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RESEARCH ARTICLE

SHRUB COMMUNITIES, SPATIAL PATTERNS, AND SHRUB-MEDIATED TREE MORTALITY FOLLOWING REINTRODUCED FIRE IN YOSEMITE NATIONAL PARK, CALIFORNIA, USA

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ABSTRACT

Shrubs contribute to the forest fuel load; their distribution is important to tree mortality and regeneration, and vertebrate occupancy. We used a method new to fire ecology—extensive continuous mapping of trees and shrub patches within a single large (25.6 ha) study site—to identify changes in shrub area, biomass, and spatial pattern due to fire reintroduction by a backfire following a century of fire exclusion in lower montane forests of the Sierra Nevada, California, USA. We examined whether trees in close proximity to shrubs prior to fire experienced higher mortality rates than trees in areas without shrubs. We calculated shrub biomass using demography subplots and existing allometric equations, and we developed new equations for beaked hazel (*Corylus cornuta* ssp. *californica* [A. de Candolle] E. Murray)

RESUMEN

Los arbustos contribuyen en la carga de combustibles de los ecosistemas forestales. Su distribución es importante en la mortalidad y regeneración de los árboles y en la ocupación del espacio por los vertebrados. Nosotros usamos un nuevo método en ecología del fuego—mapeo continuo de parches de árboles y arbustos dentro de un sitio de estudio (25,6 ha)—para identificar cambios en el área cubierta por arbustos, su biomasa y los patrones de distribución causados por la reintroducción del fuego en bosques montanos en la Sierra Nevada de California, EEUU. Examinamos si árboles muy próximos a arbustos antes del fuego experimentaban una mayor mortalidad que árboles en áreas sin arbustos. Calculamos la biomasa de los arbustos usando patrones de densidad y ecuaciones alométricas, y desarrollamos nuevas ecuaciones para el arbusto *Corylus cornuta* (*Corylus cornuta* ssp. *californica* from full dissection of 50 stems. Fire decreased shrub patch area from 15.1% to 0.9%, reduced live shrub biomass from 3.49 Mg ha^{-1} to 0.27 Mg ha^{-1}, and consumed 4.41 Mg ha^{-1} of living and dead shrubs. Distinct (non-overlapping) shrub patches decreased from 47 ha^{-1} to 6 ha^{-1}. The mean distance between shrub patches increased 135%. Distances between montane chaparral patches increased 285%, compared to a 54% increase in distances between riparian shrub patches and an increase of 267% between generalist shrub patches. Fire-related tree mortality within shrub patches was marginally lower (67.6% versus 71.8%), showing a contrasting effect of shrubs on tree mortality between this forest ecosystem and chaparral-dominated ecosystems in which most trees are killed by fire.

[A. de Candolle] E. Murray) mediante la disección de 50 tallos. El fuego hizo decrecer el área de los parches de arbustos del 15,1% al 0,9%, redujo su biomasa viva de 3,49 Mg ha^{-1} a 0,27 Mg ha^{-1}, y consumió 4,41 Mg ha^{-1} tanto de su biomasa viva como muerta. Los parches de arbustos no solapados con árboles decrecieron de 47 ha^{-1} a 6 ha^{-1}. La distancia media entre parches de arbustos se incrementó un 135%. Las distancias entre parches del chaparral se incrementaron un 285%, comparado con un incremento del 54% entre parches de arbustos generalistas. La muerte de árboles relacionados con el fuego en parches de arbustos fue marginalmente baja (67,6% versus 71,8%), mostrando un efecto contrastante de los arbustos en la mortalidad de árboles entre este ecosistema forestal y los ecosistemas dominados por vegetación de chaparral, en los cuales la mayoría de los árboles mueren por efectos del fuego.

Keywords: allometric equations, *Corylus cornuta* ssp. *californica*, Rim Fire, Smithsonian ForestGEO, Yosemite Forest Dynamics Plot

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INTRODUCTION

Shrubs constitute a small proportion of forest biomass, but their spatial arrangement can amplify local effects of fire on surrounding vegetation by propagating fire and increasing fire intensity (Collins and Stephens 2010). Through their ability to persist in a wide range of light and moisture regimes, and their fire-adapted life history traits such as vegetative reproduction (van Wagtendonk and Fites-Kaufman 2006), shrubs provide structural elements for invertebrate (Marra and Edmonds 2005) and vertebrate habitat (North *et al.* 2005, Fontaine *et al.* 2009), as well as food for birds and rodents (Smucker *et al.* 2005, Roberts *et al.* 2008, Fontaine *et al.* 2009, Fontaine and Kennedy 2012). In shrub-dominated chaparral systems, fire behavior is characterized by rapid and complete combustion of shrubs (e.g., Keeley 2000, 2006). Large, contiguous patches of montane chaparral are often mixed with forests in the Sierra Nevada, California, USA (Nagel and Taylor 2005, Lauvaux *et al.* 2016), and these patches can inhibit forest development through repeated high-severity burns (Lauvaux *et al.* 2016).

Fire effects in the shrub understory of closed-canopy forests remain poorly understood, especially where the area and continuity of montane chaparral species are constrained by light and nutrient limitations (Conard *et al.*

1985, Halpern and Lutz 2013, Lutz *et al.* 2014*b*). Although the aboveground portions of most shrub species in Sierra Nevada forests are killed in fire, they often regenerate asexually by sprouting from root crowns in the spring following fire. The immediate fire-induced reduction in aboveground portions of shrubs could facilitate tree seedling development through a reduction in competition (Oakley *et al.* 2006), and a concurrent reduction in shrub reproductive output during the time required for tree seedlings to gain sufficient stature. Sprouting shrubs do not generally flower in periods following wildfire, effectively reducing food resources for invertebrates and vertebrates. Therefore, post-wildfire landscapes could enhance tree recruitment and reduce the distribution and abundance of invertebrate and vertebrate species.

In the Sierra Nevada, shrub community composition and structure vary along a soil moisture gradient (North *et al.* 2005, Keeler-Wolf *et al.* 2012), with moister vegetation communities correlating positively with tree vigor and negatively with fire intensity (Van de Water and North 2011, Kane *et al.* 2015*b*). The distinct shrub communities of xeric areas could be positively correlated with higher severity fire and greater tree mortality. Shrubs, even in discontinuous patches in the forest understory, could exacerbate local fire effects by spreading fire through the understory (e.g., Weise *et al.* 2005) and heightening fire intensity (Collins and Stephens 2010). Shrub combustion is characterized by large and rapid release of heat that rises through tree canopies and damages leaves (Smith *et al.* 2016*b*). The long burning times for the woody stems of shrubs and their associated litter (Engber and Varner 2012) would be expected to contribute to cambial heating and higher levels of damage to low foliage, leading to higher mortality of trees near shrubs. In contrast, shrub communities associated with riparian areas might produce lower intensity fire and lower tree mortality. When conditions are conducive to fire, however, the severity of fire in riparian shrub communities could be higher due to greater fuel loads (e.g., Olson and Agee 2005, Van de Water and North 2011). Finally, although the aboveground portion of shrubs burns, some patches would likely remain unburned in isolated refugia (e.g., Hylander and Johnson 2010; Kolden *et al.* 2012, 2015), making the net effect of shrubs on tree mortality unclear.

Recognizing that distinct shrub communities arise depending on microenvironment (North *et al.* 2005, Lutz *et al.* 2014*b*), we investigated the relationship between fire-induced tree mortality and shrub communities characterizing xeric, moist, and intermediate environments. We hypothesized that more xeric shrub communities would burn at higher intensity, while riparian shrub communities would burn at lower intensity. We further hypothesized that post-fire tree mortality in drier upland areas characterized by montane chaparral species would be higher within shrub patches because shrub combustion produces considerable heat that could damage tree canopies (Weise *et al.* 2005, Collins and Stephens 2010, Smith *et al.* 2016*b*). We also hypothesized that riparian areas would have more vigorous trees that could resist fire, or less active fire behavior, resulting in lower post-fire tree mortality. We compared pre-fire and post-fire shrub maps of a closed-canopy forest and used species-specific allometric equations in combination with tree demographic data to explore the relationship between fire effects on the area of shrubs, shrub biomass, continuity of shrubs, and the contribution of shrubs to fire-induced tree mortality.

