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RESEARCH ARTICLE

Fire Regime Alteration in Natural Areas Underscores the Need to Restore a Key Ecological Process

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ABSTRACT: Research Natural Areas (RNAs) are federal lands designated to protect exemplary, relatively undisturbed ecosystems where ecological processes may proceed unencumbered with minimal human intervention. Ideally, RNAs serve as properly functioning reference sites for more heavily managed landscapes. However, many RNAs have been modified to some degree by past and ongoing human actions. In the western United States, these actions commonly result in altered disturbance regimes, most notably fire. Ecological disturbance regimes are important components of natural ecosystems, and major changes to such regimes challenge the usefulness of the RNA system as a reference network. To assess the extent of modern departure from their pre-Euroamerican settlement (i.e., pre-1850) fire regimes, we examined 64 RNAs on Forest Service lands in California. We found that 76% exhibited moderate to high fire regime departure. Of these, 87% are burning much less frequently than they would have under the presettlement fire regime and 13% are burning more frequently. Within RNAs, ecosystems historically characterized by frequent, mostly low-severity fire have missed multiple fire cycles and tend to burn at higher fire severities than expected under the presettlement fire regime. We present four case studies that demonstrate how recent wildfires have affected California RNAs. We also indicate where and how future fire management strategies could address altered fire regimes and more effectively sustain target ecosystems within RNAs. Our findings suggest that a re-examination of the hands-off approach to management in some protected natural areas like RNAs is needed.

Index terms: California, fire regime interval departure, fire severity, reference conditions, Research Natural Area

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INTRODUCTION

Research Natural Areas (RNAs) are part of a national network of federal lands set aside for research, baseline monitoring, education, and biodiversity protection. The USDA Forest Service defines them as: A physical or biological unit in which current natural conditions are maintained insofar as possible. These conditions are ordinarily achieved by allowing natural physical and biological processes to prevail without human intervention (USDA 2005).

In the Forest Service, RNAs are selected to protect unique ecosystems as well as a representative range of terrestrial vegetation and habitat types administered by the agency. These ecosystems are generally classified by their dominant vegetation and are referred to as RNA target elements. One of the principal purposes of RNA designation is to provide a baseline or reference landscape that land managers may use to evaluate long-term ecological change, ecosystem sustainability, or the effects of management actions in equivalent ecosystems not subject to RNA protections (USDA 2005). RNAs are ideally envisioned as an important part of the adaptive management cycle, but their value as unmanipulated controls is subject to at least one major caveat: some of the most important ecological processes occurring in natural landscapes are disturbances, and human management within and adjacent to RNAs has resulted in major alterations to disturbance regimes. For terrestrial ecosystems, this effect is most apparent with fire, and nowhere is this more evident than in forested ecosystems of the western United States (Agee 1993; Sugihara et al. 2006; Parks et al. 2015).

Prior to Euroamerican settlement in the mid-19th century, fire ignited by lightning and Native Americans played a major ecological role in vegetation succession, nutrient and water cycling, and fuel and carbon dynamics (Agee 1993; Sugihara et al. 2006; Safford and Stevens 2017). However, fire suppression policies initiated in the early 20th century with the establishment of the National Forest Reserve System virtually eliminated fire in forests of the western United States. In forest types where presettlement fire was very frequent, the exclusion of fire has had profound ecological effects, including alteration of forest structure, species composition, and ecosystem function (Agee 1993; Sugihara et al. 2006; Knapp et al. 2013; Keeley and Safford 2016; Safford and Stevens 2017). Notable among these effects is the accumulation of fuels and cohorts of younger, fire-intolerant trees that contribute to changes in fire behavior that ultimately increase fire severity (a measure of the ecological impact of fire, quantified often by mortality or biomass loss) when fires burn after long fire-free periods (Steel et al. 2015). The ecological integrity of RNAs in these types of landscapes may be greatly compromised by the long-term lack of fire, resulting in areas that no longer represent the natural condition of the target ecosystems.

At the same time, some landscapes are experiencing notably more fire today than they did before Euroamerican settlement. In southern California, an increase in human-caused ignitions (Keeley and Fotheringham 2001; Syphard et al. 2007), coupled with invasion by easily combustible nonnative annual grasses (D'Antonio and Vitousek 1992), has increased the frequency of fire in highly flammable shrubland ecosystems like sage scrub and chaparral (Underwood et al. 2018). Some moist coastal forests in northern California and sagebrush ecosystems in the Great Basin are also experiencing more fire today than was typical before Euroamerican settlement (Billings 1994; Sugihara et al. 2006). The reference value of RNAs in these landscapes is liable to be compromised by too much fire rather than too little, and under such conditions the ecological sustainability of RNA target vegetation types may be under great threat (Zedler et al. 1983; Haidinger and Keeley 1993).

In this study, we examined contemporary fire regimes in RNAs on Forest Service lands in California. The California national forests support 64 formally established RNAs (Cheng 2004). Dozens of forest and shrubland vegetation types are protected in the California RNA system. These target elements represent the full range of fire regimes presented in Table 1, from vegetation types characterized historically by frequent, mostly low-severity fire (e.g., yellow pine and mixed conifer forests), to ecosystems historically characterized by infrequent, mostly stand-replacing fire (e.g., pinyon-juniper woodlands and chaparral). Our overall objective was to quantify the extent to which vegetation types within the California RNAs are departed from their natural (presettlement) fire regime in terms of fire frequency and severity. Specifically, we asked (1) how far departed are California's RNAs from their presettlement fire frequency, and (2) when contemporary fires burn RNAs, are fire effects (measured as fire severity) similar to what would be expected under the presettlement fire regime? We address these questions and evaluate four specific RNA case studies in California. We conclude by identifying management strategies to promote the long-term sustainability of protected natural areas like RNAs where passive management has been the predominant management action.

METHODS

Study Area

Our study area included 64 formally established RNAs that occur on Forest Service lands in California (Figure 1). California's large land base (423,970 km^2) includes a wide range of climatic zones, elevational gradients, and geology, resulting in exceptionally high plant diversity and endemism (Sugihara et al. 2006). RNAs are distributed across the state, ranging from the coast to the inland desert and from low-elevation valley grasslands to high-elevation alpine ecosystems (Cheng 2004). Elevations range from sea level to nearly 4000 m. California RNAs range in size from 30 ha to over 3000 ha, with an average area of 632 ha; the total area within these RNAs is 40,444 ha. Although it comprises less than 0.5% of Forest Service lands in the state, the RNA network represents most of the dominant terrestrial vegetation types present on Forest Service lands in California. The RNA target elements range from relatively common ecosystems (e.g., yellow pine forest, California black oak

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Table 1. Fire regimes groups (FRGs) categorized by fire frequency and severity (Schmidt et al. 2002).

