

ARTICLE

Recurring wildfires provoke type conversion in dry western forests

Deborah G. Nemens^{1,2}  | Kathryn R. Kidd³ | J. Morgan Varner⁴  | Brian Wing^{5†}¹School of Environmental and Forest Sciences, University of Washington, Seattle, Washington, USA²Pacific Wildland Fire Sciences Laboratory, USDA Forest Service Pacific Northwest Research Station, Seattle, Washington, USA³Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, Nacogdoches, Texas, USA⁴Tall Timbers Research Station, Tallahassee, Florida, USA⁵USDA Forest Service Pacific Southwest Research Station, Redding, California, USA

Correspondence

Deborah G. Nemens
Email: dnemens@uw.edu

Funding information

U.S. Forest Service, Grant/Award Number: National Fire Plan; USDA Forest Service, Grant/Award Number: 15-JV-11272139-027; USDA Forest Service, Grant/Award Number: 19-JV-11261987-139

Handling Editor: Carrie Levine

Abstract

Recent wildfires across western North America have burned with uncharacteristically high severity, representing a substantial departure from natural fire regimes. In mixed-conifer and pine-oak ecosystems of the southern Cascade Range, widespread shifts in stand structure and composition have led to a diversity of post-wildfire vegetation responses. When recent wildfire “footprints” reburn in subsequent fires, their recovery pathways are complex. In order to understand the effects of overlapping mixed-severity fires, we quantified changes in overstory and midstory structure and species composition for time periods prior to and following two large overlapping wildfires in the southern Cascades: the 2000 Storrie and 2012 Chips Fires. Plots were stratified into 16 severity combinations (unburned, low, moderate, and high in the Storrie Fire combined with the same four categories in the Chips Fire: e.g., moderate Storrie/high Chips) across the 9000-ha overlapping burned area. Following the two fires, tree quadratic mean diameter and stand density declined for most species, but changes were species-specific. Compared with preburn values, importance values for fire-sensitive white fir (*Abies concolor*) were reduced by 66%, while resprouting fire-resilient California black oak (*Quercus kelloggii*) importance values increased by 37% in severity combinations that included at least one high-severity fire. Greatest shifts were documented in sites that burned twice at high severity, where resulting vegetation was dominated by oak sprout clumps and resprouting and fire-stimulated montane chaparral species, while unburned and low-severity strata retained a substantial component of Douglas-fir (*Pseudotsuga menziesii*) and white fir. Results suggest that repeated moderate- and high-severity fires can result in ecosystem state shifting toward fire-resilient oak-shrub communities in this fire-prone landscape. Managers seeking greater landscape resilience can implement treatments such as thinning and prescribed burning, while taking advantage of fire-created patches such as these in areas where the likelihood of a

† Deceased

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

hotter and drier future makes the reestablishment of continuous forest cover unrealistic.

KEYWORDS

alternative stable states, Cascade Range, fire regime, positive feedback, *Quercus kelloggii*, reburn, resprouting

INTRODUCTION

Disturbance regimes play a major role in determining ecosystem composition and structure worldwide. When severe, these perturbations have the ability to alter the distribution of plants and animals on the landscape (Kane et al., 2017; Staver et al., 2011). Both frequent, low-severity and infrequent, high-severity disturbances are key ecosystem processes, maintaining the structure and composition of many ecosystems worldwide (Agee, 1993; Foster et al., 1998; Turner & Romme, 1994). Frequent, low-severity fire was particularly prevalent in the landscapes of the past, where it promoted fire-tolerant species and prevented the accumulation of fuels that could increase the intensity (and often severity) of future fires (Agee, 1993; Agee & Skinner, 2005; Hessburg et al., 2005; Taylor, 2000). When anthropogenic activity removes key ecological processes such as low-severity fire, subsequent changes in vegetation can have long-lasting ecological consequences (Agee, 1993; Hessburg et al., 2005).

Prior to Euro-American settlement, many fire regimes in western North America were self-limiting, as ingrowth and fuel accumulation were limited by frequent natural and anthropogenic fire. More than a century of timber harvesting, grazing, and fire exclusion have led to drastic alterations in forest composition and structure (Hagmann et al., 2021; Hessburg et al., 2019). The aggregate effect is the accumulation of fuels and the proliferation of dense, homogenous vegetation, with considerable ingrowth of shade-tolerant and often fire-intolerant species in many western forests (Hessburg et al., 2005; Parsons & DeBenedetti, 1979; Scholl & Taylor, 2010). Conditions in these uncharacteristically fuel-rich forests can transform wildfires that would formerly have had subtle impacts into severe disturbances, resulting in the increased incidence of catastrophic wildfires and shifting fire regimes (Agee & Skinner, 2005; Mallek et al., 2013; Miller, Safford, et al., 2009; Skinner & Chang, 1996).

This departure from past fire regimes can have severe consequences for ecosystems and their future trajectories. Following a stand-replacing wildfire, fire-adapted species are able to exploit the postfire environment by quickly recovering and/or recolonizing, while others often exhibit poor or failed regeneration (Keeley, 1991; Stevens

et al., 2019). Particularly where stand-replacing patches are large, forests composed of seed-obligate conifer species can fail to reestablish (Donato et al., 2009; Welch et al., 2016). Even conifers that are able to regenerate despite adverse climatic conditions are impeded in large patches which have burned at high severity (Harris & Taylor, 2020). These species are vulnerable to being replaced by shrubs, which benefit from fire adaptations such as resprouting and fire-stimulated germination (Cocking et al., 2014; Donato et al., 2009; Keeley, 1991; Odion et al., 2010; Welch et al., 2016). This can lead to the appearance of a distinct suite of vegetation, potentially resulting in shifts in ecological state (Cocking et al., 2014; Coop et al., 2020; Johnstone et al., 2016; Romme et al., 1998). Climate change puts additional pressure on ecosystems, testing their resilience, increasing the likelihood of fire regime shifts (Flannigan et al., 2013; Littell et al., 2009; Moritz et al., 2012), and triggering subsequent type conversion in some ecosystems (Johnstone et al., 2016; Stephens et al., 2013; Stevens-Rumann et al., 2018).

The compounding effects of novel landscape conditions, coupled with the top-down impacts of climate change on fire regimes, may be increasing the likelihood of wildfire recurrence within the same physical boundaries. Atmospheric warming is predicted to increase the size, frequency, and severity of wildfires in the near and long term (Abatzoglou & Williams, 2016; McKenzie et al., 2004; Miller, Safford, et al., 2009; Westerling et al., 2006). Under these circumstances, reburns are probable, particularly in areas where rapid understory recovery and other factors reduce the ability of previous burn scars to act as barriers to subsequent fires (Coppoletta et al., 2016; McGinnis et al., 2010; Parks et al., 2015; Prichard et al., 2017; Thompson & Spies, 2010; van Wagtenonk et al., 2012). Repeated high-severity wildfire can cause long-lasting state shifts in formerly frequent-fire forests, restructuring ecosystems, and altering future fire regimes (Collins & Roller, 2013; Coop et al., 2016, 2020; Coppoletta et al., 2016; Lydersen et al., 2019; Nemens et al., 2018). These observed patterns may have substantial implications for forest resilience, as dry forests are replaced by shrubs and herbaceous vegetation with divergent structure and ecological function.

In order to examine the consequences of multiple wildfires on species composition and future recovery

trajectories, we characterized the structure and composition of a forested landscape that had recently experienced two large mixed-severity wildfires. Across a spectrum of fire severity combinations (from unburned to high severity for each fire), we measured overstory and midstory composition in the intersectional area of the 2000 Storrie Fire and the 2012 Chips Fire in Northern California, USA. Using field data compiled from 93 plots, we asked the following questions: (1) What was the relationship between fire severity and compositional change in the two fires? (2) Were the patterns established in the first wildfire amplified in the second fire? and (3) What influence did cumulative fire severity have on the trajectory of future forest composition? We hypothesized that repeated fire would cause shifts toward shrub species in composition and stand structure in these long fire-excluded forests and that these changes would be more dramatic with greater burn severity in each fire. As stand-replacing wildfire affects more forested land in the western United States, and the risk of reburns increases, a greater understanding of postfire processes will assist land managers in preparing for large-scale landscape changes (Hessburg et al., 2016; Swanston et al., 2020).

METHODS

Study location

The study sites were located in the Lassen National Forest (hereafter Lassen) situated at the southern terminus of the Cascade Range in Northern California. Volcanic soils are dominant in the Cascades, although the southernmost portion of the study area, where it adjoins the Sierra Nevada, includes granitic soils (Kliewer, 1994). The Lassen experiences a Mediterranean climate, with warm, dry summers and cool, wet winters, during which 95% of the annual precipitation occurs (Kliewer, 1994). The terrain in the study area is generally steep, with elevations ranging from 900 to 1800 m above sea level. Vegetation in our study area was dominated by Sierra mixed-conifer forest (McDonald, 1980), interspersed with montane chaparral shrublands. Common tree species were white fir (*Abies concolor* [Gord. & Glend.]), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*), ponderosa pine (*Pinus ponderosa* var. *ponderosa* C. Lawson), sugar pine (*Pinus lambertiana* Douglas), California black oak (*Quercus kelloggii* Newb.), and incense-cedar (*Calocedrus decurrens* [Torr.] Florin). Common midstory species were deerbrush (*Ceanothus integerrimus* Hook. & Arn.), greenleaf manzanita (*Arctostaphylos patula* Greene), snowbrush (*Ceanothus velutinus* Douglas ex Hook. var. *velutinus*), Sierra gooseberry (*Ribes roezlii* Regal var. *roezlii*), mountain whitethorn (*Ceanothus cordulatus* Kellogg), and trailing snowberry (*Symphoricarpos mollis* Nutt.).

