorus. The post-fire increases in phosphorus we observed at Garrapata and Soberanes Creeks (Figures. 2 and 3) may be caused by two mechanisms. The increase in phosphorus could be due to a decrease in surrounding vegetation taking up nutrients. Alternatively, it
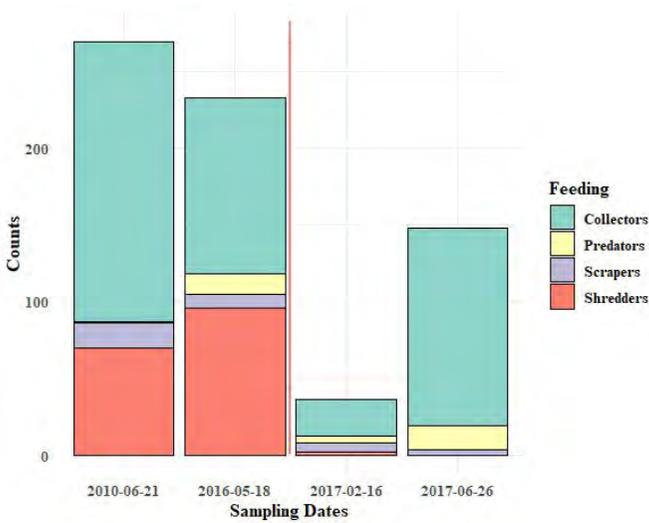
Figure 8. Pre and post functional feeding groups by count of organisms. The two sample dates before October 2016 represent data available on CEDEN. Post-fire data is represented in the two bars right of the red line.
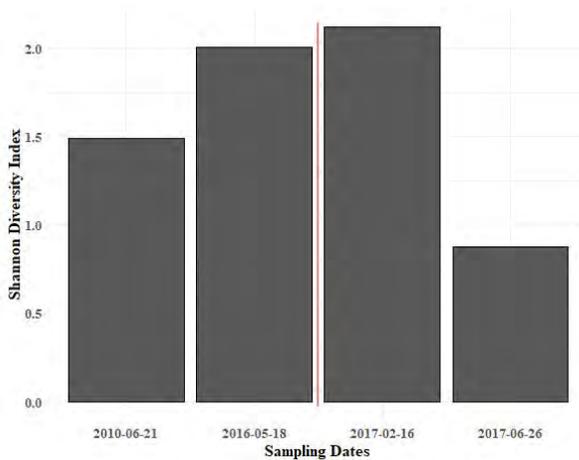
**Figure 9.** Pre and post wildfire, genus level Shannon diversity index scores for each sample timeframe. Red line represents the Soberanes Wildfire start event in October of 2016.

may also be due to increased phosphorus-enriched sediments in the water. Both Garrapata and Soberanes Creek's watersheds had areas greater than 80% burned and could be experiencing one or both mechanisms. At Soberanes Creek post-fire we observed an increase of fine sediments (Figure 4) which indicates increased erosion of the surrounding watershed due to wildfire. Increasing bioavailable phosphorus from phosphorus-enriched sediments is known to be a key mechanism that impacts streams and large watersheds (Emelko et al. 2015). Diemer et al. (2015) showed that fires in boreal forests alter stream chemistry for many years after by altering the retention of nutrients in streams. The legacy this increase in bioavailable phosphorus may have downstream is still unknown but long-term monitoring may be able to explain the recovery or long-term impacts of this change.

Increases in nutrient concentrations can also lead to changes in algal response, specifically increases in phosphorus in post-fire settings are known to increase algal biovolume (Klose et al. 2015). Increased light could also increase algae (Cooper et al. 2015, Coombs and Melack 2013), but because we measured algae below where the fire affected the stream,

light was not changed between before and after the fire. We saw an increase in microalgae thickness at all sampled creeks and rivers post-fire (Figure 6) which could indicate that the increase in nutrients is contributing to an increase in microalgae growth. Microalgae thickness also increased post-fire in the unburned watershed, but this watershed had the greatest microalgae thickness pre-fire which could be due to previous fires in the region such as the Chalk Fire which occurred in 2008. Algal levels are known to be higher in streams post-fire where riparian vegetation has burned (Cooper et al. 2015). This increase in algae growth could impact stream food webs and basal resources (Cooper et al. 2015). It should be noted that algal growth after fires depends on many factors such as sediment deposition, light availability, canopy cover, and flooding so not all algal growth could be attributed to the increase in nutrients (Coombs and Melack 2013).