Fire Regime Group (FRG)	Frequency	Severity
1	0–35 years	Low to mixed severity; surface fires common; less than 25% of the dominant overstory vegetation replaced
2	0–35 years	High severity; stand-replacement; greater than 75% of the dominant overstory vegetation replaced
3	35–100+ years	Mixed severity; between 25% and 75% of the dominant overstory vegetation replaced
4	35–100+ years	High severity; stand-replacement; greater than 75% of the dominant overstory vegetation replaced
5	200+ years	High severity; stand-replacement; greater than 75% of the dominant overstory vegetation replaced

[*Quercus kelloggii* Newb.], mixed conifer forest, and chaparral) to unique and endemic types (e.g., bristlecone pine [*Pinus longaeva* D.K. Bailey], gabbro chaparral, and serotinous conifers). In some cases, these elements represent plant assemblages, unique habitats, or individual species that are not protected in other conservation units (Evenden et al. 2001).

Fire Frequency Departure

We used the California Fire Return Interval Departure (FRID) database (Safford et al. 2015) to assess the similarity between modern and presettlement fire frequencies. This spatially explicit dataset was developed by the USDA Forest Service and quantifies the percent departure based on comparisons between the modern fire return interval (FRI; in this case based on the period 1908–2015) and estimates of the presettlement FRI (i.e., prior to 1850; Van de Water and Safford 2011; Safford and Van de Water 2014). FRI is a measure of the average number of years between fire events (California Department of Forestry and Fire Protection 2017). FRID values are calculated using Eq. (1) when the current FRI is longer than the presettlement estimate and Eq. (2) when the current FRI is shorter than the presettlement estimate (Safford and Van de Water 2014).

$$\text{FRID} = [1 - (\text{Presettlement FRI}) / (\text{Current FRI})] \times 100 \qquad (1)$$

$$\text{FRID} = -[1 - (\text{Current FRI}) / (\text{Presettlement FRI})] \times 100 \qquad (2)$$

FRID values range from −100 to 100, with positive values indicating that vegetation is currently burning less frequently than it would under the presettlement fire regime, and negative values denoting that it is burning more frequently. FRID values are further categorized by the following departure condition classes (CC): (1) low departure, represented by CC1 (FRID: 0% to 33%) and CC-1 (FRID: 0% to −33%), indicating a modern FRI that is 1–1.5 times greater or less than the presettlement FRI; (2) moderate departure, represented by CC2 (FRID: 33% to 67%) and CC-2 (FRID: −33% to −67%), indicating a modern FRI that is 1.5–3 times greater or less than the presettlement FRI; and (3) high departure, represented by CC3 (FRID: >67%) and CC-3 (FRID: < −67%), indicating a modern FRI that is more than 3 times greater or less than the presettlement FRI (Safford and Van de Water 2014).

For this analysis, we used ArcGIS to clip FRID polygons to RNA boundaries and quantified the degree of departure using mean and median percent FRID (Safford and Van de Water 2014). FRID data are only available for ecosystems dominated by woody vegetation, therefore polygons that were dominated by herbaceous vegetation (e.g., meadows, fens, alpine) were excluded from our analysis. Time since last fire was calculated by subtracting the year of the last fire in each polygon from the year the dataset was updated (i.e., 2015); in this analysis, polygons that had not burned since prior to 1908 were assigned a default value of 107 y.

Fire Severity Departure

Fire severity data were obtained from the USDA Forest Service for all fires greater than 40 ha that burned within the California RNAs between 1984 and 2016 (USDA 2017). This dataset estimates fire severity using the Relative differenced Normalized Burn Ratio (RdNBR), which is derived from LANDSAT Thematic Mapper imagery acquired either immediately after the fire or during the first growing season after fire containment (Miller and Thode 2007). For each fire, the USDA Forest Service identified the acquisition that best represented fire effects based on factors such as vegetation type, seasonality, and satellite image quality. In California, RdNBR data have been validated and calibrated using field data, originally using the Composite Burn Index (CBI; Key and Benson 2006; Miller and Thode 2007) and more recently using standard measures of tree mortality, tree basal area, and canopy cover (Miller et al. 2009, 2016). The continuous RdNBR data are then divided into four fire severity categories: (1) unchanged, where post-fire vegetation conditions were indistinguishable from pre-fire conditions; (2) low, where there was little change in cover and low mortality (0–25%); (3) moderate, where conditions were intermediate between low and high with a mixture of effects (25–75% mortality); and (4) high, where the dominant vegetation experienced high to complete loss of cover and, in conifer forest systems, high to complete mortality (>75%; USDA 2017).

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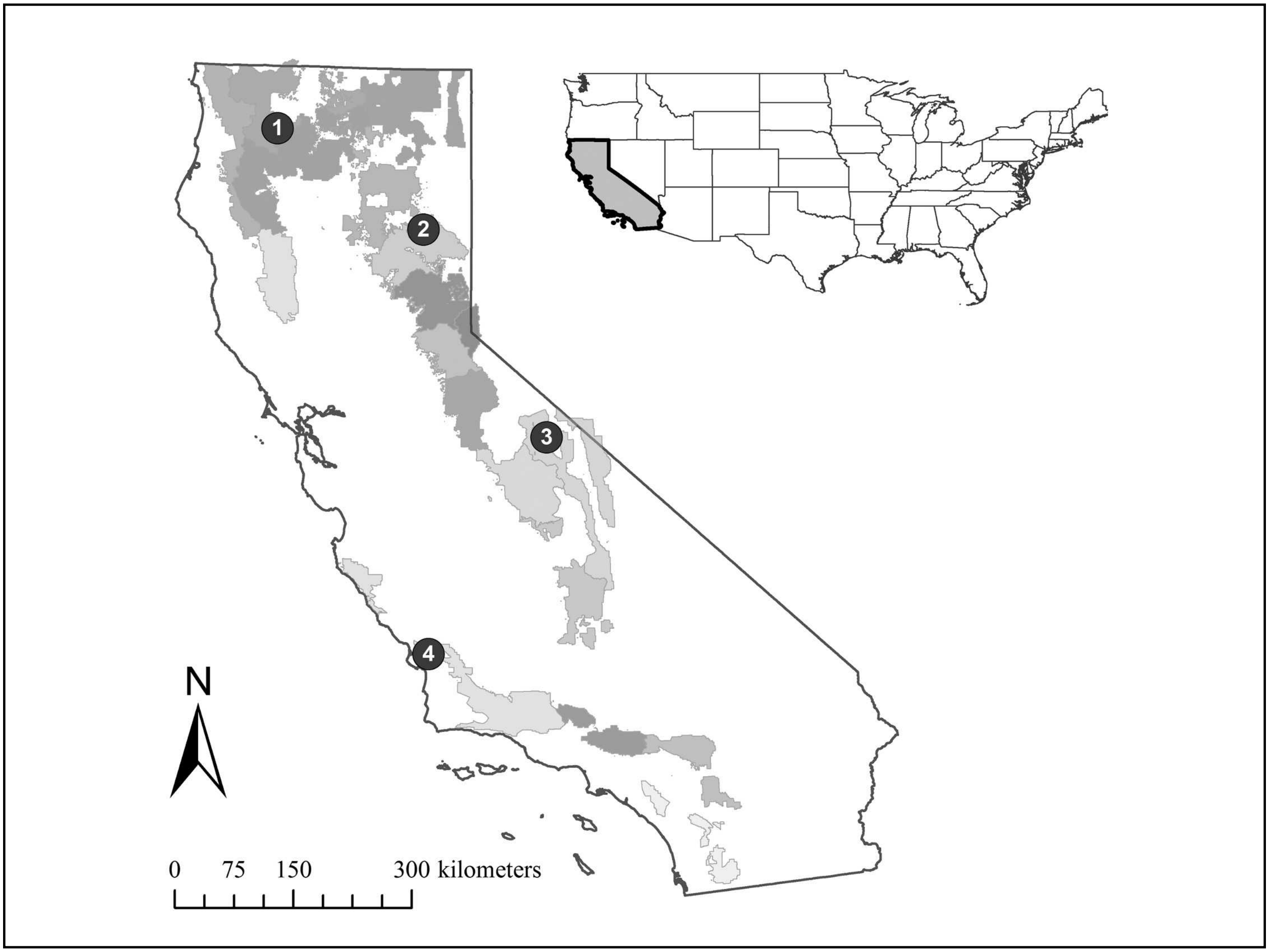