The mixed-severity Storrie Fire burned approximately 23,000 ha of the Lassen and Plumas National Forests in 2000. The fire ignited after a prolonged period of warm and dry conditions and was characterized by rapid initial spread through steep terrain in dense forests that had not experienced fire in nearly a century. Twelve years following this event, the Chips Fire started in the Plumas and quickly spread into the Storrie Fire footprint, burning intensely in dry and continuous fuels on steep slopes. Fuel loading in high-severity areas of the Storrie Fire footprint was high, due to the large quantity of snags, downed wood, and dense shrub regrowth that followed the fire. Along with topography, weather, and fuel moisture conditions, these fuels contributed substantially to both the rate of spread and fireline intensity of this subsequent fire. The Chips Fire eventually burned approximately 30,000 ha at a mix of severities, 9,900 ha of which was inside of the footprint of the Storrie Fire (Figure 1). The intersection of these two mixed-severity fires allowed the examination of fire effects across a complete spectrum of fire severity combinations, from unburned in both fires to repeated high-severity burns.

Field sampling

Within the 9,900-ha intersection of the two wildfire footprints, we established 93 plots, encompassing the full range of fire severity combinations. Plots were circular, 0.045 ha in area. We used both remote sensing data and field verification in order to characterize burn severity for each fire in each plot. We used satellite-derived relative differenced normalized burn ratio (RdNBR) values following each fire (Miller, Knapp, et al., 2009; Miller & Thode, 2007) to separate plots into categories of unburned, and low, moderate, and high severity. RdNBR is a satellite-derived metric calculated from the analysis of pre- and 1-year postfire imagery using LANDSAT bands 3 and 7, which are sensitive to chlorophyll content. This allows fire severity to be calculated by determining the amount of change in the “greenness” of the images pre- and postfire (differenced NBR [dNBR]). This value is then calibrated in order to remove the influence of prefire vegetation type by dividing it by the square root of the prefire NBR, resulting in a RdNBR (Miller, Knapp, et al., 2009). This unitless measure can be used to approximate the composite burn index (CBI, a field-derived measure of severity; Key & Benson, 2006) in the categorization of a given 30 × 30 m grid cell. The RdNBR thresholds for fire severity categories are defined in Miller and Thode (2007) as unchanged (<69), low (69–315), moderate (316–640), and high (>641), corresponding to the calibrated CBI metrics. Thus, combined fire severity in a

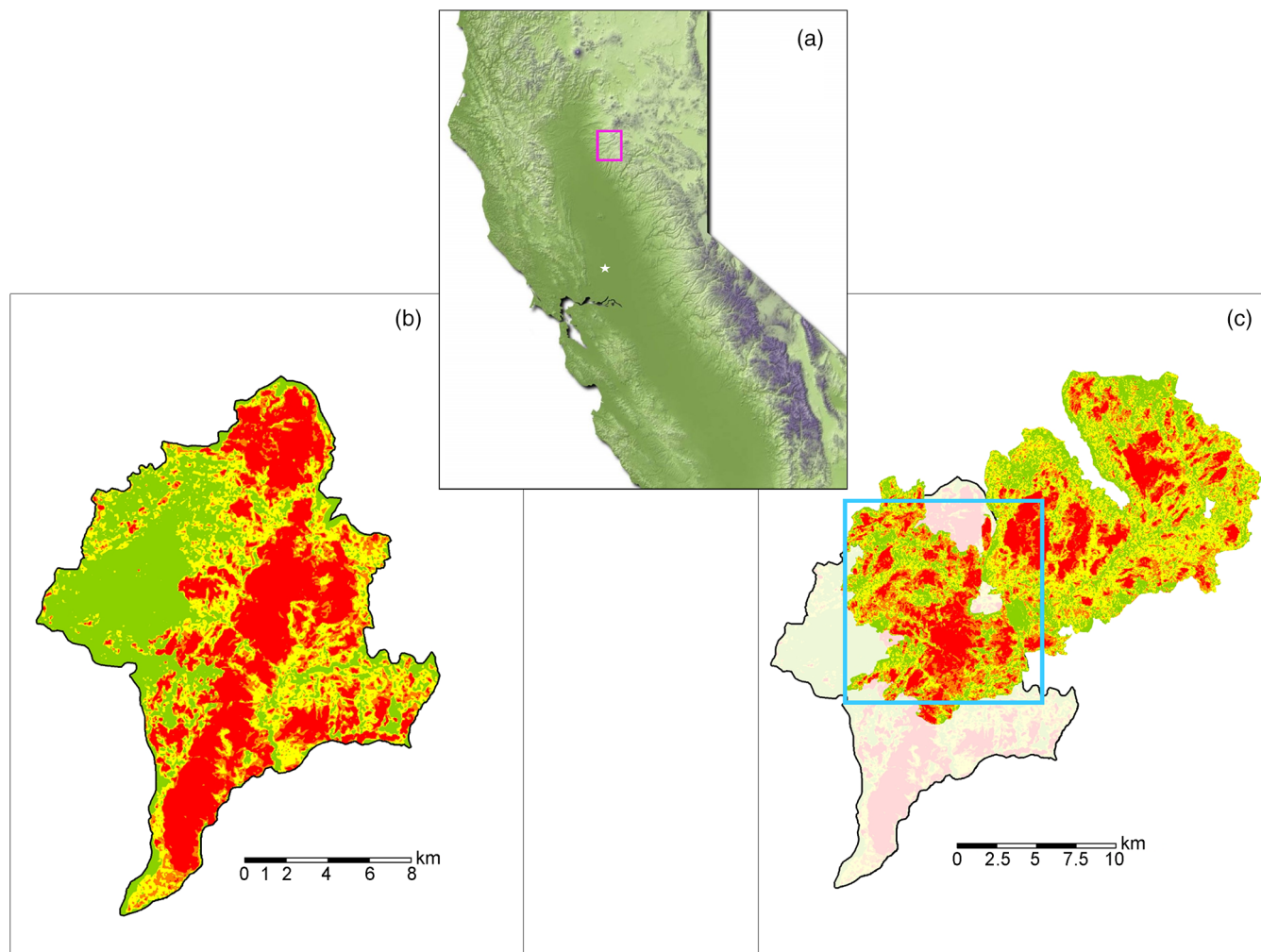


FIGURE 1 Map of the two studied fires in the southern Cascade Range in California (a, pink rectangle): the 2000 Storrie Fire (b) and the 2012 Chips Fire (c). Study area was located in the region where the two fires overlapped (blue rectangle).

given plot could have any of 16 distinct designations: unburned in the Storrie Fire, then high severity in the Chips Fire, moderate severity in both fires, etc.

Due to the large size of these cells in comparison with the area of our plots (0.09 ha compared with 0.045 ha), field observations were necessary to ascertain whether severity categories were correctly assigned. This was important due to the stratified nature of our sampling design (capturing all severity classes for each fire in all possible combinations). Field cues used to determine severity for each fire included the presence of bark and small twigs on snags (which would indicate age of less than 10 years), substantial consumption of snags and logs (which would indicate a fire-killed tree burning in a second fire), age of conifer regeneration, and rates of overstory mortality. We used these field observations to verify satellite-derived categories and recategorize severity classes where necessary in order to capture a single severity combination in each plot.

In each of these plots, for every overstory tree (>2.5 cm in dbh) we determined species, dbh (measured 1.37 m above ground level), percent live crown, and “fire history” status (e.g., top-killed in the Storrie Fire and subsequently resprouted, or survived the Storrie Fire but killed in the Chips Fire). For the purpose of prefire stand reconstruction, snags and stumps were treated similarly, except that basal diameter was used where dbh could not be measured. Midstory (saplings, seedlings >10 cm tall, and shrubs) characteristics were recorded in a smaller 0.0056-ha subplot, centered on the same point as the larger plot. In these midstory plots, we identified species and measured crown area (from two orthogonal measurements) and height in the following classes: 10–25 or 25–50 cm for seedlings and 50–75, 75–137, and >137 cm but ≤2.5 cm dbh for saplings. Seedlings <10 cm tall were considered ephemeral and were not measured (as in Crotteau et al., 2013). Additional measurements were taken on a randomly selected “focal oak” or oak sprout

clump (multiple sprouts originating from a single oak snag or stump) in each plot. Individual sprout basal diameter at 20 cm above ground level, number of sprouts, height, and crown diameter of oak clumps were recorded for each focal oak. Two orthogonal crown width measurements were taken from three additional randomly selected oak sprout clumps and, along with oak clump counts, were used to calculate oak sprout clump area for each plot.

Data analyses

In order to characterize structural changes in stands after fires, metrics were summarized across three fire “condition stages”: prefire, post-Storrie Fire, and post-Chips Fire, using stand reconstruction methods. For each of these stages, we calculated tree basal area (BA; in square meters per hectare), stand density (in trees per hectare [TPH]), quadratic mean diameter (QMD; in centimeters; Appendix S1: Formula S1), and stand density index (SDI; Reineke, 1933; Appendix S1: Formula S2) for each of the six most common tree species.

Importance values (IVs) were determined by calculating dominance (BA of the species), density (number of stems per hectare of the species), and frequency (number of plots where present) for each species in each severity category (Curtis, 1959). Each of these components was converted into a relative value (component value for species A/combined component value for all species $\times$ 100) so that the influence of disparity in a number of growing seasons following each fire (15 for the Storrie Fire vs. 3 for the Chips Fire) was removed. Components were then summed to arrive at a relative IV for each species in each severity class (range of IVs: 0–300). The IVs were compared based on fire severity categories for each fire to assess structural and compositional changes due to burn severity.

Resprouting oaks were included in the overstory for the purposes of this analysis, as they were generally >2 m tall and can reasonably be expected to continue to mature into overstory trees. Dominance metrics for these oaks were extrapolated from the diameter of sprouts measured on the single “focal oak” that was the subject of detailed measurements. These values were extrapolated to the oak clumps recorded in each plot. As oaks were reliably top-killed with moderate or high severity in either fire, combined fire severity largely determined oak dimensions (by determining sprout age and thus size—consistent across ages). As severity was homogenous within each plot, we anticipate errors from this methodology to be negligible (Crotteau et al., 2013; Hammett et al., 2017; Kidd & Varner, 2019).