Here we introduce a new method, not to our knowledge used previously in fire ecology, but used extensively in studies of forest diversity and pattern (e.g., Anderson-Teixeira *et al.* 2015). Pre fire, we extensively mapped woody vegetation in the Yosemite Forest Dynamics Plot (YFDP), a single, large (800 m × 320 m; 25.6 ha) permanent plot. Previously, the largest fire-related study plots with the similar level of mapping extent and precision were the 4 ha plots at Teakettle Experimental Forest, about 150 km southwest of the YFDP in the Sierra Nevada (North *et al.* 2005).

METHODS

Ecological inference is inherently tied to the scale of investigation (e.g., Chisholm *et al.* 2013, Réjou-Méchain *et al.* 2014), and fire-mediated changes to spatial pattern are rarely examined. Although using a single contiguous area precludes within-fire replication, it allows an analysis of spatial patterns at inter-organismal distances of tens of meters (e.g., Lutz *et al.* 2012, 2014*a*; Larson *et al.* 2016). A single large plot extends research possibilities by enabling spatial analysis of fire effects that cannot be captured in smaller plots (i.e., because the scale of detection of spatial patterns is limited to one quarter of the minimum plot dimension; Wiegand and Moloney 2004). For example, distances between patches of vegetation, which may be important to vertebrate occupancy and dispersal, can only be determined from surveys of larger contiguous areas. The approach is philosophically different from the more traditional approach of sampling large numbers of smaller plots because the vegetation in the large plot is measured in its entirety (subject to minimum sizes) rather than sampled. As a consequence, more spatial information is available, but inferences to the larger landscape need to be carefully evaluated. This approach only provides insight into a single fire burning under a specific set of conditions. Nevertheless, results from single large plots can provide complementary data to studies using traditional methods (e.g., Condit 1995, Hubbell *et al.* 1999, Anderson-Teixeira *et al.* 2015, Lutz 2015).

Study Area

We conducted this study in the Yosemite Forest Dynamics Plot (YFDP), a 25.6 ha permanent plot in old-growth (oldest trees >500 yr) white fir–sugar pine (*Abies concolor–Pinus lambertiana*) mixed-conifer forest in Yosemite National Park located between 1774 m and 1911 m elevation (Keeler-Wolf *et al.* 2012; Lutz *et al.* 2012, 2013). The YFDP was established in the summers of 2009 and 2010, in vegetation characteristic of the white fir superassociation (Keeler-Wolf *et al.* 2012). Tree mapping methods followed those of the Smithsonian ForestGEO network (Condit 1998), and involved the establishment of a 20 m grid surveyed in place with professional grade total stations with grid points accurate to within ≤10 cm to the North American Datum of 1983 (see Lutz *et al.* 2012 for details). All trees were mapped with reference to the grid, identified and measured at DBH (diameter at breast height, 1.37 m). Shrub mapping methods followed North *et al.* (2005). In 2010, all patches of shrubs ≥2.0 m^2 and with ≥40 % cover were identified to species and individually mapped as polygons, with the vertices referenced to known locations within the YFDP (either trees or reference pins; methods adapted from North *et al.* 2005). The 2.0 m^2 sampling size for shrubs was selected to capture mature individuals or clumps of stems. For each shrub patch, we measured average height and maximum height. All trees were censused annually in 2011, 2012, and June 2013, two months before the plot was burned in a backfire ignited to control the spread of the Rim Fire, a large wildfire (Harris and Taylor 2015, Kane *et al.* 2015*a*). Pre-fire tree composition (n = 34 458) was primarily *Abies concolor* (Gordon & Glend.) Hildebrand (956 trees ha^{-1}) and *Pinus lambertiana* Douglas (185 trees ha^{-1}), with lower densities of incense-cedar (*Calocedrus decurrens* [Torrey] Florin), Pacific dogwood (*Cornus nuttallii* Audubon ex Torr. & A. Gray), and California black oak (*Quercus kelloggii* Newb.). Basal areas of *Abies* (29.28 m^2 ha^{-1}) and *Pinus* (28.75 m^2 ha^{-1}) were approximately equal. Canopy metrics were calculated from LiDAR data taken on 21 July 2010 by Watershed Sciences (now Quantum Spatial;

Kane *et al.* 2014). The pre-fire forest had canopy heights to 66.8 m, with a median canopy height of 19.3 m. Median canopy cover was 89 % at 30 m resolution. The 25th percentile canopy height ranged from 0 m to 53.1 m, with a median of 8.0 m. Nomenclature follows Flora of North America (Flora of North America Editorial Committee 1993+).

The YFDP was historically characterized by a fire return interval of 29.5 years (Barth *et al.* 2015), a return interval well within the range for this forest type (Van de Water and Safford 2011), perhaps because of its generally northerly aspect. Lightning-ignited fires have occurred since 1900, but fire has successfully been excluded from the YFDP since the last widespread fire event in 1899 (Scholl and Taylor 2010).

The YFDP burned in a backfire ignited at the Crane Flat lookout (Figure 1A), approximately 1 km distant, on 31 August 2013. Specific information about burning conditions was obtained from a Fire Behavior Assessment Team (FBAT) that placed four instrument packages, each containing a video camera and three thermocouples, in front of the advancing fire (Ewell *et al.* 2015; four videos of the fire behavior in the Yosemite Forest Dynamics Plot during the Rim Fire as captured by the USFS Fire Behavior Assessment Team [Ewell *et al.* 2015]: http://doi.org/10.15142/T3HP4D). Because of the requirement to ignite the backfire in the afternoon and in mixed forest–chaparral, burning conditions were less benign than most management ignitions (Kelly Martin, Chief of Fire and Aviation, Yosemite National Park, personal communication; Figure 1B through 1E), and the backfire was not managed subsequent to the initial ignition (Figure 1A). After ignition, the fire backed downslope to the north (Figure 1F) and triggered the first FBAT instrument package at 0139 hours on 1 September 2013 (Figure 1G; Ewell *et al.* 2015). Approximately half of the YFDP burned during the night of 1 September 2013 (Figure 1H), with the remainder burning during the morning of 2 September 2013 (Figure 1I), with the end of active consumption at about 1130 hours on 2 September 2013 (Ewell *et al.* 2015). The fire was active in the area of the YFDP for approximately 30 hours, and burned at moderate (Figure 1G) and low (Figure 1I) severities, lower than that of the plume-dominated portions of the Rim Fire proper (e.g., Harris and Taylor 2015, Kane *et al.* 2015*a*). At the four FBAT monitoring points, the fire ranged from a low intensity to a high intensity surface fire with some torching. The twelve thermocouples recorded maximum temperatures from 96 °C to 1105 °C (average 468 °C), with heat duration above 80 °C between 1 minute and 180 minutes (average 26 minutes; Ewell *et al.* 2015). Flame lengths ranged from 0.3 m to 3 m. Some smoldering of large woody debris continued until November. Subsequent to the fire, in May 2014, all trees were relocated (or their consumption was confirmed), and DBH remeasured. Shrub patches were remapped in May to July 2014 with the same field methods used pre fire.