Figure 1. The 64 established RNAs on Forest Service lands (shaded in gray) in California. Numbers correspond to case studies presented in the text: (1) Sugar Creek RNA, (2) Mud Lake RNA, (3) Indiana Summit RNA, and (4) Black Butte RNA.

We examined the potential influence of FRID on fire severity by calculating the proportional distribution of severity classes within each FRID condition class. FRID data corresponding to the year prior to each fire were used for this calculation. We used a simple linear regression to investigate temporal trends (1984–2016) in total area burned, as well as total area burned at high severity, within RNAs. In order to meet the assumption of normality, the total number of hectares was log transformed. For both sets of analyses, we grouped our vegetation data into Presettlement Fire Regime Groups (PFRs, see Table 2; Van de Water and Safford 2011; Safford and Van de Water 2014), and then into Fire Regime Groups (FRGs; Tables 1 and 2). The FRG groupings, which are based on both fire frequency and severity, offer a convenient way to classify, describe, and analyze fire patterns within diverse landscapes. For comparison, we focused on the three most common FRGs found within RNAs (see Table 2): those historically characterized by frequent, low- to moderate-severity fire (FRG 1; 54% of PFRs) and those characterized by more infrequent, high-severity fire (FRGs 4 and 5; 31% of PFRs).

One important caveat for the interpretation of fire severity using NBR-based methodologies is that most assessments that we utilized were completed approximately 1 y after the fire. This method has been shown to accurately capture fire-related structural change in conifer-dominated forests (Lydersen et al. 2016). However, many shrubland and hardwood forest types in California resprout vigorously after fire (Keeley et al. 2008; Cocking et al. 2014). As a consequence, in areas that are dominated by resprouting species, extended fire severity assessments can underestimate the areal extent of stand-replacing fire (Lydersen et al. 2016).

RESULTS

How Far Departed are California's RNAs from Their Presettlement Fire Frequencies?

Our analysis suggests that more than 75%

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Table 2. The 17 presettlement fire regime (PFR) groups identified by Safford and Van de Water (2014) that are represented within California's RNAs. Estimates of presettlement fire return intervals (FRI) are compared to average-weighted means of current FRI, time since last fire (TSLF), and percent fire return interval departure (FRID) metrics. PFRs are presented in order of greatest percent departure to least. Negative values indicate that the PFR is burning more frequently than the reference FRI. Positive values indicate that the PFR is burning less frequently.

Presettlement Fire Regime (PFR)[a]	Characteristic dominant woody species[b]
Yellow pine	*Pinus ponderosa* , *P. jeffreyi* , *P. ponderosa* var. *washoensis* (H. Mason & Stockw.) J.R. Haller & Vivrette, *P. lambertiana* , *Quercus kelloggii*
Oak woodland	*Quercus douglasii* Hook & Arn, *Q. lobata* Née, *Q. wislizeni* A. DC., *Pinus sabiniana* D. Don
Dry mixed conifer	*Pinus ponderosa* , *P. lambertiana* , *Calocedrus decurrens* (Torr.) Florin, *Abies concolor, Quercus kelloggii*
Moist mixed conifer	*Abies concolor, Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* , *Calocedrus decurrens* , *Pinus ponderosa* , *P. lambertiana* , *P. contorta* ssp. *murrayana* (Grev. & Balf.) Critchf., *Sequoiadendron giganteum* (Lindl.) J. Buchholz
Lodgepole pine	*Pinus contorta* ssp. *murrayana*
Red fir	*Abies magnifica* A. Murray bis, *A. concolor* , *Pinus montícola* Douglas ex D. Don, *P. contorta* ssp. *murrayana*
Coastal sage scrub	*Artemisia californica* Less., *Baccharis pilularis* DC., *Eriogonum fasciculatum* Benth., *Salvia* spp.
Montane chaparral	*Arctostaphylos* spp., *Ceanothus* spp., *Quercus vacciniifolia* Kellogg, *Prunus ilicifolia* (Nutt. ex Hook. & Arn.) D. Dietr., *Chrysolepis sempervirens* (Kellogg) Hjelmq., other shrubs
Big sagebrush	*Artemisia tridentata* Nutt., *Purshia tridentata* (Pursh) DC., *Chrysothamnus* spp.
Curl-leaf mountain mahogany	*Cercocarpus ledifolius* Nutt.
Black and low sagebrush	*Artemisia nova* A. Nelson, *A. arbuscula* Nutt.
Mixed evergreen	*Pseudotsuga menziesii* , *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, C.H. Cannon & S. Oh, *Quercus agrifolia* Née, *Q. chrysolepis* Liebm. , *Umbellularia californica* (Hook. & Arn.) Nutt., *Arbutus menziesii* Pursh, *Acer macrophyllum* Pursh, *Taxus brevifolia* Nutt.
Bigcone Douglas-fir	*Pseudotsuga macrocarpa* (Vasey) Mayr, *Quercus chrysolepis*
Chaparral/ serotinous conifers	*Adenostoma* spp., *Arctostaphylos* spp., *Ceanothus* spp., *Quercus berberidifolia* Liebm. other shrubs; *Pinus attenuata* , *P. muricata* D. Don, *Hesperocyparis* spp., other serotinous conifers
Redwood	*Sequoia sempervirens* (D. Don) Endl.
Pinyon juniper	*Pinus monophylla* Torr. & Frém., *Juniperus* spp.
Subalpine forest	*Tsuga mertensiana* (Bong.) Carrière, *Pinus albicaulis* Engelm., *P. monticola* , *P. contorta* ssp. *murrayana* , *P. flexilis* James, *P. balfouriana* Grev. & Balf., *P. longaeva* , *Abies magnifica*