We compared mean overstory IVs for each species in two ways: between pre- and post-Storrie values, and

along a continuous gradient of satellite-derived fire severity values (RdNBR) for both fires. For categorical analyses, we used *t* tests to compare pre- and post-Storrie Fire IVs for each species. Due to the interactive effects of multiple fires on vegetation, the effect of Chips Fire on IVs could not be analyzed solely using Chips Fire severity categories without also considering the Storrie Fire severity. Dividing plots this way, however, yielded sample sizes too small ($n = 6$) for these analyses. Thus, the effect of the Chips Fire on IVs was examined using only continuous fire severity metrics described above (satellite-derived RdNBR). This was applied using multiple linear regression analysis for both Storrie and Chips Fire severity values and their interaction. Models were selected following evaluation using Akaike information criterion (AIC), root mean square error (RMSE), and R^2 values.

We calculated midstory IVs for the six most common tree and shrub species using similar methods as for the overstory. For these analyses, we used crown area (a direct measure of cover, calculated using two orthogonal crown diameter measurements) as a metric of a species' dominance within a plot. It should be noted that the lack of prefire data meant that midstory species abundance data were only collected following the Chips Fire, and some assumptions were necessary as to prefire species composition based on nearby unburned areas. Thus, the influence of the earlier Storrie Fire on the midstory could not be directly assessed but only inferred from species present after the Chips Fire. Results of models using RdNBR values from the Storrie Fire should thus be interpreted with caution.

We constructed generalized additive models (GAMs) of midstory species abundance and RdNBR values for each fire, and tested the effects of both fires, as well as their interaction, on the IV of each of the most common midstory species. To examine larger patterns of change in woody plant community composition, we used nonmetric multidimensional scaling (NMDS) ordination. We conducted NMDS using Bray–Curtis distance matrices of abundance data (overstory BA) for each common tree species alive at each condition stage evaluated (prefire, post-Storrie Fire, and post-Chips Fire). Stress was calculated by comparing the distances in the original matrices with the fitted distances in ordination space and used to evaluate the interpretive ability of each ordination. The influence of continuous fire severity (RdNBR) on the composition of the overstory in each fire was quantified using the *ordisurf* function in the *vegan* package in R (version 2.5-1; R Core Team, 2016; Oksanen et al., 2018). *ordisurf* fits a smooth response surface of a continuous predictor variable onto an unconstrained ordination (such as an NMDS), and uses a GAM to evaluate the relationship between a continuous nonlinear variable and a matrix of response variables

(in this case, species abundance) in ordination space (Bennion et al., 2012; Oksanen et al., 2018; Raut et al., 2018). This technique was repeated by combining overstory and midstory data to give a more complete picture of the influence of combined fire severity on future vegetation trajectories. As these data were only available following the second fire (Chips Fire), the effects of burn severity on midstory vegetation following the Storrie Fire could not be assessed.

RESULTS

Before accounting for fire severity, we found dramatic changes in stand structure between condition stages. Of particular note were the declines in tree BA, density, SDI, and size for fire-sensitive white fir, and the near-constant stem density values for resprouting black oak (Table 1).

When compared to prefire values, IVs for several overstory species were significantly changed by the Storrie Fire, but these changes were contingent on fire severity

(Figure 2). Results of paired comparisons showed a significant decline in white fir and sugar pine importance, but only in plots that experienced high-severity fire in the Storrie Fire ($t = 2.98$, $p = 0.005$ for white fir and $t = 4.33$, $p > 0.001$ for sugar pine). We observed the opposite effect for California black oak, whose IVs increased significantly in plots that burned at high severity ($t = -4.45$, $p > 0.001$). Other species did not show significant change following the Storrie Fire. Importance values did not change for any species in plots that were unburned or those that burned at low or moderate severity.

When postfire IVs were modeled using continuous burn severity indices for each fire, a clear pattern emerged, with all conifers declining in importance as burn severity increased for each fire, and black oak increasing in importance along this same gradient (Figure 3). Increasing fire severity explained nearly half of the observed variation in white fir and Douglas-fir IVs ($R^2 = 0.45$ and 0.48 , respectively, $p < 0.0001$ for both models), and more than half of the increase in black oak importance ($R^2 = 0.51$, $p < 0.0001$). For half

TABLE 1 Summary of basal area (BA), trees per hectare (TPH), stand density index (SDI), and quadratic mean diameter (QMD) for the six most common overstory tree species at three fire condition stages, regardless of severity.

Condition	Species	BA (m ² ha ⁻¹)	TPH	SDI	QMD (cm)
Prefire	ABCO	20.66 (22.82)	250.15 (277.58)	50.38 (77.98)	30.05 (20.92)
	CADE	2.52 (5.06)	42.05 (82.33)	5.49 (17.97)	11.31 (17.99)
	PILA	15.16 (34.55)	30.58 (50.32)	159.93 (579.2)	32.89 (42.99)
	PIPO	8.36 (19.98)	48.74 (108.32)	100.45 (443.43)	25.71 (42.16)
	PSME	15.08 (30.38)	45.4 (95.51)	173.65 (578.17)	32.27 (47)
	QUKE	11.43 (13.53)	321.11 (291.57)	12.62 (21.78)	19.78 (10.6)
Total		73.21	738.03	502.52	152.01
Post-Storrie Fire	ABCO	14.38 (19.07)	204.76 (286.19)	34.48 (61.93)	24.48 (22.71)
	CADE	2.31 (4.77)	39.42 (82.11)	6.34 (27.67)	10.44 (19.52)
	PILA	3.64 (8.58)	11.71 (20.87)	28.25 (90.27)	17.21 (32.51)
	PIPO	4.15 (10.04)	41.1 (105.24)	21.04 (82.08)	16.41 (26.15)
	PSME	8.58 (15.95)	37.99 (95.66)	67.06 (180.85)	23.48 (40.02)
	QUKE	9.27 (12.56)	325.42 (293.19)	9.43 (16.18)	17.07 (11.14)
Total		42.33	660.4	166.6	109.09
Post-Chips Fire	ABCO	6.23 (10.32)	87.45 (194.04)	15.83 (33.81)	17.8 (24.09)
	CADE	0.95 (2.82)	19.83 (55.35)	1.72 (6.29)	5.68 (13.15)
	PILA	2.49 (7.79)	5.5 (14.15)	22.1 (86.78)	10.85 (29.4)
	PIPO	2.36 (6.09)	15.29 (34.82)	17.38 (71.12)	13.62 (28.48)
	PSME	4.78 (10.68)	30.34 (83.45)	24.78 (80.77)	13.99 (27.78)
	QUKE	6.08 (9.95)	342.62 (295.95)	4.84 (12.39)	13.12 (8.02)
Total		22.89	501.03	86.65	75.06

Note: Prefire and post-Storrie Fire data are estimates based on field reconstructions of fire history. Means and SDs are presented for each species.

Abbreviations: ABCO, *Abies concolor*; CADE, *Calocedrus decurrens*; PILA, *Pinus lambertiana*; PIPO, *Pinus ponderosa*; PSME, *Pseudotsuga menziesii*; QUKE, *Quercus kelloggii*.

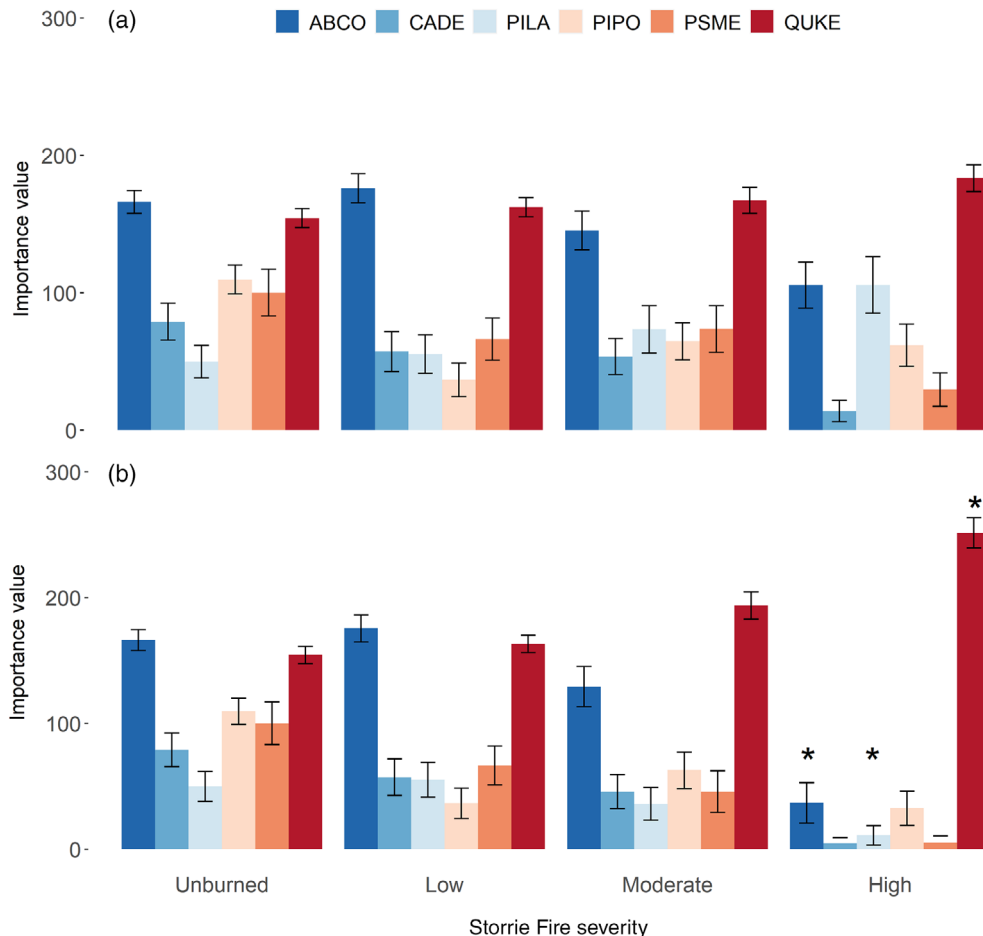


FIGURE 2 Mean importance values for the six most common overstory species in two condition stages: (a) prefire and (b) post-Storrie Fire. Species acronyms are as follows: ABCO, *Abies concolor*; CADE, *Calocedrus decurrens*; PILA, *Pinus lambertiana*; PIPO, *Pinus ponderosa*; PSME, *Pseudotsuga menziesii*; and QUKE, *Quercus kelloggii*. Asterisks denote species whose importance value showed a significant change between condition stages in certain severity classes in paired *t* tests.

of the dominant species, model selection criteria resulted in our choice of linear models of IVs for each species containing three terms: RdNBR values for both the Storrie and Chips Fires, and an interaction term for severity in both fires. In these cases, substantial improvements over models that did not include an interaction term were demonstrated by model selection metrics (AIC, RMSE, and R^2). For the other three species, the interaction of the two fires was not significant, and so models without interaction terms were used in analyses (Table 2).