Shrub Demography

A total of 24 slope-adjusted plots (2 m × 2 m) were established pre fire (2011) to track the demography of the 10 most abundant shrub species. The location of demography plots was selected after the establishment and initial tree mapping of the YFDP. When there were three demography plots for a given species, they were selected from high, medium, and low elevations within the YFDP, with representation in the eastern, middle, and western sections of the YFDP. When species were represented by two plots, they were selected from high and low elevations within the YFDP in the eastern and western sections of the YFDP. All plots for a given shrub species were separated by ≥83 m (average 328 m) to minimize potential pseudoreplication. Within the shrub demography plots, the diameter of each living and dead stem was measured at the base

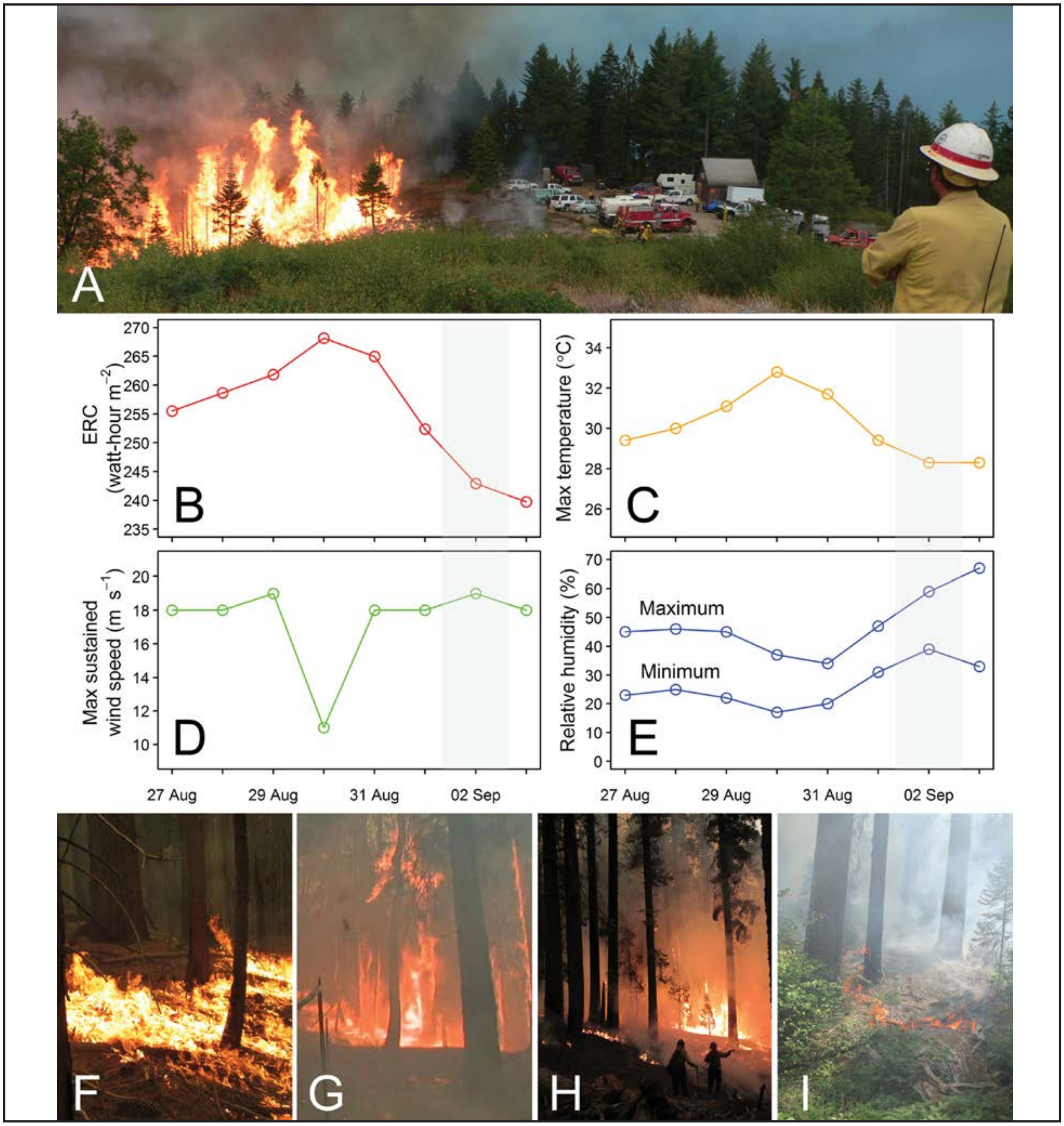

Figure 1. Burning conditions in the Yosemite Forest Dynamics Plot during the 2013 Rim Fire backfire. The backfire was ignited at the Crane Flat Lookout (A) during the afternoon of 1 September 2013, approximately 1 km from the plot. The energy release component (B), maximum temperature (C), maximum sustained wind speed (D), and relative humidity (E) during the period of fire activity were higher than typical for management ignitions. The shaded area (B through E) delineates the period of active burning. The fire backed downslope to the plot (F) and burned within the plot at moderate (G) to lower severities during the night of 1 September 2013 (H) and the morning of 2 September 2013 (I). Fire weather data from Ewell *et al.* (2015). Photo credits: Andrew "Boots" Davenport (A), Gus Smith (F, H, and I). Photo G is a video still from an FBAT camera, eight minutes after the video was triggered by thermocouple. (See four videos of the fire behavior in the Yosemite Forest Dynamics Plot during the Rim Fire as captured by the USFS Fire Behavior Assessment Team [Ewell *et al.* 2015]: http://doi.org/10.15142/T3HP4D).

(DBA), and, if the stem extended beyond 1.37 m, diameter was also measured at DBH. All branches of stems reaching 1.37 m in height were measured and tagged with stainless steel tags attached with stainless steel wire. Shrub demography patches were re-censused once pre fire in 2012, with new stems, stem growth, stem death, and stem breakage (for dead stems) recorded. Therefore, differences in pre-fire and post-fire biomass reflected fire effects but also growth that occurred since the 2012 census. Post fire, the shrub demography patches were revisited and the condition of each stem was determined (alive, killed but not by fire, killed by fire, killed and consumed by fire, previously dead and unaffected by fire, or previously dead and consumed by fire).

Shrub Biomass

We calculated biomass from allometric equations selected from the literature (Table 1) and from an equation for *Corylus cornuta* ssp. *californica* (A. de Candolle) E. Murray that we developed from 50 plants selected from within 100 m of the YFDP, using the field methods of Lutz *et al.* (2014*b*) and the lab methods of Williamson and Wiemann (2010). We fit biomass data to log-log (natural logarithms) curves of the form $\ln(biomass) = A + B \times \ln(DBA)$ using DBA (Kauffman and Martin 1990), and, if the stem was longer than 1.37 m, DBH as well, as predictors. We calculated the correction factor for bias related to log-log regressions. We fit both DBA and DBH to age. Analyses were performed with R version 3.3.1 (R Core Team 2016).

Shrub Guilds and Tree Mortality

We grouped the shrubs into three guilds: montane chaparral, riparian (or mesic), and generalist based on life history traits (McGinnis *et al.* 2010) and their distribution throughout the YFDP. We analyzed all shrubs as a group and each of the three guilds. The xeric montane chaparral guild included *Arctostaphylos patula* Greene, *Ceanothus cordulatus* Kellogg,

Table 1. Allometric equations used for computing shrub biomass in the Yosemite Forest Dynamics Plot, with all equations in the form $\ln(biomass) = A + B \times \ln(DBA)$, where DBA is basal diameter and ln is the natural logarithm. The number of shrub demography plots for each species (used to generate biomass figures from patch areas) is indicated by *n*.