[a] Excludes PFRs with less than 100 ha (total) in RNAs.
[b] From Van de Water and Safford (2011); species names have been updated to reflect current taxonomy.
[c] weighted-area mean

of the area encompassed by RNAs in California exhibits moderate to high departures from presettlement FRIs (Figure 2). Across the California RNAs, 44% of lands are currently classified as highly departed (CC3 and CC-3) and 32% are moderately departed (CC2 and CC-2); only 23% are estimated to have low departure (CC1 and CC-1). Of the 26,848 ha estimated to be moderately to highly departed, 87% are burning less frequently than they would have under the presettlement fire regime and 13% are burning more frequently. Seventeen RNAs (27% of total) have not had a wildfire or prescribed fire recorded within their boundary since before 1908, and 50% of the total area contained within RNAs has not burned in at least 107 y.

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Table 2. (*Continued*)

Number of RNAs with PFR	Fire Regime Group	Total area (ha) in RNA (% of total)	Mean reference FRI (yrs)[b]	Current FRI (yrs)[c]	TSLF (yrs)[c]	Mean FRID (%)[c]	Median FRID (%)[c]
29	1	3193.4 (9%)	11	91.2	83.7	85.6	90.8
11	1	1057.2 (3%)	12	81.3	77.1	83	83
23	1	3506.8 (10%)	11	71.6	53	80.8	84.3
36	1	5714.5 (16%)	16	82.2	67.6	76.9	82.7
10	4	772.4 (2%)	37	104.8	102.4	63.7	64.7
18	3	2087.4 (6%)	40	102.6	99	59.2	66.3
6	4	150.1 (<1%)	76	34.8	28.7	−54.4	−65.2
34	2/4	2380.4 (7%)	26	67.6	44	53.8	57.4
11	4	987 (3%)	35	87.8	83	52.9	45
4	3	334.3 (1%)	52	106.7	105.1	50.7	41.3
9	5	734.3 (2%)	66	105	103.8	35.7	48.2
33	1	5084.5 (15%)	29	53.9	34.3	33.8	70.1
6	3	635.6 (2%)	31	50.4	14.4	31.7	33.8
34	4	4696.4 (13%)	55	46.1	33.7	−21.7	−26.3
2	1	185.6 (1%)	23	47	36.8	17.6	45.7
7	4	1431.1 (4%)	151	101.6	101.6	−7.4	6.3
15	4	1849.7 (5%)	133	105.7	103.7	−2.5	−2.5

The degree of departure varied among the 17 PFR groups represented within California's RNAs (Table 2). The highest departures (area-weighted mean FRID >67%) were in yellow pine forest, oak woodland, and dry and moist mixed conifer forest types. These PFRs are currently burning much less frequently than before Euroamerican settlement, with current FRIs between five and eight times longer than estimated presettlement return intervals. Coastal sage scrub, which is found primarily in southern California, had a mean departure of −54%, indicating that on average, this PFR is burning more than twice as often as under the presettlement fire regime. Chaparral/serotinous conifer also had a shorter FRI compared to the reference estimate (statewide area-weighted mean: −21.7%) and was generally more departed in southern California RNAs

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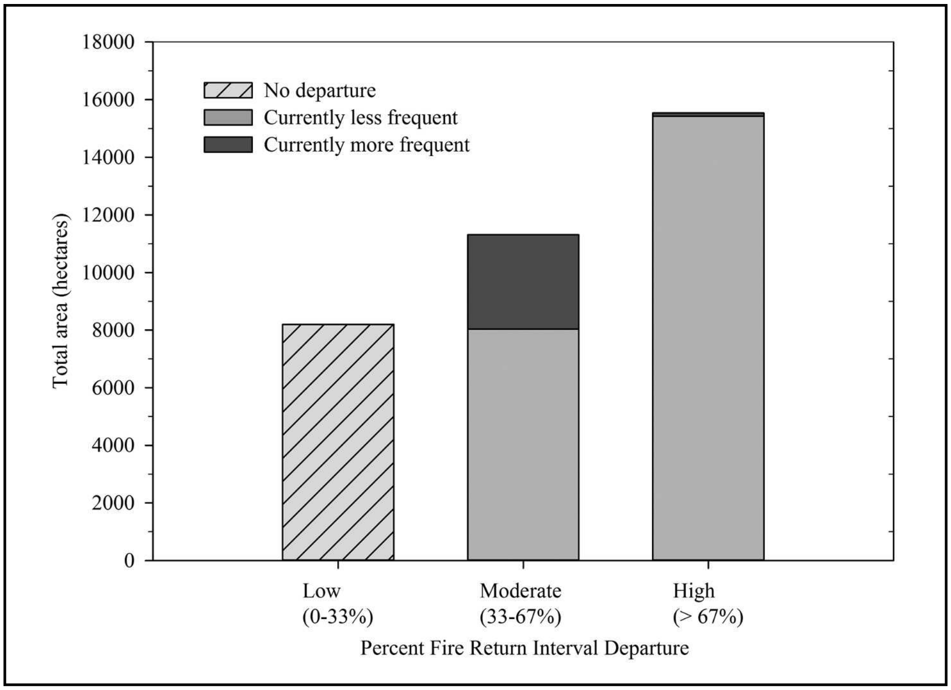

Figure 2. Estimate of the percent departure in fire return interval for the 64 established RNAs in California. Light gray bars represent the total number of hectares currently burning less frequently than expected under a presettlement fire regime (PFR). Dark gray bars represent the total hectares within RNAs currently burning more frequently than the PFR. Percent departure is classified as low (0–33% departure), moderate (33–67% departure), or high (greater than 67% departure).

(mean FRID −36%) than in the rest of the study area (mean FRID: −3%).

When RNAs Burn, are Modern Fire Severities Similar to Presettlement Fire Severities?

Fire severity data were available for 46 fires within 34 RNAs. The area burned within the RNAs ranged in size from 0.7 ha to 2010 ha (average 441 ha). In areas characterized historically by a more frequent, low- or moderate-severity fire regime (FRG 1), the greatest proportion (35%) of high-severity fire occurred in areas that had burned much less frequently over the previous 107 y than was characteristic of the presettlement fire regime (CC3; Figure 3a). In contrast, fires burning in areas with low (CC1 and CC-1) and moderate (CC2) departure had smaller proportions of the landscape burn at high severity (9% and 18%, respectively).