Midstory species were also impacted by fire severity. While we do not have data for midstory species abundance prior to the Chips Fire, it is clear that in areas that experienced high severity in the Storrie Fire, shrubs were abundant. In plots that burned twice at high severity, vigorous shrub regeneration was coupled with a complete exclusion of tree regeneration (Figure 4). Despite high variability, significant effects of fire severity on the IV of whitethorn were found ($p < 0.0001$, $R^2 = 0.24$). Whitethorn responded

strongly to repeated high-severity (HS) fire, where the mean IV for plots that burned severely twice was more than three times the mean IV for lower severity (LS) plots (mean $IV_{HS} = 146$ vs. mean $IV_{LS} = 43.6$). In contrast, mean white fir IVs increased with decreasing burn severity (mean $IV_{HS} = 7.5$ vs. mean $IV_{LS} = 53$).

Overstory composition shifted drastically following each wildfire. With each successive high- and moderate-severity burn, shade-tolerant and fire-sensitive species decreased in dominance, while fire-tolerant black oak became the dominant overstory species. Ordinations of relativized abundance data for common overstory species prefire, post-Storrie, and post-Chips Fire yielded three-dimensional solutions with stresses of 0.12, 0.08, and 0.05, respectively. These ordinations revealed changes in species composition between each fire event, with clear distinctions between prefire, post-Storrie Fire, and post-Chips Fire ordinations (Figure 5). The application of GAMs to postfire overstory ordinations revealed that increased RdNBR values explained a significant portion

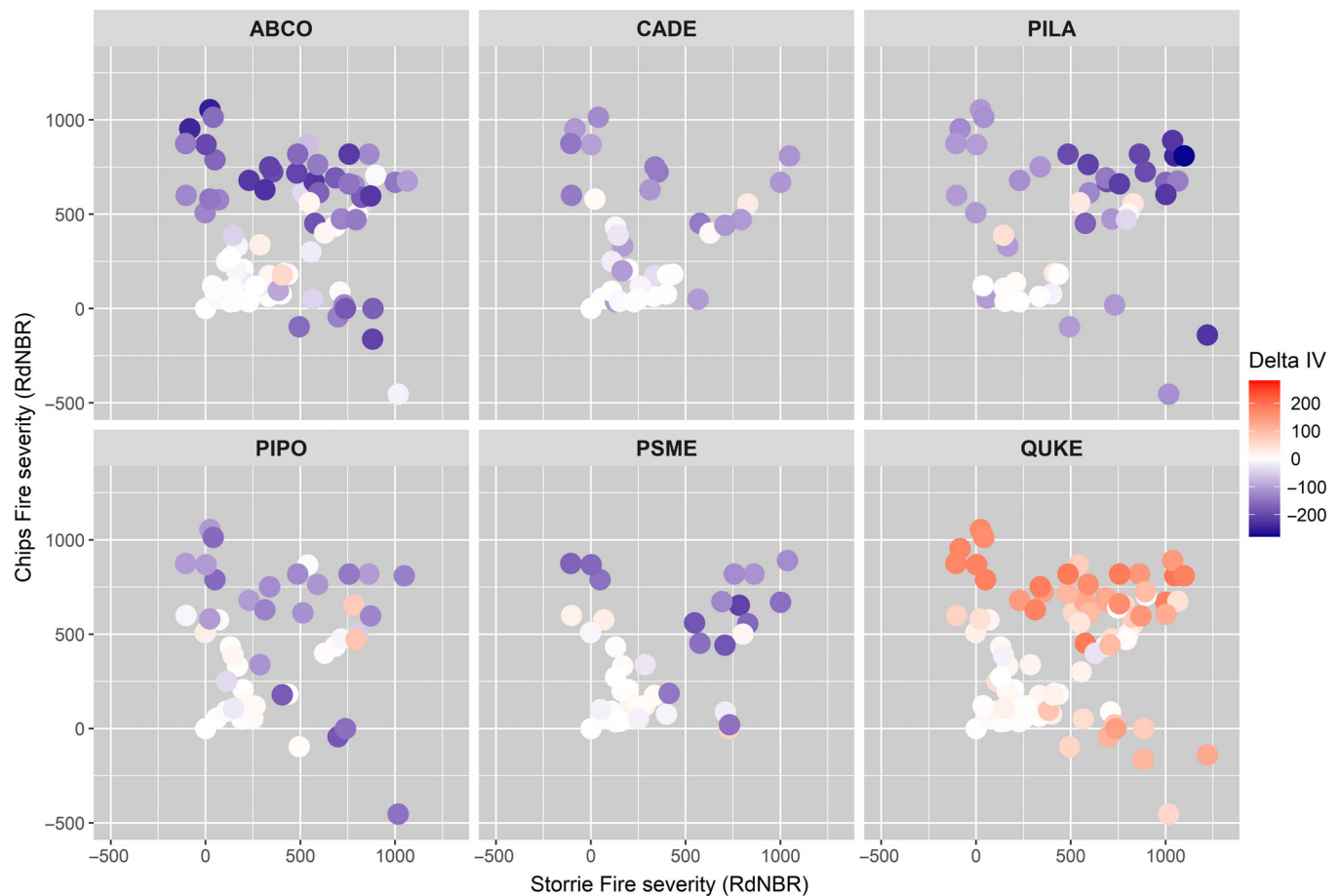


FIGURE 3 Total change in the importance value (Delta IV) from original condition stage (prefire) to final condition stage (post-Chips Fire) for six most common overstory species compared with fire severity values for each fire. Species acronyms are as follows: ABCO, *Abies concolor*; CADE, *Calocedrus decurrens*; PILA, *Pinus lambertiana*; PIPO, *Pinus ponderosa*; PSME, *Pseudotsuga menziesii*; and QUKE, *Quercus kelloggii*.

TABLE 2 Model coefficients for linear models of the effect of continuous fire severity (relative differenced normalized burn ratio) on importance values for each overstory species.

Species	R^2	p		
		Storrie Fire	Chips Fire	Interaction term
ABCO	0.45	0.00002	<0.00001	0.00006
CADE ^a	0.38	0.76700	0.00002	n.s.
PILA ^a	0.42	0.00010	0.00022	n.s.
PIPO	0.24	0.00122	0.00037	0.00321
PSME ^a	0.48	0.01587	0.00015	n.s.
QUKE	0.51	<0.00001	<0.00001	0.00015

Abbreviations: ABCO, *Abies concolor*; CADE, *Calocedrus decurrens*; PILA, *Pinus lambertiana*; PIPO, *Pinus ponderosa*; PSME, *Pseudotsuga menziesii*; QUKE, *Quercus kelloggii*.

^aModels for which fire interaction terms were nonsignificant.

of the deviance in species composition ordinations (49% and 34%, respectively).

Plant community composition as a whole also changed in response to increased fire severity. When we

combined overstory and midstory strata, an ordination of post-Chips species abundance values displayed patterns consistent with a transition to a shrub- and oak-dominated community along a gradient of increasing fire