Shrub species	*n*	Proxy species	A	B	Reference
Arctostaphylos patula	3	*A. columbiana*	3.3186	2.6846	Means *et al.* 1994
Ceanothus cordulatus	3	*C. velutinus*	3.6167	2.2043	Means *et al.* 1994
Ceanothus integerrimus	2		3.6672	2.65018	Means *et al.* 1994
Ceanothus parvifolius	2	*C. integerrimus*	3.6672	2.65018	Means *et al.* 1994
Chrysolepis sempervirens	3		3.888	2.311	Lutz *et al.* 2014*b*
Corylus cornuta ssp. *californica*	3		3.570	2.372	This study
Cornus sericea	3		3.315	2.647	Lutz *et al.* 2014*b*
Leucothoe davisiae	2		2.749	2.306	Lutz *et al.* 2014*b*
Rhododendron occidentale		*V. parvifolium*	3.761	2.37498	Means *et al.* 1994
Ribes nevadense		*V. parvifolium*	3.761	2.37498	Means *et al.* 1994
Ribes roezlii		0.5 × *V. parvifolium*	3.761	2.37498	Means *et al.* 1994
Rosa bridgesii		0.5 × *V. parvifolium*	3.761	2.37498	Means *et al.* 1994
Rubus parviflorus		*V. parvifolium*	3.761	2.37498	Means *et al.* 1994
Sambucus racemosa		*C. cornuta*	3.570	2.372	This study
Symphoricarpos mollis		0.5 × *V. parvifolium*	3.761	2.37498	Means *et al.* 1994
Vaccinium uliginosum	3	*V. parvifolium*	3.761	2.37498	Means *et al.* 1994

C. integerrimus Hook. & Arn., *C. parvifolius* (S. Watson) Trel., *Chrysolepis sempervirens* (Kellogg) Hjelmq., and *Ribes roezlii* Regel. Riparian shrubs included *Cornus sericea* L., *Leucothoe davisiae* Torrey ex A. Gray, *Rhododendron occidentale* (Torrey & A. Gray) A. Gray, *Sambucus racemosa* L., and *Vaccinium uliginosum* L., Generalist shrubs that were present in all landscape positions in the YFDP included *Corylus cornuta* ssp. *californica*, *Ribes nevadense* Kellogg, *Rosa bridgesii* Crépin ex Rydberg, *Rubus parviflorus* Nutt., and *Symphoricarpos mollis* Nutt. We divided the YFDP into areas with shrubs and areas without shrubs using ARC software (ESRI 2011). Areas with shrubs included the mapped shrub patches and a 1 m exterior buffer to account for lateral heating to trees from shrub combustion (hereafter, buffered shrub patches). Differences in tree mortality within buffered shrub patches and outside buffered shrub patches were examined for the five most common tree species (*Abies concolor, Pinus lambertiana, Calocedrus decurrens, Quercus kelloggii*, and *Cornus nuttallii*) and five tree diameter classes (1 cm to 10 cm, 10 cm to 30 cm, 30 cm to 60 cm, 60 cm to 90 cm, and >90 cm) using χ^2 tests ($\alpha = 0.05$). We used the null hypothesis of equal mortality rates applied to the trees actually present pre fire. We applied a Bonferroni correction (Zar 2007) for multiple tests (adjusted $\alpha = 0.005$). We also assessed whether the mortality rates of trees within shrub patches differed among the shrub guilds by conducting pairwise comparisons across guilds of within-patch mortality rates for all trees, for each tree species, and for each diameter class. Our previous work (i.e., Lutz *et al.* 2014*b*) showed that both pre-fire tree species composition and basal area differed within and outside shrub patches. Therefore, we used the null hypothesis of equal mortality rates applied to the trees actually present pre fire. We applied a Bonferroni correction for multiple tests (adjusted $\alpha = 0.0014$).

Changes to Shrub Area and Biomass

We used ARC software (ESRI 2011) to compare the change in area of shrub patches between the pre-fire and post-fire periods. We applied the allometric equations (Table 1) to the shrub stems present in the shrub demography patches to determine initial shrub biomass per unit area, and then used the changes in stem status in each of the census intervals to determine the change in live biomass and the biomass lost to fire per unit area, which we then scaled to plot-level biomass calculations using the areas of mapped shrub patches. To examine the change in spatial pattern of shrub patches, we calculated the pre-fire and post-fire mean patch size, patch density, and nearest neighbor statistics. Summary statistics of nearest neighbor distances were calculated for all patches, for the three shrub guilds, and for individual species.

RESULTS

Shrub Allometry

The relationship between DBA and total biomass of *Corylus cornuta* ssp. *californica* was strong ($R^2 = 0.96$, $P < 0.001$) and DBH almost as predictive ($R^2 = 0.89$, $P < 0.001$; Figure 2, Table 2). The diameter-age relationship was strong (DBA $R^2 = 0.79$; DBH $R^2 = 0.82$; both $P < 0.001$). See Lutz *et al.* 2017 for raw data.

Shrub Area and Biomass

Live shrub biomass in the YFDP decreased 92.3 % due to fire, while shrub area decreased 94.0 % (Figure 3, Table 3), declining from 38 640 m^2 (1509 m^2 ha^{-1}, 15.1 % of the YFDP) to 2314 m^2 (90 m^2 ha^{-1}, 0.9 % of the YFDP). The fire burned 87.4 % (1053 of 1204) of patches completely (Table 3), with unburned areas lying primarily in swales (Figure 3). Shrub area and biomass reductions varied

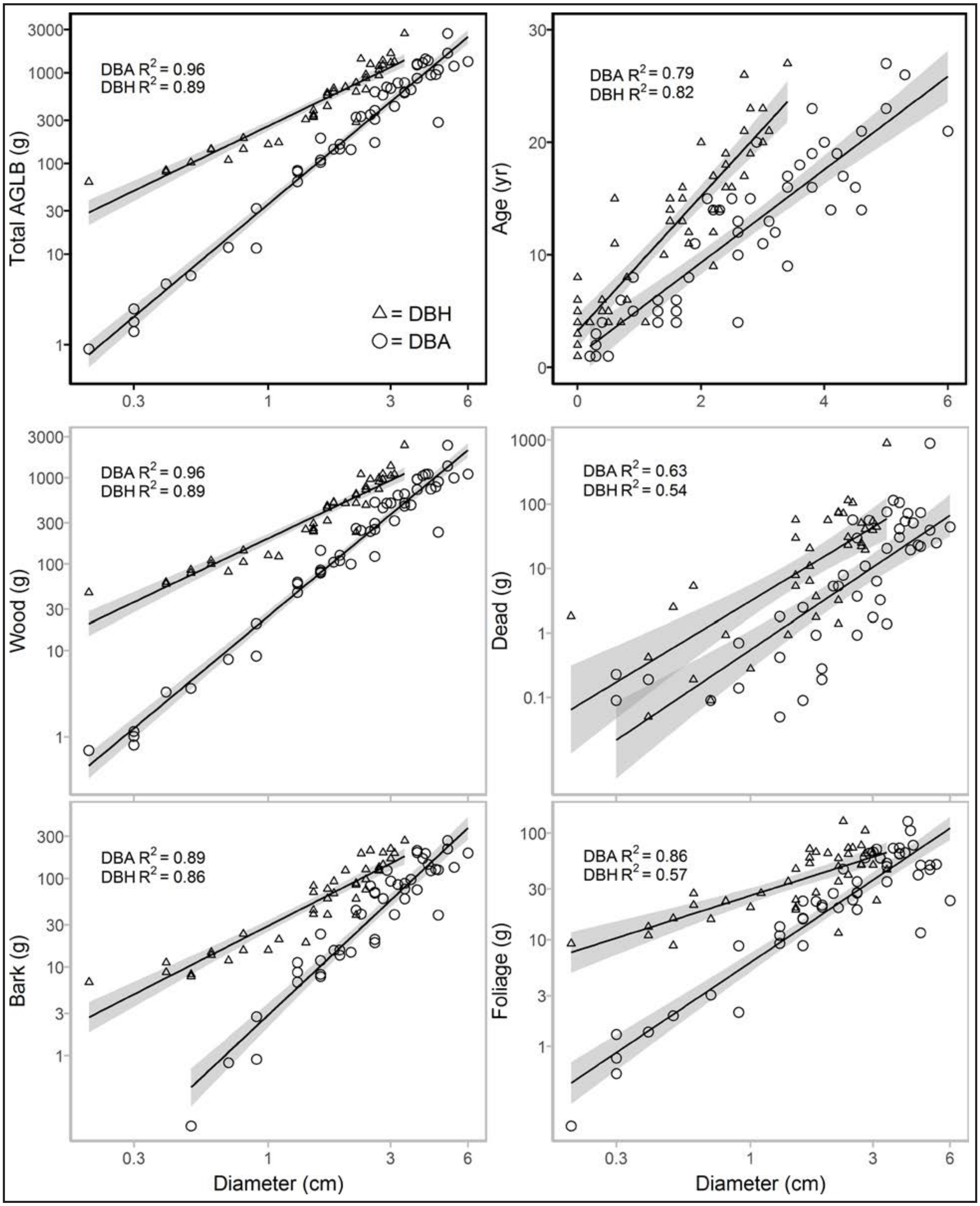

Figure 2. Allometry of *Corylus cornuta* ssp. *californica* based on dissection of 50 plants collected within 100 m of the Yosemite Forest Dynamics Plot. Shaded regions indicate 95% confidence intervals. Axis scaling differs among figure panels. The *y*-axis for biomass graphs is logarithmic. The diameter-age relationship is linear. DBA = basal diameter (circular symbols); DBH = diameter at breast height (triangular symbols).