Systematic differences among departure classes were less apparent in areas that were characterized by more infrequent, high-severity presettlement fire regimes (FRGs 4/5; Figure 3b). Areas that are currently burning more frequently than expected under a presettlement fire regime (CC-3) had the lowest proportion of high-severity fire (20%). In all other condition classes, high-severity fire comprised the largest proportion of the burned landscape, ranging from 37% to 60%. These results indicate that the relationship between FRI and severity in these ecosystem types is not inversely related as it is in FRG 1 systems (Steel et al. 2015; Safford and Stevens 2017). However, it is also important to note that the actual amount of high-severity fire in FRG 4/5 ecosystems may be higher than our data suggest, due to the resprouting of vegetation between the fire date and the date of postfire LANDSAT imagery capture (see Methods for details).

Our analysis of high-severity fire patterns over time revealed differences between FRG 1 and FRGs 4/5 (Figure 4). For FRG 1, we found a statistically significant linear increase in the total number of hectares burned at high severity within RNAs between 1984 and 2016 ($P = 0.003$; $R^2 = 0.12$). We found no significant relationship between fire year and total number of hectares burned at high severity for FRGs 4/5. We also found no significant trend in the total area burned within the RNAs between 1984 and 2016 ($P = 0.14$; $R^2 = 0.45$).

RNA CASE STUDIES

The case studies presented below demonstrate how fire regime alteration and recent wildfires have impacted four of the California RNAs.

Indiana Summit RNA: Prescribed Burning before a Wildfire

Located on the western slope of the Glass Mountains on the Inyo National Forest, the Indiana Summit RNA (470 ha; 37°49′N, 118°55′W) was established in 1932 as the first RNA in California. The RNA protects one of the last remnant old-growth stands of Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) in the eastern Sierra Nevada, with noted importance to the local Paiute Tribe who harvest the larvae of pandora moths (*Coloradia pandora*) that are associated with mature Jeffrey pine trees. This forest type is adapted to frequent, low- to moderate-severity fire (mean FRI = 11 y, range 5–40 y; Van de Water and Safford 2011, Safford and Stevens 2017). However, prior to 2016, only one 16-ha wildfire had burned in 1986 within the RNA boundary and the mean FRID for the unit was 89%.

In the late 1990s, managers treated 30 ha (6%) of the RNA with prescribed fire (Ryan et al. 2013), which resulted in reduced small tree densities, decreased surface fuel loading, and increased mean tree diameter (Figure 5, upper left). In 2016, the Clark Fire ignited after 4 y of drought and burned most of the RNA under high wind conditions. An estimated 35% of the RNA experienced high-severity fire effects (i.e., >75% loss in canopy cover), including one large (115 ha) high-severity patch that covered 25% of the RNA. Comparisons between areas that were treated prior to the Clark Fire and areas that were untreated found that fire severity patterns (e.g., proportion of high-severity fire and patch size) within the prescribed burn units were similar to what would be expected under

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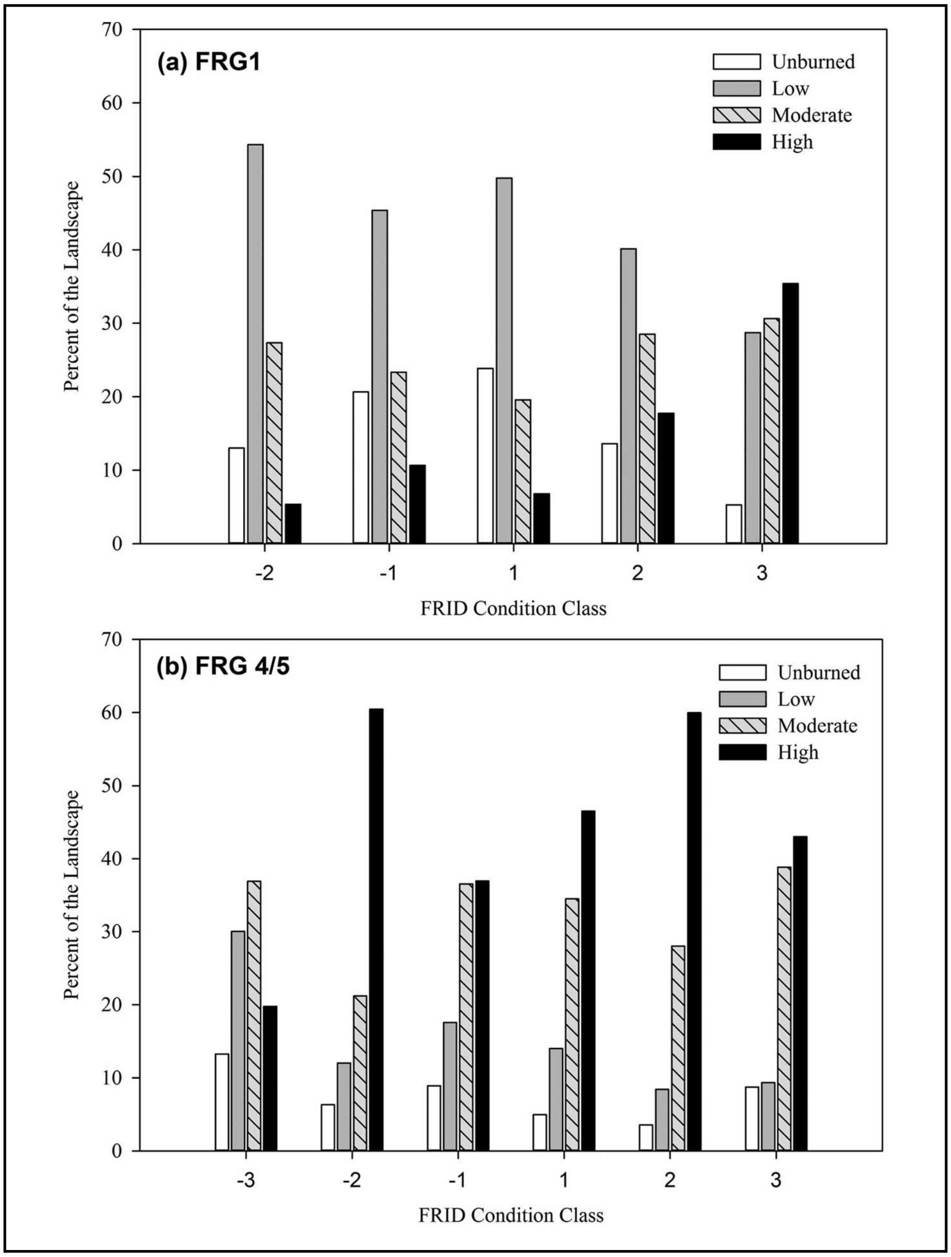

Figure 3. Proportional distribution of fire severity classes within each FRID condition class, across all RNAs that burned between 1984 and 2016. Top figure (a) includes presettlement fire regime groups characterized by frequent and low- to mixed-severity fire (FRG 1) and the lower figure (b) includes those characterized by infrequent, high-severity fire (FRG 4/5).