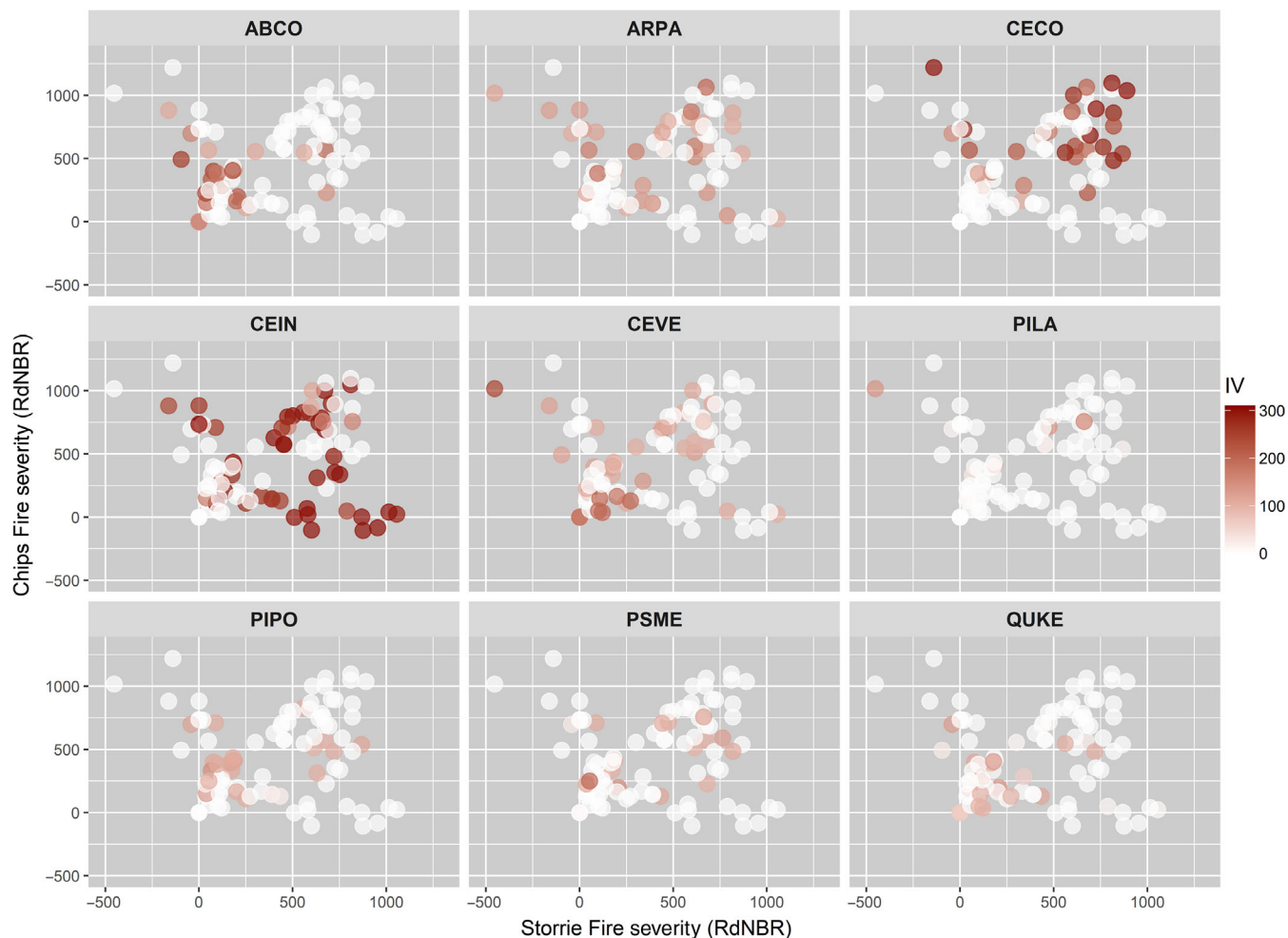


FIGURE 4 Importance values (IV) of nine most common midstory species, including shrubs and tree seedlings, as compared to fire severity values for each fire. Species acronyms are as follows: ABCO, *Abies concolor*; ARPA, *Arctostaphylos patula* Greene; CECO, *Ceanothus cordulatus* Kellogg; CEIN, *Ceanothus integerrimus*; CEVE, *Ceanothus velutinus*; PIPO, *Pinus ponderosa*; PILA, *Pinus lambertiana*; PSME, *Pseudotsuga menziesii*; and QUKE, *Quercus kelloggii*.

severity (Figure 6). An NMDS ordination of these combined values yielded a three-dimensional solution with a stress of 0.17. When a GAM was applied in order to overlay continuous fire severity (RdNBR) for each fire on the ordination, significant interactions between fire severity and community composition were revealed for both the Storrie (deviance explained = 38%) and Chips (deviance explained = 36%) Fires.

DISCUSSION

Past land use practices and the interruption of pre-Euro-American settlement fire regimes have caused a cascade of ecological effects that continue to manifest in contemporary fire-prone landscapes. The increased size and severity of wildfires in many dry western forests is a striking example of this legacy (Collins et al., 2011; Miller,

Safford, et al., 2009; Parks & Abatzoglou, 2020; Steel et al., 2018). The changes to forests wrought by increasingly severe fire are obvious in the near term, but the longer term consequences of these fires on vegetation trajectories and thus future fires are less clear (Barton, 2002; Collins & Roller, 2013; Lydersen et al., 2019).

There is increasing evidence that high-severity wildfire can act as a novel disturbance in previously frequent-fire forests from which fire has been excluded. While high-severity fire played a role in these landscapes in the past, the size, shape, and pattern of stand-replacing patches have increased since the advent of fire exclusion and suppression (Miller, Safford, et al., 2009; Stephens et al., 2015; Stevens et al., 2017). The excess of fuels available in these ecosystems can convert a wildfire that would have resulted in a low incidence of injury to overstory trees into a catastrophic event that replaces entire stands (Hessburg

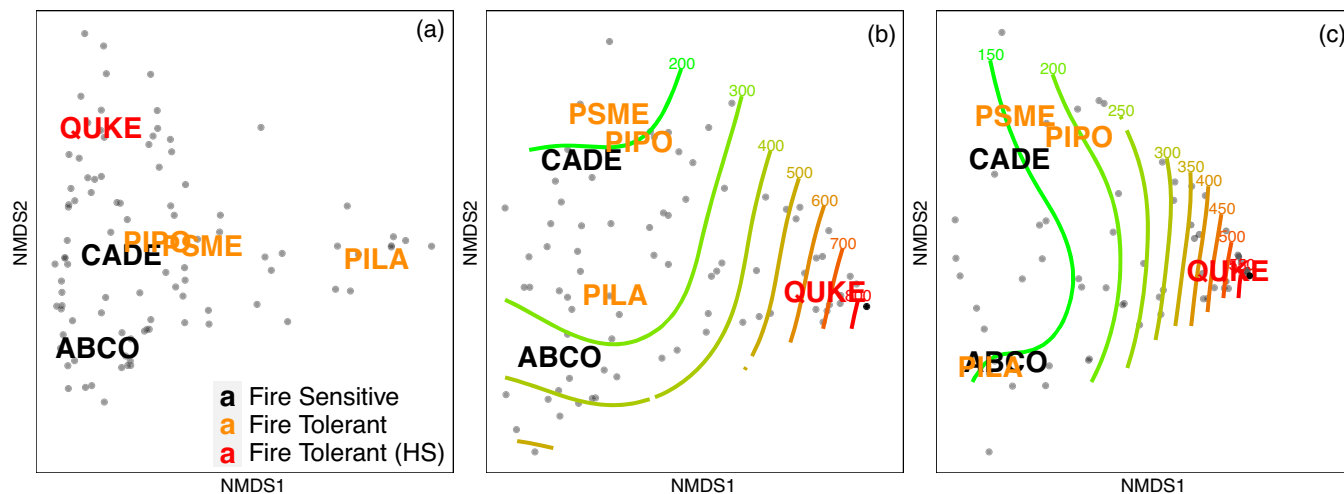


FIGURE 5 Ordinations of common overstory species composition showing species centroids: (a) prefire, (b) post-Storrie Fire, and (c) post-Chips Fire. Overlaying continuous fire severity (relative differenced normalized burn ratio) values for each fire on these ordinations explained significant portions of the deviance in species composition matrices following the Storrie ($R^2 = 0.49$) and Chips ($R^2 = 0.34$) Fires. Species acronyms are as follows: ABCO, *Abies concolor*; CADE, *Calocedrus decurrens*; PILA, *Pinus lambertiana*; PIPO, *Pinus ponderosa*; PSME, *Pseudotsuga menziesii*; and QUKE, *Quercus kelloggii*. NMDS, nonmetric multidimensional scaling.

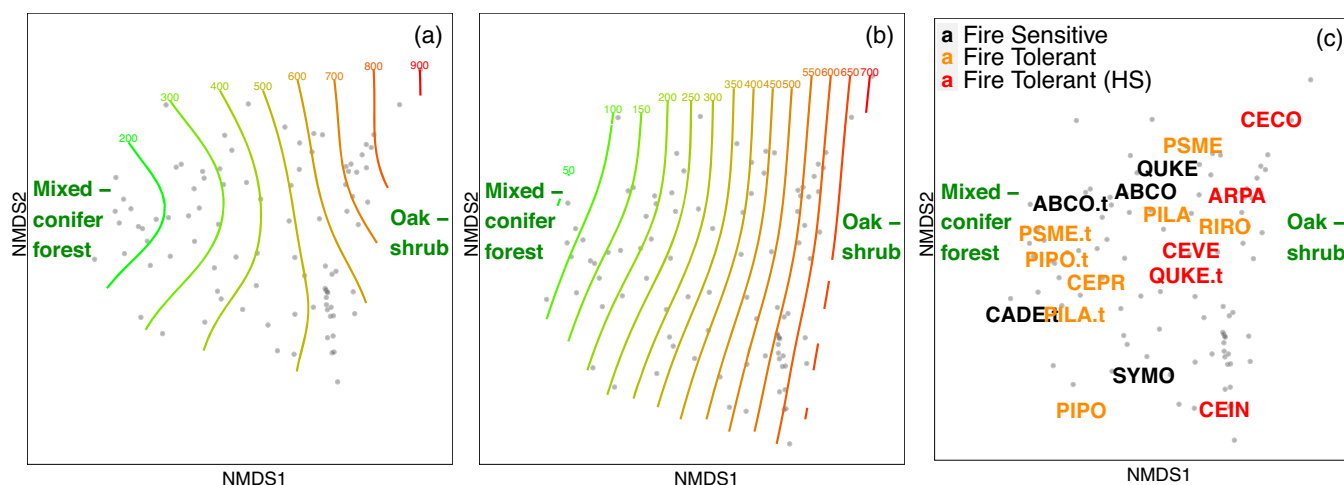


FIGURE 6 Nonmetric multidimensional scaling (NMDS) ordination of entire woody plant community composition, including trees, saplings, seedlings, and shrubs. Fire severity for each fire is overlaid showing effects of the (a) Storrie Fire ($R^2 = 0.32$) and the (b) Chips Fire ($R^2 = 0.35$) on species composition. Species colored in red are tolerant of high-severity (HS) fire. Species centroids (c) of combined overstory and understory (trees in overstory denoted with .t following the species codes). Species acronyms are as follows: ABCO, *Abies concolor*; CADE, *Calocedrus decurrens*; PILA, *Pinus lambertiana*; PIPO, *Pinus ponderosa*; PSME, *Pseudotsuga menziesii*; QUKE, *Quercus kelloggii*; CEIN, *Ceanothus integerrimus* Hook. & Arn.; ARPA, *Arctostaphylos patula* Greene; CEVE, *Ceanothus velutinus* Douglas ex Hook. var. *velutinus*; RIRO, *Ribes roezlii* Regal var. *roezlii*; CECO, *Ceanothus cordulatus* Kellogg; and SYMO, *Symphoricarpos mollis* Nutt.

et al., 2005; Mallek et al., 2013; Miller, Safford, et al., 2009). These disturbance events can have drastic effects, particularly when the disturbance is repeated, as is the case in reburns. Several authors have noted substantial changes following reburns and have posited that these constitute potentially long-lasting shifts in vegetative state (Coop et al., 2016, 2020; Coppoletta et al., 2016; Stevens-Rumann & Morgan, 2016).