Table 2. Regression coefficients for biomass of foliage, bark, living wood, dead wood, and total aboveground live biomass (AGLB) for *Corylus cornuta* ssp. *californica* in the form ln(*biomass*) = *A* + *B* × ln(*diameter*), where ln is the natural logarithm, and *diameter* is either basal diameter (DBA) or diameter at breast height (DBH) in cm. SEE = standard error of the regression in arithmetic units. CF = correction factor for A (see Methods). Regression coefficients for age are linear; *Age* = *A* + *B* × (*diameter*). All relationships $P < 0.001$.

	Basal diameter (DBA)						**Diameter at breast height (DBH)**					
	A	**B**	**R^2**	**SEE**	**CF**	***n***	**A**	**B**	**R^2**	**SEE**	**CF**	***n***
Foliage	1.818	1.617	0.865	0.5428	1.159	50	3.259	0.761	0.575	0.4483	1.106	41
Bark	1.057	2.717	0.891	0.5392	1.156	45	3.377	1.478	0.865	0.4034	1.085	41
Wood	3.215	2.476	0.965	0.4028	1.085	50	5.293	1.411	0.891	0.3408	1.060	41
Dead	–0.600	2.685	0.629	1.5101	3.127	44	1.141	2.407	0.542	1.5001	3.081	38
Total AGLB	3.570	2.372	0.964	0.3901	1.079	50	5.555	1.364	0.894	0.3247	1.054	41
Age	1.039	4.138	0.786	3.2674		49	3.229	5.994	0.816	3.0329		49

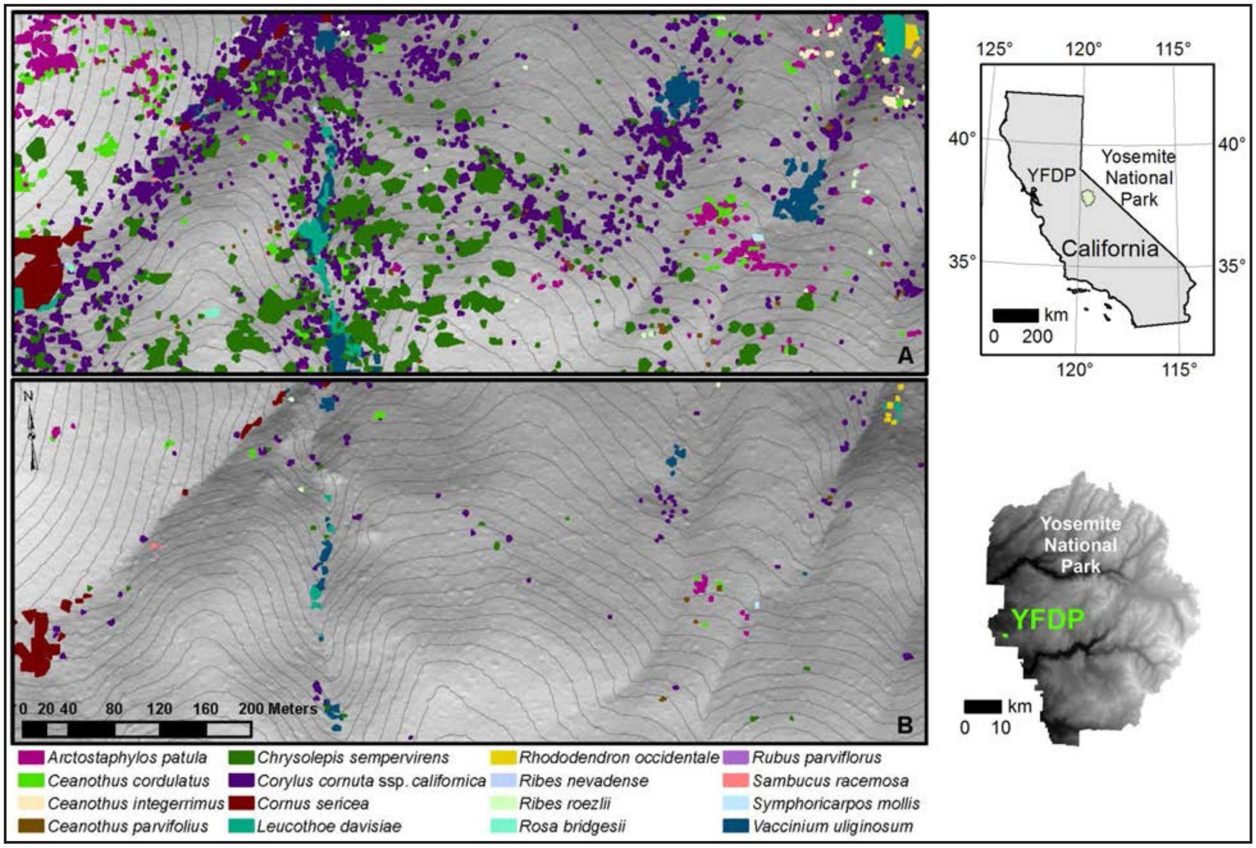

Figure 3. Shrub patches by species in the Yosemite Forest Dynamics Plot for continuous patches of shrubs ≥2.0 m². Shrub area before the backfire (mapped in July 2010; A) was 38 640 m² (15.1% of the 25.6 ha). Shrub area after the backfire (mapped in July 2014; B) was 2314 m² (0.9% of the 25.6 ha).

Table 3. Fire effects on shrub patches within the Yosemite Forest Dynamics Plot (25.6 ha). Pre-fire aboveground live biomass (AGLB) for each species was higher than standing dead biomass except for *A. patula* and *C. integerrimus*. Totals reflect live and dead stems that were burned across all habitat types. Total pre-fire fuel loading of the shrub strata (live and dead) was 6447 kg ha^{-1}. All shrub stems that were dead pre fire were consumed. t = trace (<1 kg ha^{-1}).

	Pre fire		**Post fire**		**Fire effects (kg ha^{-1})**			
Shrub species	**Area (m^2)**	**AGLB (kg ha^{-1})**	**Area (m^2)**	**AGLB (kg ha^{-1})**	**Killed only**	**Killed-consumed**	**Dead-consumed**	**Total consumed**
Montane chaparral								
Arctostaphylos patula	2 524	469	111	16	90	296	1 865	2 161
Ceanothus cordulatus	1 222	84	58	4	9	66	30	96
Ceanothus integerrimus	194	67	0	0	20	61	280	341
Ceanothus parvifolius	187	20	25	3	8	2	t	3
Chrysolepis sempervirens	12 998	1 006	73	6	669	707	173	879
Ribes roezlii	66	2	9	t	t	1	t	1
Total montane chaparral	17 191	1 648	276	29	796	1 133	2 348	3 481
Generalist								
Corylus cornuta ssp. *californica*	13 224	406	407	12	234	76	4	81
Ribes nevadense	7	1	0	0	t	t	t	t
Rosa bridgesii	58	2	0	0	t	1	t	1
Rubus parviflorus	8	1	0	0	t	t	t	t
Symphoricarpos mollis	29	1	6	t	t	t	t	t
Total generalist	13 326	411	413	12	234	77	4	82
Riparian								
Cornus sericea	2 320	309	1 114	147	101	8	24	31
Leucothoe davisiae	2 151	850	134	53	17	772	8	780
Rhododendron occidentale	687	51	36	3	7	13	1	13
Sambucus racemosa	13	t	6	t	t	t	t	t
Vaccinium uliginosum	2 952	221	335	25	29	51	3	54
Total riparian	8 123	1 431	1 625	228	154	844	36	878
Total	38 640	3 490	2 314	269	1 184	2 054	2 388	4 441

among guilds, with montane chaparral species showing the greatest decreases, led by *Chrysolepis sempervirens*, which declined in area by 99.4 %. Riparian shrubs were least affected by fire, primarily due to patches of *Cornus sericea* that remained protected in moist swales, which led that species to exhibit the smallest proportional decline in area (52.0 %). Counter to these trends, some completely unburned shrub patches remained in all landscape positions (Figure 3). Although the aboveground area in shrubs and live biomass decreased, a large proportion of shrubs was observed to be sprouting in 2014. However, growth of sprouts was slow, with no new shrub sprouts reaching the minimum mapping size in the immediate post-fire sampling year 2014 (nor did any sprouts reach the minimum mapping size in 2015, with only some sprouts reaching the minimum size in 2016). Shrub species that develop from seed banks post fire (e.g., Knapp *et al.* 2012) also had not met the minimum sampling size in 2016.