a presettlement fire regime (Safford and Stevens 2017). Monitoring data collected following the Clark Fire documented bole char and tree scorch heights that were 3 and 2.5 times lower, respectively, in prescribed burn units than untreated areas. Post-fire live tree densities (140 trees/ha) in prescribed burn units were almost identical to the average tree densities reported from reference landscapes and historic stand inventories of yellow pine forests (144 trees/ha; Safford and Stevens 2017). Moreover, the density of large trees (>75 cm dbh) within the prescribed burn units did not change as a result of the Clark Fire, while large tree densities declined by half in portions of the RNA that had not been treated. These observations suggest that the Clark Fire helped to restore stand structure and resilience within the portion of the RNA that was previously treated with prescribed fire, but had the opposite effect in areas that were left untreated. Many of the untreated areas burned at high severity, where the current absence of live trees, tree regeneration, and other vegetation cover (e.g., shrubs) could result in the permanent loss of Jeffrey pine forest.

Mud Lake RNA: Managed Wildfire as a Restoration Tool

Mud Lake RNA (154 ha in two units; northern unit: 40°10′N, 120°42′W), situated in the northern Sierra Nevada on the Plumas National Forest, is one of the few RNAs currently burning at a frequency similar to the presettlement FRI. Mud Lake RNA was established in 1989 to protect two isolated stands of Baker cypress (*Hesperocyparis bakeri* [Jeps.] Bartel), a rare serotinous conifer that is adapted to infrequent, stand-replacing fire (FRI range = 30–90 y; Van de Water and Safford 2011). High-severity fire in these stands facilitates seed dispersal by opening cones, creates conditions for seed germination and establishment, and reduces competition from other conifers (Vogl et al. 1977). Under a natural fire regime, many cypress stands grow in almost pure monocultures of even-aged individuals with few other conifer species (Vogl et al. 1977). Monitoring of the RNA in 2006 after a long period of fire exclusion (estimated 95 y), documented an increase in the abundance of white fir (*Abies concolor* [Gordon & Glend.] Lindl. ex Hildebr.) and high levels of cypress mortality. Baker cypress represented only 28% of total stand density, and 87% of cypress individuals were dead or dying. There was significant concern that without immediate action to reintroduce fire to this population, the Baker cypress might be extirpated.

In 2007, the Moonlight Fire burned the northern unit of the Mud Lake RNA. Clear and immediate communication between resource specialists and fire management personnel prevented suppression of the fire within the RNA and allowed for a significant portion (67%) of the Baker cypress stand to burn at high intensity. Post-fire monitoring documented substantial Baker cypress regeneration after the Moonlight Fire (Figure 5, upper right). Seedling densities of up to 85 individuals

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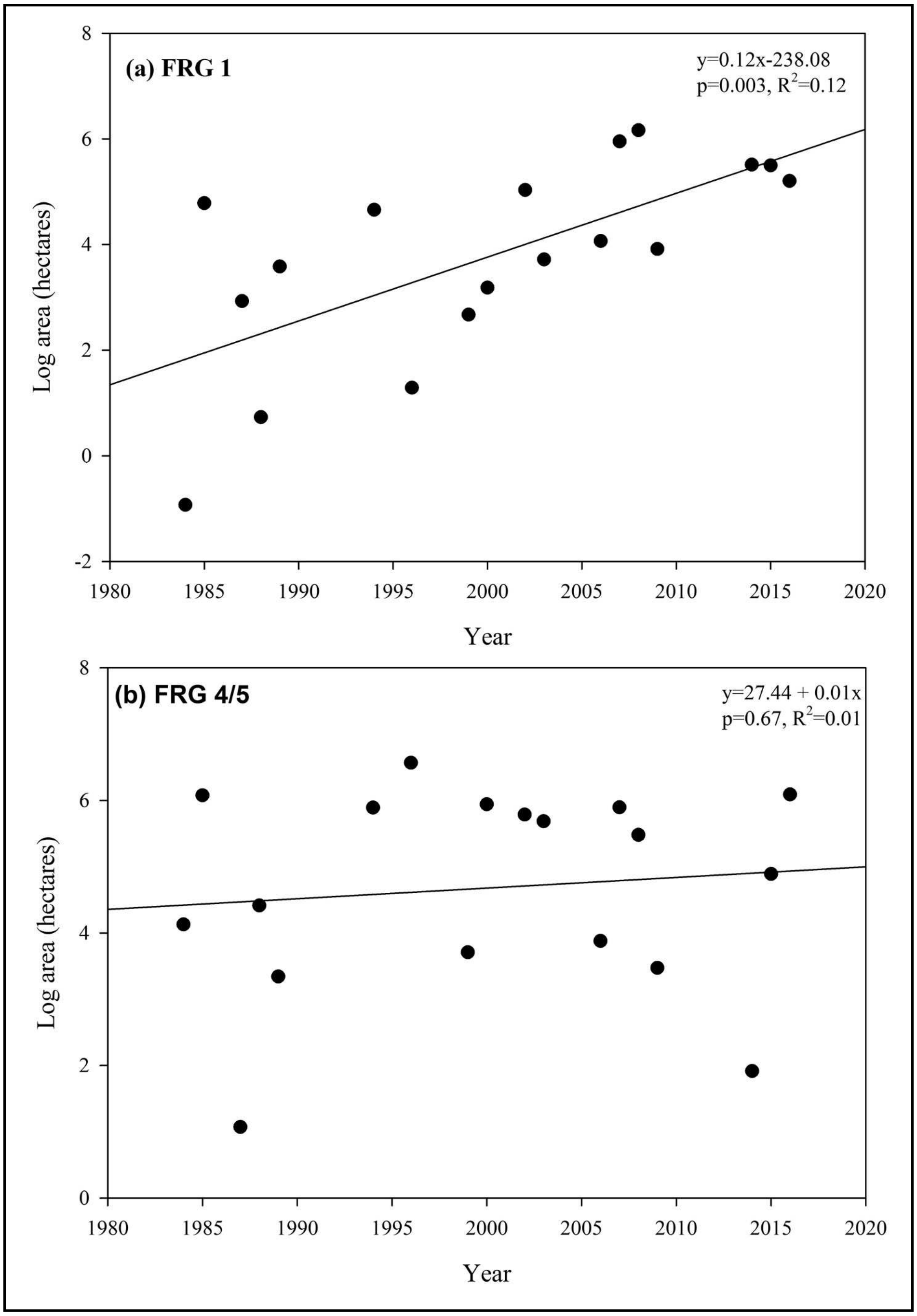

Figure 4. Trend in total area (log hectares) burned by high-severity fire between 1984 and 2016 within California's RNAs. The top figure (a) includes data for areas historically characterized by a frequent, low-severity fire regime (FRG 1) and the lower figure (b) includes areas historically characterized by infrequent, high-severity fire (FRG 4/5).

m^{-2} were recorded in plots with only three living cypress trees prior to the fire, and fire severity was the strongest predictor of post-fire seedling density. Although the Baker cypress stands in the Mud Lake RNA are currently burning at a frequency consistent with their presettlement FRI, the developing stand now faces another management dilemma. The high abundance of white fir (70% of total stand density) in the Baker cypress stands prior to the Moonlight Fire resulted in a high density of snags (72 trees ha^{-1}) throughout most of the RNA, creating a potential fire hazard that will likely increase over time as snags fall and contribute to surface fuel loads (Coppoletta et al. 2016). The Baker cypress that germinated after the Moonlight Fire have not yet produced cones, and another fire in the Mud Lake RNA would likely eliminate the population if it were to occur before cypress trees mature (35–50 y; Rentz and Merriam 2009).