We expected that as microalgae increased we would see a corresponding increase in the amount of benthic macroinvertebrates belonging to the scraper functional feeding group. However, our results indicate a decrease in the number of scrapers post-fire (Figure 7), which may be due to other factors such as increased fine sediment deposition (Jones et al. 2012). We also found a complete loss of shredders post-fire which could be attributed to a decrease in vegetative inputs from the riparian communities. Similar to the results of Rodríguez-Lozano et al. (2015), we saw a recovery of most functional feeding groups within a year post-wildfire. However, we did not see the shredders feeding group recover in the first year.

Although nitrate concentrations and organic inputs such as CPOM are also reported to respond to fire, we did not see changes in levels of either nitrate or CPOM post-fire. CPOM may increase post-fire with pulses of leafy matter or decrease as materials get mobilized and transported downstream (Copper et al. 2015, Beakes et al. 2014; Britton 1990). Robinson et al. (2005) and Bendix and Cowell (2015) noted that riparian tree damage and organic inputs may take many years after a fire to fall into rivers, so we may not have captured changes in CPOM in the first year of post-fire monitoring. Nitrogen released post-fire may have been taken up by the increasing microalgal biomass, indicating that these coastal streams are normally nitrogen limited (Feminella et al. 1989).

Overall, we determined that phosphorus concentrations, the amount of fine sediments, the composition and abundance of the benthic macroinvertebrate assemblage, and amounts of microalgae are the factors in coastal streams most affected by wildfire. Additional monitoring is needed to determine when all of the abiotic and biotic factors have fully recovered. In the future, long-term post-fire monitoring of all aspects of streams should be planned for and resourced to determine if the same impacts we observed occur and how fast streams recover. Other natural events such as drought may be exacerbating stress on these streams and watersheds and incorporating them in future work is critical to deepening our understanding of the impacts caused by fire.

ACKNOWLEDGMENTS

Author Contributions

Conceived and designed the study: JD, JO, and MB

Collected the data: MB and JD

Performed data analysis: JD

Authored the manuscript: JD and JO

Provided critical revision of the manuscript: all authors

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APPENDIX I

Predictor Variables	Source	Description
A__SB2	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Moderate load activity fuel or low load blowdown, 7-12 t/ac, 0-3 inch diameter class, depth about 1 foot, blowdown scattered with many still standing, spread rate and flame low
A__TL5	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: High load conifer litter, light slash or dead fuel, spread rate and flame low
BFIWs	USEPA StreamCat	Baseflow is the component of streamflow that can be attributed to ground-water discharge into streams. The Baseflow Index (BFI) is the ratio of baseflow to total flow, expressed as a percentage, within watershed.
CaOWs	USEPA StreamCat	Mean % of lithological calcium oxide (CaO) content in surface or near surface geology within watershed
ClayWs	USEPA StreamCat	Mean % clay content of soils (STATSGO) within watershed
CompStrgthWs	USEPA StreamCat	Mean lithological uniaxial compressive strength (megaPascals) content in surface or near surface geology within watershed
DamDensWs	USEPA StreamCat	Density of georeferenced dams within watershed (dams/ square km) based on the National Inventory of Dams (https://catalog.data.gov/dataset/national-inventory-of-dams)
ElevWs	USEPA StreamCat	Mean watershed elevation (m)
GR1	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Short, sparse dry climate grass is short, naturally or heavy grazing, predicted rate of fire spread and flame length low
GR2	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Low load, dry climate grass primarily grass with some small amounts of fine, dead fuel, any shrubs do not affect fire behavior
GS1	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Low load, dry climate grass-shrub shrub about 1 foot high, grass load low, spread rate moderate and flame length low
GS2	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Moderate load, dry climate grass-shrub, shrubs are 1-3 feet high, grass load moderate, spread rate high, and flame length is moderate
HighSqKm	BAER Soil Burn	% of watershed area with high burn soil severity
LowSqKm	BAER Soil Burn	% of watershed area with low burn soil severity
MaxRelief	USGS National Map	Using the 30-meter resolution DEM from National Map, max relief was calculated by taking the max elevation from the minimum elevation

APPENDIX I CONT.

Predictor Variables	Source	Description
ModSqKm	BAER Soil Burn	% of watershed area with moderately burn soil severity
NB1	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Non Fuel Vegetation: Urban
NB3	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Non Fuel Vegetation: Agriculture
NB8	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Non Fuel Vegetation: Water
NB9	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Non Fuel Vegetation: Barren
OmWs	USEPA StreamCat	Mean organic matter content (% by weight) of soils (STATSGO) within watershed
PctConif2011Ws	USEPA StreamCat	% of watershed area classified as evergreen forest land cover (NLCD 2011)
PctDecid2011Ws	USEPA StreamCat	% of watershed area classified as deciduous forest land cover (NLCD 2011)
PctFire2000Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2000 within catchment
PctFire2001Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2001 within catchment
PctFire2002Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2002 within catchment
PctFire2003Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2003 within catchment
PctFire2004Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2004 within catchment
PctFire2005Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2005 within catchment
PctFire2006Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2006 within catchment
PctFire2007Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2007 within catchment
PctFire2008Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2008 within catchment
PctFire2009Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2009 within catchment
PctFire2010Ws	USEPA StreamCat	% Forest loss to fire (fire perimeter) for 2010 within catchment

APPENDIX I cont.