Distinct (non-overlapping) shrub patches decreased from 47 ha^{-1} to 6 ha^{-1}. Of the shrub patches that remained post fire, mean patch size decreased from 31 m^2 to 15 m^2, but the reduction in patch size was different among species (Figure 4). The post-fire shrub patch density was 3 ha^{-1} for *Corylus cornuta* ssp. *californica* and 1 ha^{-1} for *Chrysolepis sempervirens*, *Cornus sericea*, and *Vaccinium uligi-*

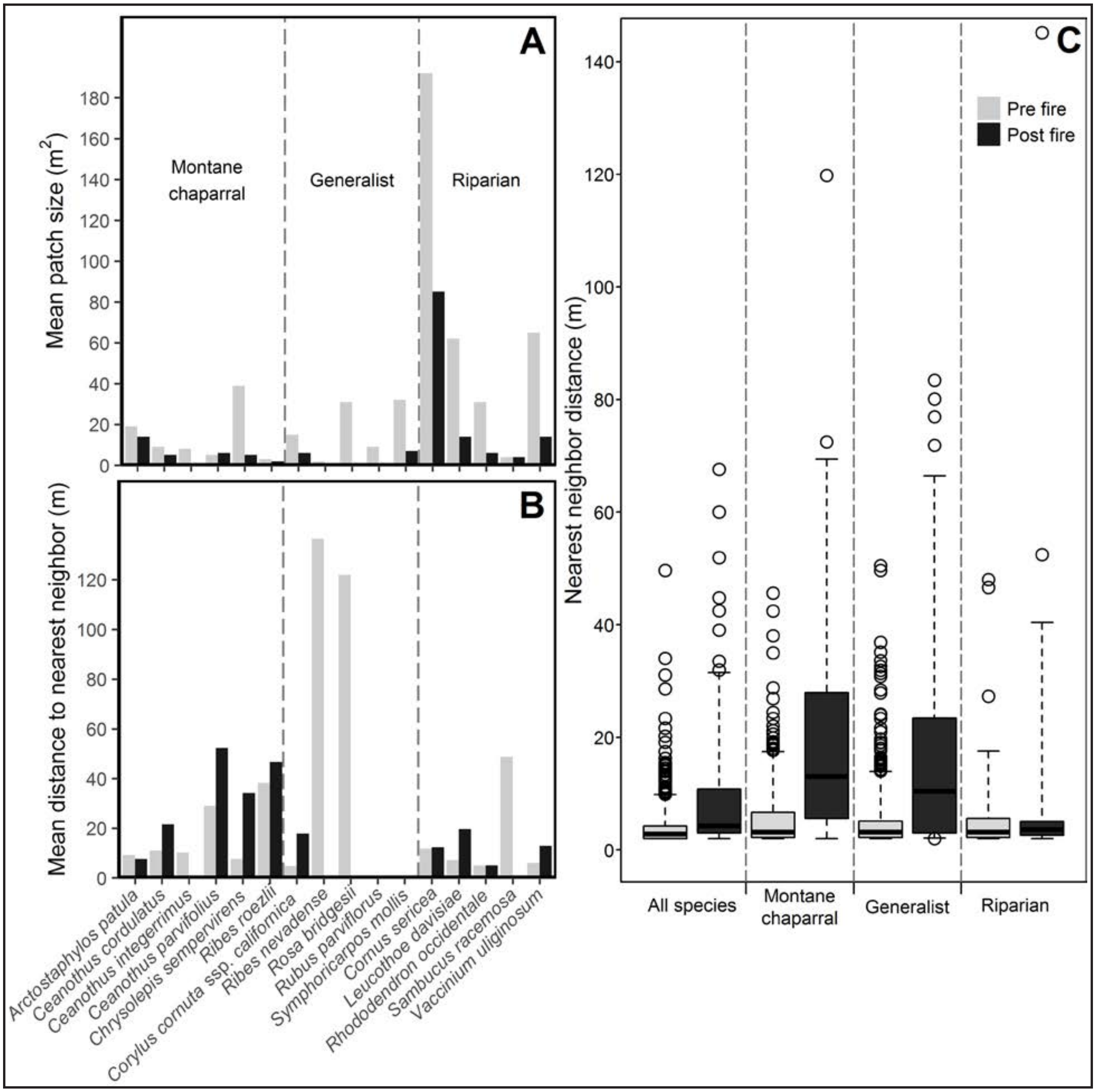

Figure 4. Mean patch size (A) and mean nearest-neighbor distances (B) before (gray) and after (black) reintroduced fire in the Yosemite Forest Dynamics Plot for individual shrub species and for montane chaparral, generalist, and riparian guilds as well as all shrubs combined (C). Species constituents of shrub guilds are grouped between dashed vertical lines.

nosum—all other species had a post-fire patch density <1 ha^{-1}. The mean distance between shrub patches of any kind increased 135 % (from 3.9 m to 9.2 m), but again the results varied by guild and species (Figure 4). Mean distances between montane chaparral patches increased 285 % (from 5.6 m to 21.7 m); between generalist shrub patches 267 % (from 4.9 m to 17.9 m); and between riparian shrub patches 54 % (from 6.1 m to 9.4 m). Among individual species, the conspecific nearest neighbor distance increased the most for *Chrysolepis* (from 7.7 m to 46.1 m), followed by *Vaccinium* (from 6.1 m to 25.3 m) and *Co-*

rylus (from 4.8 m to 17.6 m). Some species changed little, but for different reasons. Conspecific nearest neighbor distances increased 6 % for *Cornus*, primarily because fire did not advance into the interior of these very mesic patches. The nearest-neighbor distance for *Arctostaphylos* stayed approximately the same. The consumption of *Arctostaphylos* patches, which would have increased nearest-neighbor distance, was balanced by the fragmentation of partially burned patches, which created separate patches that were close together.

Shrub-Mediated Tree Mortality

Buffered shrub patches covered 64 532 m^2 (25.2 % of the YFDP, compared to their actual area of 15.1 % of the YFDP). Buffered shrub patches of montane chaparral covered 30 330 m^2, buffered riparian shrub patches covered 9667 m^2, and buffered generalist shrub patches covered 29 126 m^2. Trees as a whole had lower mortality rates within buffered shrub patches than outside buffered shrub patches (67.6 % versus 71.8 %, $P < 0.001$; Table 4). The tree mortality rate was higher in montane chaparral (72.7 %), but lower in generalist (63.7 %) and riparian (61.6 %) shrub patches compared to areas outside shrub patches (71.8 %, all $P < 0.001$; Table 5). Pairwise comparisons of tree mortality rates within shrub patches of different guilds showed successive decreases in tree mortality rate from the montane chaparral to the generalist, and finally the riparian guild ($P < 0.001$; Table 5).