Black Butte RNA: Fire Exclusion as the Appropriate Course of Action

The rugged topography and steep elevational gradients within Black Butte RNA (218 ha; 35°18′N, 120°40′W) support a diverse flora, including knobcone pine (*Pinus attenuata* Lemmon) and chaparral stands dominated by chamise (*Adenostoma fasciculatum* Hook. & Arn.) in drier areas and interior live oak (*Quercus wislizeni* A. DC.) on more mesic slopes (Figure 5, lower right). Most vegetation types in the RNA are adapted to stand-replacing fire, occurring at intervals ranging between 30 and 90 y (mean FRI = 55 y; Van de Water and Safford 2011). However, like many chaparral and serotinous conifer–dominated RNAs in southern California, the Black Butte RNA is burning more frequently (mean FRID: −54%) than was characteristic of the presettlement fire regime. The RNA is embedded within the Santa Lucia Wilderness on the Los Padres National Forest. However, it is also located in close proximity to a major highway and dense suburban housing. As a result of anthropogenic ignitions, the vegetation within the RNA has burned multiple times during the analysis period, with seven fires recorded between 1916 and 2015 (California Department of Forestry and Fire Protection 2017).

High fire frequencies in chaparral and serotinous conifer ecosystems can cause localized extinction of obligate-seeding shrubs and serotinous trees, while favoring disturbance-tolerant nonnative annual grasses (Zedler et al. 1983; Haidinger and Keeley 1993). In 1994, the Highway 41 Fire burned an 8-year-old stand of knobcone pine in the Black Butte RNA. An evaluation of the stand's immaturity risk (i.e., inability to establish a suitable seed bank between disturbance events) by Keeley and others (1999) determined that, while the

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Figure 5. Photographs from the four RNA case studies. Clockwise from the top left: Jeffrey pine stand within a prescribed fire unit in the Indiana Summit RNA; dense regeneration of Baker cypress following the 2007 Moonlight Fire; a fuel break constructed along the southern edge of the Black Butte RNA; and a diverse coniferous forest within the Sugar Creek RNA.

knobcone pine were able to produce cones between fires (1985 to 1994), 20% of the surveyed landscape lacked any regeneration. They concluded that post-fire seedling recruitment would likely be insufficient to replace pre-fire stand densities. Since the establishment of Black Butte RNA in 1998, numerous human-caused fires have been extinguished before reaching the RNA, and three fires have been held along its edges, underscoring the persistent threat from frequent wildfires to this RNA.

Sugar Creek RNA: On the Brink and in Need of Action

Sugar Creek RNA (1604 ha; 41°17′N, 122°56′W) is located in the Russian Wilderness on the Klamath National Forest (Figure 5, lower left) and supports the most diverse coniferous forest in the world (Kauffmann 2012). The intersection of four distinct floristic provinces, as well as high geological and topographic variation, results in exceptional biological diversity, including 18 conifer species, almost 500 native herbaceous plant species, and habitat for rare and endangered wildlife. Lower elevations support a mosaic of old-growth mixed conifer forest with >500-year-old sugar pine (*Pinus lambertiana* Douglas) and ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) and younger successional stands associated with past fire activity (FRG 1; 35% of the RNA). Higher elevations support open upper montane and subalpine forests

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with rock outcroppings, low understory vegetation, and low fuel loads (FRGs 3 and 4; 49% of the RNA). The RNA has not experienced a large fire in over 100 y and the lower-elevation forests are highly departed from historical reference conditions (mean FRID = 77%). Fire exclusion has led to high densities of shade-tolerant firs (*Abies* spp.), very heavy fuel loads and continuity, and the loss of large old-growth fire-dependent ponderosa and sugar pines, particularly within the lower elevations of the RNA. The Klamath National Forest recently completed a management plan for the RNA that identifies areas of concern and proposes mitigation measures, such as the introduction of prescribed fire. If these management actions are not implemented, a lightning-caused wildfire or human ignition from adjacent private lands below the RNA could pose a significant threat to the maintenance of this unique, species-rich assemblage of conifers.

DISCUSSION

Our examination of RNAs in California revealed patterns of fire regime departure that closely align with other studies conducted at broader scales on public lands across the western United States (Mallek et al. 2013; Safford and Van de Water 2014; Parks et al. 2015; Steel et al. 2015). Anthropogenic alterations to natural fire regimes have resulted in significant changes in fire frequency, with fewer fires occurring in forests historically characterized by frequent fire (FRG 1 ecosystems) and more frequent fires occurring in vegetation types that experienced infrequent stand-replacing fires prior to Euroamerican settlement (FRG 4/5 ecosystems). We demonstrate that these broader patterns are also occurring in natural areas like RNAs, which were set aside with the explicit goal of allowing ecological processes to proceed with minimal human intervention (Agee 2002).

Like many protected areas, a hands-off course of action has been the predominant approach to stewardship in California's RNAs. However, these natural areas are embedded within a matrix of federal lands, where in many cases fire as a natural process has not been allowed to perform its historical role due to fire suppression policies implemented across the larger landscape. This lack of fire was evident in our comparison of presettlement and contemporary fire regimes, where we found that 44% of California's RNAs were highly departed in terms of fire frequency (CC3, Figure 2). Within these areas, many historically frequent-fire ecosystems (FRG 1) have missed three or more fire cycles. When contemporary fires re-enter these RNAs after a long fire-free period, there is increased risk that they will burn at high severity (Figure 3a), and our data indicate that this trend has significantly increased over the past 30 y (Figure 4a). Safford and Stevens (2017) conducted an extensive review of historical accounts and empirical studies and estimated that the proportion of high-severity fire in presettlement yellow pine–mixed conifer forest types in California rarely exceeded 10% (natural range of variation 3–15%). In the RNAs that we studied, highly departed areas (CC3) that supported historically frequent-fire vegetation types (FRG 1) had approximately 35% of the landscape burn at high severity over the past 32 y. In these same vegetation types, we found that areas with fire frequencies approximating the presettlement FRI (CC1 and CC-1) had a lower proportion of high-severity fire (6% and 11%), well within Safford and Stevens's (2017) estimated natural range of variation. This greater proportion of high-severity fire in CC3 ecosystems is likely due to increased live and dead fuel loads and greater horizontal and vertical continuity of fuels, both of which have been linked to fire exclusion in historically frequent-fire forests of the western United States (Safford and Stevens 2017).