A number of elements combine to provoke this situation. Uncharacteristically intense fires often result in near-complete mortality of mature seed-bearing trees, resulting in large open patches where seedling establishment is poor, due to both harsh growing conditions and lack of seed sources (Coop et al., 2020; Stevens et al., 2017; Welch et al., 2016). These elements combine to reduce the likelihood of tree seedling establishment

following high-severity fire (Chambers et al., 2016; Kemp et al., 2019; Welch et al., 2016). Competition from shrub species employing fire-adaptive strategies such as heat-stimulated germination and prolific basal sprouting compounds the impediments for conifer regeneration in postfire environments, particularly in fire-adapted Mediterranean ecosystems (Conard & Radosevich, 1982; Keeley, 1991; Keeley & Zedler, 1978). In dry Californian and southwestern US regions, these conditions can result in the transition of mixed-conifer forests into hardwood and shrub-dominated landscapes (Barton, 2002; Collins & Roller, 2013; Coop et al., 2016; Coppoletta et al., 2016).

In this study, we observed similar patterns of change following reburn. After two successive wildfires, overstory structure was radically changed in sites that experienced repeated moderate- and high-severity fire. Resprouting oaks dominated these stands, while formerly dominant conifer species declined sharply in importance (Figures 2 and 3). These trends were repeated in the midstory, where following the Chips Fire, we found few conifer seedlings and saplings in plots that experienced multiple high-severity burns, likely due to the increased distance to seed sources and poor growing conditions common in high-severity burn patches (Chambers et al., 2016; Owen et al., 2017; Stevens et al., 2017; Welch et al., 2016). Shrub species dominated the midstory in these plots, particularly deerbrush and whitethorn, both of which are adapted to high-severity fire. These plots also lacked oak seedlings, an artifact of this species' high fire sensitivity in the juvenile stage (Kidd & Varner, 2019). While oaks dominated the overstory of reburned plots, oak overstory recruitment was almost exclusively in the form of sprouts from top-killed rootstocks. This regrowth increased in vigor with greater fire severity, likely due to lack of competition from overtopping conifers (Cocking et al., 2012; Nemens et al., 2018).

When we combined overstory and midstory abundance data, a trend of plant community change was apparent. Following the Storrie Fire, plant communities in severely burned plots shifted from dominance by shade-tolerant, fire-sensitive species (white fir and Douglas-fir) to oak- and shrub-dominated communities (Figure 2). This change appeared to be amplified by the second fire, as we observed a near-total lack of conifer seedling recruitment or survival in plots, which burned twice at high and moderate severity (Nemens et al., 2018). This is likely due, at least in part, to the depletion of the seed bank following short-interval reburns (Coop et al., 2016, 2020; Turner et al., 2019). There were also a marked decline in all conifer species' dominance following multiple wildfire events that

included at least one severe burn, and a concurrent increase in the dominance of black oaks and montane chaparral species (Figure 6). These findings support the idea that multiple wildfires can cause the transition of forested areas into shrublands, leading to a shift in ecological state. Positive feedback (such as the regular burning and resurgence of montane chaparral species) perpetuates these postfire changes in vegetation and fire regime, increasing the potential for short-interval reburns at severities that preclude the development of mature forests (Coop et al., 2020; Tepley et al., 2018).

In the intersection of the Storrie and Chips Fires, observed vegetative state transitions were directly influenced by fire severity. In plots that did not experience at least one high-severity fire, we observed no significant changes in overstory dominance. In plots that sustained a substantial loss of existing overstory, particularly those that burned twice at moderate or high severity, a measurable transition to shrub and oak dominance occurred (Figure 7). Much of this variation was explained by fire severity: As severity increased, there was a greater departure from prefire structure and composition (Figure 6). This was evident following both the Storrie Fire and the subsequent Chips Fire, as the effects of the first fire were compounded by the second fire for some species (Table 2).

The consequences of these changes for future forests can be dramatic and long-lasting: Others have documented that non-forest patches created by a high-severity fire can remain on the landscape for decades (Coop et al., 2016; Lauvaux et al., 2016; Nagel & Taylor, 2005). As reburns increase burn patch size and reduce seed source proximity, these shrub-dominated areas are likely to become more persistent. Additionally, these patches may be sustained for long periods via a self-reinforcing mechanism of increased high-severity fire that selects for species that are advantaged in this novel regime (Coppoletta et al., 2016; Guiterman et al., 2018; Lauvaux et al., 2016; Tepley et al., 2018). The risk of repeated reburn has recently demonstrated itself, as the 2021 Dixie Fire burned nearly 390,000 ha, including the entire intersection of the Storrie and Chips Fires.

Management implications

Restoration of historic forest structure and composition is often cited as a goal of forest managers, but the forests of the past may not be well suited to future climatic conditions and forecasted shifts in fire regimes (Chambers et al., 2016; Collins & Roller, 2013). Climate change is likely to increase the incidence of severe fire in the Cascades and other similarly semiarid regions



FIGURE 7 Areas of shrub dominance in single (a) and multiple (b) high-severity burn areas in the Lassen National Forest, California.

(Abatzoglou & Williams, 2016; McKenzie et al., 2004; Miller, Safford, et al., 2009; Westerling et al., 2006), and postfire regeneration is expected to experience declines with warmer and drier conditions (Kemp et al., 2019; Stevens-Rumann et al., 2018). In light of these predictions, restoration of forested landscapes following severe wildfire will require a substantial investment by land managers

(Chambers et al., 2016; Collins & Roller, 2013). The problem is particularly salient in the case of reburns, as postfire vegetative shifts create positive feedback with fire severity, perpetuating a plant community that itself fosters stand-replacing fire (Coppoletta et al., 2016; Nagel & Taylor, 2005; van Wagtenonk & Fites-Kaufman, 2006). Facing a warmer and drier future, managers will need to

take a multipronged approach to effect the objective of increased forest and landscape resilience. Forest treatments that interrupt fuel continuity, such as thinning and prescribed fire, have demonstrated successful outcomes in the reduction in both size and severity of wildfires, even under extreme weather conditions (Prichard et al., 2021). These treatments, when implemented in forests that have experienced long periods of fire exclusion, can be effective in restoring historic forest structure and composition, reintroducing structural heterogeneity and reducing fuels such that crown fire spread is interrupted (Povak et al., 2020; Prichard & Kennedy, 2014). Non-forest patches created by mixed-severity wildfires should also be integrated into management strategies, as they create patchy landscapes that may be more resilient in a projected future of increased fire activity (Crotteau et al., 2013; North et al., 2019).

Land managers aiming for greater resilience on a landscape scale will need to consider non-forest patches as part of their “portfolio” of desirable conditions, particularly as the effort required to restore these areas to forest may be subject to the law of diminishing returns. Patches of non-forest vegetation created by high- and mixed-severity burns contribute to landscape heterogeneity, a characteristic that is lacking in much of the western United States due to decades of fire exclusion (Miller & Thode, 2007; Safford & Stevens, 2017). There is substantial evidence that diminished structural heterogeneity contributes to the prevalence of large high-severity patches in wildfires by providing continuous fuel to crown fires (Koontz et al., 2020; Stevens et al., 2017). Small spatially distributed non-forest patches also contribute to overall species diversity and were likely maintained by mixed-severity fire regimes in the era predating fire exclusion (Lauvaux et al., 2016; Matonis & Binkley, 2018).

A postfire mosaic landscape, characterized by patches of early seral forest, shrub fields, and mature, fire-resistant trees, is not only more resilient to severe fire but also provides substantial habitat values (Lauvaux et al., 2016; Nagel & Taylor, 2005; North et al., 2019; Stephens et al., 2020; Swanson et al., 2011). These same characteristics make postfire mosaics important to indigenous communities, whose ancestors managed many western landscapes using fire for food, medicine, and material resources (Anderson, 2005; Long et al., 2016, 2021). These cultural values must also be considered when making decisions regarding forest management following severe fire events. As the 2021 Dixie Fire illustrates, fire-prone landscapes in much of western North America will continue to undergo increased pressure from changing fire regimes. Only land management paradigms that acknowledge these impending changes

will prove successful in establishing resilient ecosystems in this challenging future.

AUTHOR CONTRIBUTIONS

Deborah G. Nemens, J. Morgan Varner, Kathryn R. Kidd, and Brian Wing conceived the ideas and designed the methodology; Deborah G. Nemens and Kathryn R. Kidd collected the data; Deborah G. Nemens analyzed the data and led the writing of the manuscript; and J. Morgan Varner and Kathryn R. Kidd contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

P. Doyle, M. Hennessey, J. Bristow, and other staff from the Lake Almanor Ranger District in the Lassen National Forest provided access to field sites, as well as helpful advice and support. We are grateful for the assistance provided by M. Schriver, J. Kreye, N. Valliant, S. Koyama Hwang, J. Restaino, and T. Tohn. Conversations with H. Podschwit greatly improved the analyses. Two anonymous reviewers helped to substantially improve the final version of this manuscript. This work was supported by Joint Venture Agreements (15-JV-11272139-027 & 19-JV-11261987-139) with the USDA Forest Service Pacific Southwest Region (Region 5), the USDA Forest Service Pacific Northwest Research Station, and the National Fire Plan.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Nemens, 2021) are available from Zenodo: <https://doi.org/10.5281/zenodo.5620972>.

ORCID

Deborah G. Nemens  <https://orcid.org/0000-0002-4388-1923>

J. Morgan Varner  <https://orcid.org/0000-0003-3781-5839>

REFERENCES

- Abatzoglou, J. T., and A. P. Williams. 2016. “Impact of Anthropogenic Climate Change on Wildfire across Western US Forests.” *Proceedings of the National Academy of Sciences of the United States of America* 113: 11770–5.
- Agee, J. K. 1993. *Fire Ecology of Pacific Northwest Forests*. Washington, DC: Island Press. <https://doi.org/10.5070/G31710279>.
- Agee, J. K., and C. N. Skinner. 2005. “Basic Principles of Forest Fuel Reduction Treatments.” *Forest Ecology and Management* 211: 83–96.
- Anderson, M. K. 2005. *Tending the Wild*. Berkeley, CA: University of California Press.