When considered by tree species alone, *Cornus nuttallii* ($P < 0.001$) was the only species with significantly lower mortality inside shrub patches of any guild relative to areas outside shrub patches (Table 4). Interactions between shrub guild and tree species were evident: mortality rates for *Abies concolor* ($P < 0.001$) and *Cornus nuttallii* ($P = 0.001$) were lower in riparian shrub patches compared to outside shrub patches (Table 5). In generalist

Table 4. Mortality rates for trees ≥1 cm DBH within and outside buffered shrub patches between the pre-fire year (2013) and the immediate post-fire year (May 2014) in the Yosemite Forest Dynamics Plot. Buffered shrub patches composed the actual area of shrubs plus a buffer of 1.0 m and totaled 64 532 m^2 (25.2 % of the YFDP). Significantly different tree mortality rates within and outside buffered shrub patches are shown in bold (χ^2 test; $\alpha = 0.005$).

		Pre-fire trees (*n*)			**Mortality rates (%)**		
	Overall abundance	**Outside shrub patches**	**Within shrub patches**	**Percent within**	**All trees**	**Outside shrub patches**	**Within shrub patches**
By species							
Abies concolor	23 991	19 938	4 053	16.9	72.5	73.0	70.2
Pinus lambertiana	4 617	3 706	911	19.7	63.8	64.7	60.0
Cornus nuttallii	2 704	1 725	979	36.2	76.4	**81.2**	**67.9**
Calocedrus decurrens	1 635	1 270	365	22.3	63.9	66.4	55.1
Quercus kelloggii	1 110	875	235	21.2	63.0	63.9	59.6
Other species	178	54	124	69.7	85.4	83.3	86.3
By diameter class							
DBH ≤1 cm to <10 cm	21 217	16 700	4 517	21.3	90.4	**92.2**	**83.9**
DBH ≤10 cm to <30 cm	9 414	7 954	1 460	15.5	50.9	**51.9**	**45.4**
DBH ≤30 cm to <60 cm	2 292	1 937	355	15.5	11.5	11.6	11.0
DBH ≤60 cm to <90 cm	691	546	145	21.0	3.6	3.3	4.8
DBH ≥90 cm	621	431	190	30.6	4.0	3.7	4.7
Total	34 235	27 568	6 667	19.5	71.0	**71.8**	**67.6**

Table 5. Mortality rates for trees within buffered shrub patches of montane chaparral, generalist, and riparian guilds from the pre-fire year (2013) and the immediate post-fire year (May 2014) in the Yosemite Forest Dynamics Plot. Tree mortality rates within buffered shrub patches that differed significantly from mortality rates outside buffered shrub patches are shown in bold (χ^2 test; $\alpha = 0.005$). All significantly different mortality rates were lower within shrub patches than outside. Significant results from pairwise comparisons of tree mortality rates within buffered shrub patches of different guilds are delineated by superscripts (χ^2 test; $\alpha = 0.0014$). Density outside shrub patches was 893.6 trees ha^{-1} for trees ≤1 cm DBH to <10 cm DBH and 1475.2 trees ha^{-1} for all trees.

	Montane chaparral		**Generalist**		**Riparian**	
	Pre-fire trees (*n*)	**Mortality rate (%)**	**Pre-fire trees (*n*)**	**Mortality rate (%)**	**Pre-fire trees (*n*)**	**Mortality rate (%)**
By species						
Abies concolor	2371	[a] 75.2	1679	[b] **65.8**	227	[c] **48.9**
Pinus lambertiana	472	63.6	441	57.6	61	41.0
Cornus nuttallii	89	67.4	342	**69.6**	648	**68.4**
Calocedrus decurrens	110	61.8	178	48.9	105	59.0
Quercus kelloggii	150	59.3	99	63.6	1	0.0
Other species	91	94.5	23	56.5	14	64.3
By diameter class						
DBH ≤1 cm to <10 cm	2288	[a] 88.2	1734	[a] **83.0**	801	[b] **72.5**
DBH ≤10 cm to <30 cm	695	49.5	688	**42.6**	153	41.2
DBH ≤30 cm to <60 cm	145	11.7	185	10.3	50	8.0
DBH ≤60 cm to <90 cm	56	3.6	74	5.4	27	3.7
DBH ≥90 cm	99	4.0	81	4.9	25	4.0
Total	3283	[a] 72.7	2762	[b] **63.7**	1056	[c] **61.6**
Density (trees ha^{-1})						
DBH ≤1 cm to <10 cm	754.4		595.3		828.6	
Total	1082.4		948.3		1092.4	

shrub patches, mortality was lower for *Abies concolor* ($P = 0.001$), but only marginally lower (when considered against the adjusted $\alpha = 0.005$) for *Cornus nuttallii* ($P = 0.007$) and *Calocedrus decurrens* ($P = 0.006$) relative to outside shrub patches. Individual tree species mortality rates within montane chaparral did not differ from tree species mortality rates outside shrub patches, and mortality rates of *Pinus lambertiana* and *Quercus kelloggii* exhibited no significant differences in any shrub vegetation type. *Abies concolor* was the only species that showed significant differences among mortality rates associated with different shrub guilds; paralleling the results for all trees combined, *A. concolor* mortality was highest in montane chaparral, lower in generalist, and lowest in riparian patches (all $P < 0.001$; Table 5).

When considered by diameter class, the mortality rate for trees ≥1 cm DBH to <10 cm DBH was lower inside buffered generalist ($P < 0.001$) and riparian ($P < 0.001$) shrub patches and marginally lower within patches of montane chaparral ($P = 0.008$) compared to outside buffered shrub patches (Table 5). Mortality rates for trees ≥10 cm DBH to < 30 cm DBH were lower in buffered generalist shrub patches ($P = 0.001$). No other diameter classes showed significant differences between areas within and outside buffered shrub patches for any shrub guild. Trees ≥1 cm DBH to <10 cm DBH were the only diameter class with significant differences in mortality rates associated with different shrub guilds; mortality was significantly higher in montane chaparral and generalist patches relative to riparian patches (both $P < 0.001$; Table 5).

DISCUSSION

Shrub Area and Communities

The area covered by shrubs and spatial patterns of shrubs varied by species and landscape position (Figures 3 and 4). These data show that shrubs are widespread in this closed-canopy, fire-suppressed forest, despite the resource limitations imposed on shrubs by high densities of trees (Table 5; Conard *et al.* 1985, Halpern and Lutz 2013). Before the Rim Fire, 15.1% of the forest floor in the YFDP was covered by shrub patches ≥2 m^2, which, upon ignition, could have acted as potential mortality agents for 25.2% of the area (Table 3). This value is comparable to mean shrub area (14.7%) in the Teakettle Experimental Forest, which, when established, had not burned since 1865 (North *et al.* 2005). The Teakettle Experimental Forest is drier and has lower biomass than the YFDP (North *et al.* 2005, Lutz *et al.* 2012). However, pre-fire shrub area in the YFDP was higher than the 2.5% reported in a harvested mixed-conifer stand in the 100 m distant Stanislaus National Forest, where fire had been excluded for 78 years (Knapp *et al.* 2013). Changes in shrubs during the period of fire exclusion likely are dependent on the initial shrub guilds present. Much of the 1929 cover reported by Knapp *et al.* (2013: Table 5) was shade intolerant *Arctostaphylos* and *Ceanothus*, which were not major constituents of the YFDP shrub community in 2013, likely at least partially because of the increased shading by small-diameter trees. The Knapp *et al.* (2013) data for *Chrysolepis* in 1929 and 2008 were consistent with the persistence of this species in the YFDP during the period of fire exclusion. Based on the Knapp *et al.* (2013) results, we expect that the post-fire shrub community in the YFDP will develop with greater areas of *Arctostaphylos* and *Ceanothus* in the post-fire period. The change in shrubs from pre fire to post fire reduced both the quantity (Table 3) and continuity (Figure 4) of fuels. The increasing distances between conspecific shrub patches (Figure 4) could have implications for pollination and herbivory.