An increase in fire frequency in ecosystems where fire is naturally infrequent can also have significant impacts on biodiversity patterns, community composition, vegetation structure, and ecosystem processes (Zedler et al. 1983; Sugihara et al. 2006; Safford and Stevens 2017). In California, 12 (19%) RNAs have been designated to protect serotinous conifer species, many of which are rare or endemic to California (e.g., Baker cypress and Cuyamaca cypress [*Hesperocyparis stephensonii* (C.B. Wolf) Bartel]). These species are highly sensitive to fire regime alteration (Vogl et al. 2007). Shortened fire return intervals can kill trees prior to reproductive maturity or the development of a sufficient seed bank (see Black Butte RNA case study), whereas extremely long fire-free periods can lead to population and seed bank senescence or facilitation of invasion by more shade-tolerant competitive species (see Mud Lake RNA case study; Vogl et al. 1977).

We found that many of the RNAs in our study area are highly departed from their natural ecological condition with regard to fire regime. Our case studies provide additional insight into how fire regime departure can have a substantial impact on an RNA's ecological values. These findings suggest that many California RNAs are at an important crossroads, where proactive management actions (i.e., fire use, fuel manipulation, or in some cases fire suppression) may be needed to restore and maintain the natural fire regime before ecological resilience is lost and ecological thresholds passed.

Management Strategies to Address Altered Fire Regimes

Encourage Research and Monitoring

The wide range of vegetation types and ecological conditions within RNAs, coupled with more restrictive management options, can make stewardship of these protected areas highly complex. As such, scientific research and monitoring play a crucial role in informing and developing effective RNA management strategies. Mud Lake RNA offers an excellent example of this, where prior monitoring of Baker cypress stands provided key information to support science-informed fire management decisions during the 2007 Moonlight Fire. Long-term monitoring data collected within the Sugar Creek RNA has also played an integral part in the identification of areas to target for prescribed fire treatments.

Unfortunately, aside from the original reports and surveys conducted as part of the RNA establishment process, many of the RNAs in California remain largely understudied. Encouraging research and

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monitoring within these unique landscapes can provide essential information to land managers, forming the foundation for science-based decisions that will benefit the integrity of these important reference sites as well as the managed lands beyond their borders.

Develop RNA Wildfire Management Strategies

Consideration of disturbance processes like fire is essential to natural area stewardship in California and other western states (Agee 2002). In many RNAs, appropriate fire management requires scientific input and planning on a site-specific basis, so that fires can occur at an ecologically appropriate frequency, scale, and intensity (Meyer et al. 2015). In areas where fire is likely to benefit the ecological values within the RNA, and suppression actions are not required to protect life, property, or significant resource values, management of wildfires for resource objectives is an appropriate course of action (Meyer 2015). In other areas, where RNA target elements may be threatened by too-frequent fire, measures may be required to protect fire-sensitive ecosystems or habitats. In these cases, public education and outreach may be necessary to reduce ignitions, in addition to pre-fire planning that facilitates a rapid and effective suppression response. When fire suppression within an RNA is necessary, minimum impacts suppression tactics (MIST) should be followed whenever possible (adapted from USDA 2007). These include avoiding the use of heavy equipment to construct fire lines; prioritizing the use of hand tools, hand-lines, and water drops; and allowing fires to burn to natural barriers. In almost every case, successful fire management will depend on conditions beyond the border of the RNA, requiring a cooperative, interdisciplinary, and landscape approach. An example of a fire suppression and rehabilitation policy, developed by the Pacific Southwest Region's RNA Committee, is provided in Appendix 1.

Consider Proactive Restoration to Increase Resilience to Future Disturbance

The small size of many RNAs, their proximity to private lands where the risk of fire escape is too great, or the high degree of departure from the natural fire regime may result in situations where wildfires simply cannot be allowed to burn. In some cases, prescribed burning may be utilized to maintain or restore the ecological conditions of the RNA (Ryan et al. 2013). In others, prescribed fire or thinning may be implemented to reduce fuel loading and increase the likelihood that future wildfires burn at intensities consistent with the natural fire regime. The benefits of this proactive approach were evident in the Indiana Summit RNA, where prescribed burning conducted prior to the 2016 Clark Fire reduced wildfire severity and wildfire-related large tree mortality. In portions of Sequoia, Kings Canyon, and Yosemite National Parks, managers have also successfully used prescribed fire to reduce heavy fuel loads in wilderness areas prior to managing lightning fires for resource benefits (Parsons et al. 1986).

Although direct manipulation of vegetation is discouraged in RNAs, Forest Service regulations permit tree cutting if necessary to restore an area to a more natural condition (USDA 2005). Although such actions are uncommon, thinning has been planned and/or implemented in a few of the region's RNAs. For example, beetle-killed trees were removed from Shasta Mudflow RNA to protect the neighboring town of McCloud from elevated fire hazard. Limited removal of non-cypress conifers in the Mud Lake RNA was also planned as part of a Baker cypress restoration project prior to the 2007 Moonlight Fire. Forest thinning in RNAs has also been carried out in other Forest Service regions. For example, in the Sawmill Creek RNA on the Bitterroot National Forest in Montana, managers removed small conifers in the understory in preparation for a prescribed fire treatment (Evenden et al. 2001).

CONCLUSION

Although the focus of this study is on California RNAs, the results and recommendations are likely applicable to many protected natural areas in the western United States (Agee 2002). Protected from direct manipulation, natural areas like RNAs offer some of our best approximations of minimally disturbed ecosystems on public lands. Because of this, they often provide unparalleled opportunities for non-manipulative research, monitoring of long-term ecological change, and public education, and as controls for management actions in equivalent ecosystems. The long-term exclusion of fire from historically frequent-fire ecosystems, as well as the increase in fire frequency in ecosystems adapted to long fire-free periods, puts many of the target elements within RNAs at risk of degradation or loss. In many cases, monitoring and proactive resource stewardship are essential to ensure that disturbance processes, such as fire, can proceed in an ecologically beneficial manner. Without restoration or maintenance of the natural fire regime, the ecological value of some natural areas as reference ecosystems and reservoirs of biodiversity will be lost.

NOTE: Refer to BioOne for supplementary materials Appendix 1 - Example of a fire suppression and rehabilitation policy, developed by the Pacific Southwest Region's RNA Committee

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