- Barton, A. M. 2002. "Intense Wildfire in Southeastern Arizona: Transformation of a Madrean Oak–Pine Forest to Oak Woodland." *Forest Ecology and Management* 165: 205–12.
- Bennion, H., L. Carvalho, C. D. Sayer, G. L. Simpson, and J. Wischniewski. 2012. "Identifying from Recent Sediment Records the Effects of Nutrients and Climate on Diatom Dynamics in Loch Leven." *Freshwater Biology* 57: 2015–29.
- Chambers, M. E., P. J. Fornwalt, S. L. Malone, and M. A. Battaglia. 2016. "Patterns of Conifer Regeneration Following High Severity Wildfire in Ponderosa Pine–Dominated Forests of the Colorado Front Range." *Forest Ecology and Management* 378: 57–67.
- Cocking, M. I., J. M. Varner, and E. E. Knapp. 2014. "Long-Term Effects of Fire Severity on Oak–Conifer Dynamics in the Southern Cascades." *Ecological Applications* 24: 94–107.
- Cocking, M. I., J. M. Varner, and R. L. Sherriff. 2012. "California Black Oak Responses to Fire Severity and Native Conifer Encroachment in the Klamath Mountains." *Forest Ecology and Management* 270: 25–34.
- Collins, B. M., R. G. Everett, and S. L. Stephens. 2011. "Impacts of Fire Exclusion and Recent Managed Fire on Forest Structure in Old Growth Sierra Nevada Mixed-Conifer Forests." *Ecosphere* 2: 1–14.
- Collins, B. M., and G. B. Roller. 2013. "Early Forest Dynamics in Stand-Replacing Fire Patches in the Northern Sierra Nevada, California, USA." *Landscape Ecology* 28: 1801–13.
- Conard, S. G., and S. R. Radosevich. 1982. "Growth Responses of White Fir to Decreased Shading and Root Competition by Montane Chaparral Shrubs." *Forest Science* 28: 309–20.
- Coop, J. D., S. A. Parks, S. R. McClernan, and L. M. Holsinger. 2016. "Influences of Prior Wildfires on Vegetation Response to Subsequent Fire in a Reburned Southwestern Landscape." *Ecological Applications* 26: 346–54.
- Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, S. D. Crausbay, P. E. Higuera, M. D. Hurteau, A. Tepley, et al. 2020. "Wildfire-Driven Forest Conversion in Western North American Landscapes." *Bioscience* 70: 659–73.
- Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. "Post-Fire Vegetation and Fuel Development Influences Fire Severity Patterns in Reburns." *Ecological Applications* 26: 686–99.
- Crotteau, J. S., J. M. Varner, and M. W. Ritchie. 2013. "Post-Fire Regeneration across a Fire Severity Gradient in the Southern Cascades." *Forest Ecology and Management* 287: 103–12.
- Curtis, J. T. 1959. *The Vegetation of Wisconsin: An Ordination of Plant Communities*. Madison, WI: University of Wisconsin Press.
- Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009. "Conifer Regeneration in Stand-Replacement Portions of a Large Mixed-Severity Wildfire in the Klamath–Siskiyou Mountains." *Canadian Journal of Forest Research* 39: 823–38.
- Flannigan, M., A. S. Cantin, W. J. De Groot, M. Wotton, A. Newbery, and L. M. Gowman. 2013. "Global Wildland Fire Season Severity in the 21st Century." *Forest Ecology and Management* 294: 54–61.
- Foster, D. R., D. H. Knight, and J. F. Franklin. 1998. "Landscape Patterns and Legacies Resulting from Large, Infrequent Forest Disturbances." *Ecosystems* 1: 497–510.
- Guiterman, C. H., E. Q. Margolis, C. D. Allen, D. A. Falk, and T. W. Swetnam. 2018. "Long-Term Persistence and Fire Resilience of Oak Shrubfields in Dry Conifer Forests of Northern New Mexico." *Ecosystems* 21(5): 943–59.
- Hagmann, R. K., P. F. Hessburg, S. J. Prichard, N. A. Povak, P. M. Brown, P. Z. Fulé, R. E. Keane, et al. 2021. "Evidence for Widespread Changes in the Structure, Composition, and Fire Regimes of Western North American Forests." *Ecological Applications* 31: e02431.
- Hammett, E. J., M. W. Ritchie, and J.-P. Berrill. 2017. "Resilience of California Black Oak Experiencing Frequent Fire: Regeneration Following Two Large Wildfires 12 Years Apart." *Fire Ecology* 13: 91–103.
- Harris, L. B., and A. H. Taylor. 2020. "Rain-Shadow Forest Margins Resilient to Low-Severity Fire and Climate Change but Not High-Severity Fire." *Ecosphere* 11: e03258.
- Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. "Dry Forests and Wildland Fires of the Inland Northwest USA: Contrasting the Landscape Ecology of the Pre-Settlement and Modern Eras." *Forest Ecology and Management* 211: 117–39.
- Hessburg, P. F., C. L. Miller, S. A. Parks, N. A. Povak, A. H. Taylor, P. E. Higuera, S. J. Prichard, et al. 2019. "Climate, Environment, and Disturbance History Govern Resilience of Western North American Forests." *Frontiers in Ecology and Evolution* 7: 239.
- Hessburg, P. F., T. A. Spies, D. A. Perry, C. N. Skinner, A. H. Taylor, P. M. Brown, S. L. Stephens, et al. 2016. "Tamm Review: Management of Mixed-Severity Fire Regime Forests in Oregon, Washington, and Northern California." *Forest Ecology and Management* 366: 221–50.
- Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, et al. 2016. "Changing Disturbance Regimes, Ecological Memory, and Forest Resilience." *Frontiers in Ecology and the Environment* 14: 369–78.
- Kane, J. M., J. M. Varner, M. R. Metz, and P. J. van Mantgem. 2017. "Characterizing Interactions between Fire and Other Disturbances and their Impacts on Tree Mortality in Western US Forests." *Forest Ecology and Management* 405: 188–99.
- Keeley, J. E. 1991. "Seed Germination and Life History Syndromes in the California Chaparral." *The Botanical Review* 57: 81–116.
- Keeley, J. E., and P. H. Zedler. 1978. "Reproduction of Chaparral Shrubs after Fire: A Comparison of Sprouting and Seeding Strategies." *American Midland Naturalist* 99: 142–61.
- Kemp, K. B., P. E. Higuera, P. Morgan, and J. T. Abatzoglou. 2019. "Climate Will Increasingly Determine Post-Fire Tree Regeneration Success in Low-Elevation Forests, Northern Rockies, USA." *Ecosphere* 10: e02568.
- Key, C. H., and N. C. Benson. 2006. *Landscape Assessment (LA): Sampling and Analysis Methods*. USDA Forest Service General Technical Report RMRS-GTR-164-CD. LA1–LA51. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.
- Kidd, K. R., and J. M. Varner. 2019. "Differential Relative Bark Thickness and Aboveground Growth Discriminates Fire Resistance among Hardwood Sprouts in the Southern Cascades, California." *Trees* 33: 267–77.
- Kliwer, G. F. 1994. *Soil Survey of Lassen National Forest Area, California*. Albuquerque, NM: USDA Forest Service, Pacific Southwest Region, NRCS.