Shrubs are expected to recruit continuously after fire, but eventually decline as trees overtop and shade out lower statured plants (Nagel and Taylor 2005, Halpern and Lutz 2013, Lauvaux *et al.* 2016). In the YFDP, fire was most recently excluded for three to four times the 29.5 yr fire return interval estimated for the period prior to fire suppression that started *circa* 1900 (van Wagtendonk 2007, Barth *et al.* 2015). Although we were unable to describe change in shrub area over the period of fire exclusion, we can infer that relative abundance of species may have changed, likely in a manner consistent with the nearby Stanislaus National Forest (Knapp *et al.* 2013). Shade intolerant *Arctostaphylos* and *Ceanothus* species had low abundance relative to the more shade tolerant *Chrysolepis* and *Corylus* species, suggesting that, while shrubs remained an important component of the forest understory, the dominant species may change with time since fire (Conard *et al.* 1985, Halpern 1988, Halpern and Lutz 2013, Knapp *et al.* 2013). Shrub species occupied unique environmental niches (Figure 3; North *et al.* 2005), supporting our categorization of shrubs into montane chaparral, generalist, and riparian guilds.

Fire Effects on Shrubs

Within the YFDP, all components of the pre-fire fuelbed, including some shrub species, likely exhibited high fuel loading (also see van Wagtendonk *et al.* 1998, Gabrielson *et al.* 2013, Banwell and Varner 2014), a typical condition for fire-suppressed forests in the Sierra Nevada (Lauvaux *et al.* 2016), although fire-suppressed forests can also exhibit low shrub abundances (Knapp *et al.* 2013). Unsurprisingly, fire reintroduction considerably reduced shrub biomass, area, and continuity of the shrub layer (Figure 4, Table 3). Shrub biomass and area decreased by 92.3 % and 94.0 %, respectively, but these effects varied among shrub guilds, with montane chaparral exhibiting the greatest proportional reductions (98.2 % and 98.4 %, respectively), and riparian shrubs the smallest (84.1 % and 80.0 %, respectively). Shrub continuity also decreased as shown by the increase in nearest neighbor distances (Figure 4). Importantly, however, fire effects varied independently of shrub community type and topography, evidenced by some shrub patches persisting in all guilds and landscape positions (Figure 3, Table 3). The large reductions in shrub biomass, area, and continuity that we observed constitute an immediate loss of habitat for organisms that rely on those structures and may be displaced to smaller refugia (Marra and Edmonds 2005; Fontaine *et al.* 2009; Kolden *et al.* 2012, 2015). However, because of the heterogeneous nature of Sierra Nevada forests, the fire exclusion period only appears to have reduced the abundance of shade intolerant species, and reintroduced fire, at least of low and moderate severity, does not extirpate species, with shrub patches persisting in small unburned areas or resprouting (Collins *et al.* 2011, Taylor *et al.* 2014). Seed banking species were not measured in the immediate post-fire environment (e.g., Knapp *et al.* 2012).

Shrub-Mediated Tree Mortality

In montane ecosystems, large patches of chaparral have been associated with high-severity fire, increased tree mortality, and perpetuation of montane chaparral shrub species (Nagel and Taylor 2005, Collins and Stephens 2010, Lauvaux *et al.* 2016) and a fire regime with high risks to ecological and social values (Smith *et al.* 2016*a*). Post-fire increase in shrubs after high-severity fire has been hypothesized as a mechanism by which high-severity fire begets high-severity fire (van Wagtendonk *et al.* 2012, Parks *et al.* 2014, Kane *et al.* 2015). These same chaparral species, however, did not lead to high-severity fire in the YFDP. Despite massive reductions in shrub area and biomass, tree mortality rates were actually lower within shrub patches than in the surrounding forest (67.6 % versus 71.8 %). Contrary to our hypothesis, tree mortality in montane chaparral (72.8 %), at least for this set of burning conditions, was not significantly higher than mortality outside shrub patches (71.8 %), although tree mortality within montane chaparral patches was higher than within other shrub cover types. This could indicate that damage to tree canopies by the combustion of shrubs in drier, upland environments may not be the dominant contributor to tree mortality when shrubs are present, perhaps because many tree canopies are high above the ground. One explanation could be that the fuel loading of shrubs in fire-excluded forests is not an important constituent of the total fuel bed, and that surface fuels play the dominant role in tree mortality (Larson *et al.* 2016). Alternatively, the high density and clumping of trees ≥1 cm DBH to < 10 cm DBH outside shrub patches may be inflating the mortality rates in those areas. Density of trees ≥1 cm DBH to < 10 cm DBH outside shrubs patches was higher (894 trees ha^{-1}) compared to inside them (754 trees ha^{-1}), supporting this alternative explanation (Table 5). Therefore, in long-unburned old-growth *Abies concolor–Pinus lambertiana* mixed-conifer forest, existing shrub patches may not initiate the same positive feedback with high-severity fire that has been observed in mixed-conifer forests located at less productive higher elevations sites (e.g., the Illilouette Basin, Yosemite National Park, California, USA; Collins and Stephens 2010). Alternatively, a second fire may be required to cause such positive feedbacks—one that burns montane chaparral-dominated communities that develop in patches that burned at high severity in the first fire (e.g., van Wagtendonk *et al.* 2012).

The equivocal nature of tree mortality in shrub patches may be due to the relatively small proportion of total fuel provided by shrubs. The surface fuel loading in the YFDP was 334.8 Mg ha^{-1} (influenced by the abundance of 1000-hour fuels and larger), with litter and duff 252.7 Mg ha^{-1} (litter 63.9 Mg ha^{-1}, duff 188.8 Mg ha^{-1}; Larson *et al.* 2016), compared to the shrub fuel loading of 5.8 Mg ha^{-1}. Consumption of surface fuels, litter, and duff in the YFDP was ~95 % (Larson *et al.* 2016). The YFDP fuel loadings were similar to those reported in other fire suppressed forests. In the Suwanee prescribed fire unit in Sequoia National Park, California, surface fuel was 50.65 Mg ha^{-1} with litter and duff 179.66 Mg ha^{-1} (Stephens and Finney 2002). At Blodgett Forest in the north-central Sierra Nevada, surface fuel loading was 36.0 Mg ha^{-1}, with litter and duff 119.0 Mg ha^{-1} (Hille and Stephens 2005). Consumption of fuels in all three cases was approximately 90 %. Initially, we had hypothesized that the high level of shrub cover might have provided ladder fuels that would contribute to foliar and cambial damage to trees, but the tree mortality results suggest that fuel strata other than shrubs drive fire effects in this system.

Caveats

It is difficult to replicate the effects from a wildfire under most prescribed fire conditions, posing a challenge to studies seeking to characterize the effects of wildfire. Replicated study designs require control of the timing and severity of fire, which is nearly unattainable given the variable nature of wildfire (e.g., see four videos of the fire behavior in the Yosemite Forest Dynamics Plot during the Rim Fire as captured by the USFS Fire Behavior Assessment Team [Ewell *et al.* 2015]: http://doi.org/10.15142/T3HP4D). Therefore, this study is an unreplicated one and subject to the attendant limitations (e.g., Barley and Meeuwig 2016). These results, although showing for the first time some spatial attributes of shrub patches within fire and their consequences for tree mortality, need to be verified by more study. Granted, this is the largest plot in which such fine-scale fire effects have been investigated, but it remains a single plot. These results show that shrub patch size (Figure 4A) and inter-patch distances (Figure 4B and 3C) could be corroborated (although not to the full extent) by spatially explicit plots of 1 ha (e.g., Das *et al.* 2016) to 4 ha (e.g., North *et al.* 2005).

CONCLUSION

Shrubs are an important areal component of the forest understory and contribute disproportionately to woody plant diversity in the Sierra Nevada. Their abundance and spatial pattern are highly sensitive to fire reintroduction, but may mediate fire effects on trees in drier, upland environments. This is in contrast with the effects of fire on tree mortality in shrub-dominated vegetation types (Nagel and Taylor 2005). The ability of shrubs in the Sierra Nevada to resprout and grow rapidly after fire (e.g., Cocking *et al.* 2014) warrants a better understanding of their ecology before and after fire. Moreover, the highly stochastic nature of shrub patch survival, both across landscape positions (Figure 4B and 3C) and within individual patches, reinforces the need for large, spatially explicit research plots to complement traditional multi-plot studies and to quantify the effects of pattern on post-fire vegetation development.

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