Predictor Variables	Source	Description
PctGrs2011Ws	USEPA StreamCat	% of catchment area classified as grassland/herbaceous land cover (NLCD 2011)
PctMxFst2011Ws	USEPA StreamCat	% of catchment area classified as grassland/herbaceous land cover (NLCD 2011)
PctShrb2011Ws	USEPA StreamCat	% of catchment area classified as grassland/herbaceous land cover (NLCD 2011)
PerAvgSlope	USGS National Map	30-meter resolution digital elevation acquired from the USGS National Map was used to calculate the percent average slope in each watershed
PermWs	USEPA StreamCat	Mean permeability (cm/hour) of soils (STATSGO) within watershed
Precip8110Ws	USEPA StreamCat	Mean permeability (cm/hour) of soils (STATSGO) within watershed
PrevAvgPrecip-Km	PRISM	Average watershed precipitation from PRISM datasets at 30-meter resolution
RckDepWs	USEPA StreamCat	Mean depth (cm) to bedrock of soils (STATSGO) within watershed
RunoffWs	USEPA StreamCat	Mean runoff (mm) within watershed
SandWs	USEPA StreamCat	Mean % sand content of soils (STATSGO) within watershed
SH1	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Low load dry climate shrub, woody shrubs and shrub litter, fuelbed depth about 1 foot, may be some grass, spread rate and flame low
SH2	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Moderate load dry climate shrub, woody shrubs and shrub litter, fuelbed depth about 1 foot, no grass, spread rate and flame low
SH5	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: High load, humid climate grass-shrub combined, heavy load with depth greater than 2 feet, spread rate and flame very high
SH7	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Very high load, dry climate shrub, woody shrubs and shrub litter, very heavy shrub load, depth 4-6 feet, spread rate somewhat lower than SH6 and flame very high
TBurnSqKm	BAER Soil Burn	% burned in watershed, calculated by summing the percentage of low, moderate and highly burned percent area.
TL1	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Low load compact conifer litter, compact forest litter, light to moderate load, 1-2 inches deep, may represent a recent burn, spread rate and flame low
TL2	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Low load broadleaf litter, broadleaf, hardwood litter, spread rate and flame low

APPENDIX I CONT.

Predictor Variables	Source	Description
TL3	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Moderate load conifer litter, moderate load conifer litter, light load of coarse fuels, spread rate and flame low
TL4	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Small downed logs moderate load of fine litter and coarse fuels, small diameter downed logs, spread rate and flame low
TL6	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Moderate load broadleaf litter, spread rate and flame moderate
TL7	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Large downed logs, heavy load forest litter, larger diameter downed logs, spread rate and flame low
TL8	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Long needle litter, moderate load long needle pine litter, may have small amounts of herbaceous fuel, spread rate moderate and flame low
TL9	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Very high load broadleaf litter, may be heavy needle drape, spread rate and flame moderate
Tmean8110Ws	USEPA StreamCat	PRISM climate data - 30-year normal mean temperature (°C): Annual period: 1981-2010 within the watershed
TU1	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Low load dry climate timber grass shrub, low load of grass and/or shrub with litter, spread rate and flame low
TU2	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Moderate load, humid climate timber-shrub, moderate litter load with some shrub, spread rate moderate and flame low
TU5	Landfire (40 Scott and Burgan Fire Behavior Fuel Models)	Vegetation: Very high load, dry climate shrub, heavy forest litter with shrub or small tree understory, spread rate and flame moderate
ValleySlope	USGS National Map	Valley Slope calculated from an euclidean distance raster from top to bottom of a watershed and slope raster created from 30-meter DEM
WsAreaSqKm	USEPA StreamCat	Watershed area (square km) at NHDPlus V2 stream segment outlet, i.e., at the most downstream location of the vector line segment
WtDepWs	USEPA StreamCat	Mean seasonal water table depth (cm) of soils (STATSGO) within watershed
Year	CEDEN or SWAMP Survey	Year the CEDEN or SWAMP survey was completed
YrSinceLastFire	Landfire (Fire Regimes)	Year since last wildfire within watershed using Landfire Fire Regime Groups

INFORMATION FOR AUTHORS

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Front. A wildland firefighter monitors a prescribed burn. Photo Credit: Cristin Walters, CDFW

Back. Lupine blooms in a high severity burn area several years after the 2013 Rim Fire in Stanislaus National Forest. Photo Credit: Cristin Walters, CDFW.