- Koontz, M. J., M. P. North, C. M. Werner, S. E. Fick, and A. M. Latimer. 2020. "Local Forest Structure Variability Increases Resilience to Wildfire in Dry Western US Coniferous Forests." *Ecology Letters* 23: 483–94.
- Lauvaux, C. A., C. N. Skinner, and A. H. Taylor. 2016. "High Severity Fire and Mixed Conifer Forest-Chaparral Dynamics in the Southern Cascade Range, USA." *Forest Ecology and Management* 363: 74–85.
- Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. "Climate and Wildfire Area Burned in Western US Ecoprovinces, 1916–2003." *Ecological Applications* 19: 1003–21.
- Long, J. W., R. W. Goode, R. J. Gutierrez, J. J. Lackey, and M. K. Anderson. 2016. "Managing California Black Oak for Tribal Ecocultural Restoration." *Journal of Forestry* 115: 426–34.
- Long, J. W., F. K. Lake, and R. W. Goode. 2021. "The Importance of Indigenous Cultural Burning in Forested Regions of the Pacific West, USA." *Forest Ecology and Management* 500: 119597.
- Lydersen, J. M., B. M. Collins, M. Coppoletta, M. R. Jaffe, H. Northrop, and S. L. Stephens. 2019. "Fuel Dynamics and Reburn Severity Following High-Severity Fire in a Sierra Nevada, USA, Mixed-Conifer Forest." *Fire Ecology* 15(1): 1–14.
- Mallek, C., H. Safford, J. Viers, and J. Miller. 2013. "Modern Departures in Fire Severity and Area Vary by Forest Type, Sierra Nevada and Southern Cascades, California, USA." *Ecosphere* 4: 1–28.
- Matonis, M. S., and D. Binkley. 2018. "Not Just about the Trees: Key Role of Mosaic-Meadows in Restoration of Ponderosa Pine Ecosystems." *Forest Ecology and Management* 411: 120–31.
- McDonald, P. M. 1980. "California Black Oak." In *Forest Cover Types of the United States and Canada*, edited by F. Eyre, 122. Washington, DC: Society of American Foresters.
- McGinnis, T. W., J. E. Keeley, S. L. Stephens, and G. B. Roller. 2010. "Fuel Buildup and Potential Fire Behavior after Stand-Replacing Fires, Logging Fire-Killed Trees and Herbicide Shrub Removal in Sierra Nevada Forests." *Forest Ecology and Management* 260: 22–35.
- McKenzie, D., Z. E. Gedalof, D. L. Peterson, and P. Mote. 2004. "Climatic Change, Wildfire, and Conservation." *Conservation Biology* 18: 90–902.
- Miller, J. D., E. E. Knapp, C. H. Key, and C. N. Skinner. 2009. "Calibration and Validation of the Relative Differenced Normalized Burn Ratio (RdNBR) to Three Measures of Fire Severity in the Sierra Nevada and Klamath Mountains, California, USA." *Remote Sensing of Environment* 113: 645–56.
- Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009. "Quantitative Evidence for Increasing Forest Fire Severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA." *Ecosystems* 12: 16–32.
- Miller, J. D., and A. E. Thode. 2007. "Quantifying Burn Severity in a Heterogeneous Landscape with a Relative Version of the Delta Normalized Burn Ratio (dNBR)." *Remote Sensing of Environment* 109: 66–80.
- Moritz, M. A., M. A. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. "Climate Change and Disruptions to Global Fire Activity." *Ecosphere* 3: 1–22.
- Nagel, T. A., and A. H. Taylor. 2005. "Fire and Persistence of Montane Chaparral in Mixed Conifer Forest Landscapes in the Northern Sierra Nevada, Lake Tahoe Basin, California, USA." *Journal of the Torrey Botanical Society* 132: 442–57.
- Nemens, D. 2021. "dnemens/Reburn2021: Overstory, Midstory Data (v1.0.0)." Zenodo. Dataset. <https://doi.org/10.5281/zenodo.5620972>.
- Nemens, D. G., J. M. Varner, B. Wing, and K. R. Kidd. 2018. "Do Repeated Wildfires Promote Restoration of Oak Woodlands in Mixed-Conifer Landscapes?" *Forest Ecology and Management* 427: 143–51.
- North, M. P., J. T. Stevens, D. F. Greene, M. Coppoletta, E. E. Knapp, A. M. Latimer, C. M. Restaino, et al. 2019. "Tamm Review: Reforestation for Resilience in Dry Western US Forests." *Forest Ecology and Management* 432: 209–24.
- Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. "Alternative Community States Maintained by Fire in the Klamath Mountains, USA." *Journal of Ecology* 98: 96–105.
- Oksanen, J. F., G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGinn, P. R. Minchin, et al. 2018. *Vegan: Assemblage Ecology Package. R Package Version 2.5-1*. Vienna: R Foundation for Statistical Computing.
- Owen, S. M., C. H. Sieg, A. J. S. Meador, P. Z. Fulé, J. M. Iniguez, L. S. Baggett, P. J. Fornwalt, and M. A. Battaglia. 2017. "Spatial Patterns of Ponderosa Pine Regeneration in High-Severity Burn Patches." *Forest Ecology and Management* 405: 134–49.
- Parks, S. A., and J. T. Abatzoglou. 2020. "Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests from 1985 to 2017." *Geophysical Research Letters* 47(22): e2020GL089858.
- Parks, S. A., L. M. Holsinger, C. Miller, and C. R. Nelson. 2015. "Wildland Fire as a Self-Regulating Mechanism: The Role of Previous Burns and Weather in Limiting Fire Progression." *Ecological Applications* 25: 1478–92.
- Parsons, D. J., and S. H. DeBenedetti. 1979. "Impact of Fire Suppression on a Mixed-Conifer Forest." *Forest Ecology and Management* 2: 21–33.
- Povak, N. A., V. R. Kane, B. M. Collins, J. M. Lydersen, and J. T. Kane. 2020. "Multi-Scaled Drivers of Severity Patterns Vary across Land Ownerships for the 2013 Rim Fire, California." *Landscape Ecology* 35: 293–318.
- Prichard, S. J., P. F. Hessburg, R. K. Hagmann, N. A. Povak, S. Z. Dobrowski, M. D. Hurteau, V. R. Kane, et al. 2021. "Adapting Western North American Forests to Climate Change and Wildfires: 10 Common Questions." *Ecological Applications* 31: e02433.
- Prichard, S. J., and M. C. Kennedy. 2014. "Fuel Treatments and Landform Modify Landscape Patterns of Burn Severity in an Extreme Fire Event." *Ecological Applications* 24: 571–90.
- Prichard, S. J., C. S. Stevens-Rumann, and P. F. Hessburg. 2017. "Tamm Review: Shifting Global Fire Regimes: Lessons from Reburns and Research Needs." *Forest Ecology and Management* 396: 217–33.
- R Core Team. 2016. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Raut, S., H. W. Polley, P. A. Fay, and S. Kang. 2018. "Bacterial Community Response to a Preindustrial-to-Future CO₂ Gradient Is Limited and Soil Specific in Texas Prairie Grassland." *Global Change Biology* 24: 5815–27.
- Reineke, L. H. 1933. "Perfection a Stand-Density Index for Even-Aged Forest." *Journal of Agricultural Research* 46: 627–38.
- Romme, W. H., E. H. Everham, L. E. Frelich, M. A. Moritz, and R. E. Sparks. 1998. "Are large, infrequent disturbances qualitatively different from small, frequent disturbances?" *Ecosystems* 1: 524–34.

- Safford, H. D., and J. T. Stevens. 2017. *Natural Range of Variation for Yellow Pine and Mixed-Conifer Forests in the Sierra Nevada, Southern Cascades, and Modoc and Inyo National Forests, California, USA*. Gen. Tech. Rep. PSW-GTR-256. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.
- Scholl, A. E., and A. H. Taylor. 2010. "Fire Regimes, Forest Change, and Self-Organization in an Old-Growth Mixed-Conifer Forest, Yosemite National Park, USA." *Ecological Applications* 20: 362–80.
- Skinner, C. N., and C. Chang. 1996. "Fire Regimes, Past and Present." In *Sierra Nevada Ecosystem Project: Final Report to Congress. Vol. II. Assessments and Scientific Basis for Management Options*. Wildland Resources Center Report No. 37 1041–69. Davis, CA: Centers for Water and Wildland Resources, University of California, Davis.
- Staver, A. C., S. Archibald, and S. A. Levin. 2011. "The Global Extent and Determinants of Savanna and Forest as Alternative Biome States." *Science* 334: 230–2.
- Steel, Z. L., M. J. Koontz, and H. D. Safford. 2018. "The Changing Landscape of Wildfire: Burn Pattern Trends and Implications for California's Yellow Pine and Mixed Conifer Forests." *Landscape Ecology* 33: 1159–76.
- Stephens, S. L., J. K. Agee, P. Z. Fule, M. P. North, W. H. Romme, T. W. Swetnam, and M. G. Turner. 2013. "Managing Forests and Fire in Changing Climates." *Science* 342(6154): 41–2.
- Stephens, S. L., J. M. Lydersen, B. M. Collins, D. L. Fry, and M. D. Meyer. 2015. "Historical and Current Landscape-Scale Ponderosa Pine and Mixed Conifer Forest Structure in the Southern Sierra Nevada." *Ecosphere* 6(5): 1–63.
- Stephens, S. L., A. L. Westerling, M. D. Hurteau, M. Z. Peery, C. A. Schultz, and S. Thompson. 2020. "Fire and Climate Change: Conserving Seasonally Dry Forests Is Still Possible." *Frontiers in Ecology and the Environment* 18(6): 354–60.
- Stevens, J. T., B. M. Collins, J. D. Miller, M. P. North, and S. L. Stephens. 2017. "Changing Spatial Patterns of Stand-Replacing Fire in California Conifer Forests." *Forest Ecology and Management* 406: 28–36.
- Stevens, J. T., J. E. Miller, and P. J. Fornwalt. 2019. "Fire Severity and Changing Composition of Forest Understory Plant Communities." *Journal of Vegetation Science* 30(6): 1099–109.
- Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. "Evidence for Declining Forest Resilience to Wildfires under Climate Change." *Ecology Letters* 21: 243–52.
- Stevens-Rumann, C., and P. Morgan. 2016. "Repeated Wildfires Alter Forest Recovery of Mixed-Conifer Ecosystems." *Ecological Applications* 26: 1842–53.
- Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. "The Forgotten Stage of Forest Succession: Early-Successional Ecosystems on Forest Sites." *Frontiers in Ecology and the Environment* 9: 117–25.
- Swanston, C. W., L. A. Brandt, P. R. Butler-Leopold, K. R. Hall, S. D. Handler, M. K. Janowiak, K. Merriam, et al. 2020. *Adaptation Strategies and Approaches for California Forest Ecosystems. USDA California Climate Hub Technical Report CACH-2020-1*. Davis, CA: U.S. Department of Agriculture, Climate Hubs.
- Taylor, A. H. 2000. "Fire Regimes and Forest Changes in Mid and Upper Montane Forests of the Southern Cascades, Lassen Volcanic National Park, California, USA." *Journal of Biogeography* 27: 87–104.
- Tepley, A. J., E. Thomann, T. T. Veblen, G. L. Perry, A. Holz, J. Paritsis, T. Kitzberger, and K. J. Anderson-Teixeira. 2018. "Influences of Fire-Vegetation Feedbacks and Post-Fire Recovery Rates on Forest Landscape Vulnerability to Altered Fire Regimes." *Journal of Ecology* 106: 1925–40.
- Thompson, J. R., and T. A. Spies. 2010. "Factors Associated with Crown Damage Following Recurring Mixed-Severity Wildfires and Post-Fire Management in Southwestern Oregon." *Landscape Ecology* 25: 775–89.
- Turner, M. G., K. H. Braziunas, W. D. Hansen, and B. J. Harvey. 2019. "Short-Interval Severe Fire Erodes the Resilience of Subalpine Lodgepole Pine Forests." *Proceedings of the National Academy of Sciences* 116(23): 11319–28.
- Turner, M. G., and W. H. Romme. 1994. "Landscape Dynamics in Crown Fire Ecosystems." *Landscape Ecology* 9: 59–77.
- van Wagtenonk, J. W., and J. A. Fites-Kaufman. 2006. "Sierra Nevada Bioregion." In *Fire in California's Ecosystems*, edited by N. G. Sugihara, J. W. van Wagtenonk, J. A. Fites-Kaufman, K. E. Shaffer, and A. E. Thode, 264–94. Berkeley, CA: University of California Press.
- van Wagtenonk, J. W., K. A. van Wagtenonk, and A. E. Thode. 2012. "Factors Associated with the Severity of Intersecting Fires in Yosemite National Park, California, USA." *Fire Ecology* 8: 11–31.
- Welch, K. R., H. D. Safford, and T. P. Young. 2016. "Predicting Conifer Establishment Post Wildfire in Mixed Conifer Forests of the North American Mediterranean-Climate Zone." *Ecosphere* 7: e01609.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. "Warming and Earlier Spring Increase Western US Forest Wildfire Activity." *Science* 313: 940–3.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Nemens, Deborah G., Kathryn R. Kidd, J. Morgan Varner, and Brian Wing. 2022. "Recurring Wildfires Provoke Type Conversion in Dry Western Forests." *Ecosphere* 13(8): e4184. <https://doi.org/10.1002/ecs2.4184>