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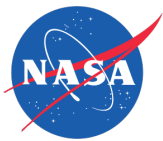
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Does short-interval fire inhibit postfire recovery of chaparral across southern California?

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Abstract

Regrowth after fire is critical to the persistence of chaparral shrub communities in southern California, which has been subject to frequent fire events in recent decades. Fires that recur at short intervals of 10 years or less have been considered an inhibitor of recovery and the major cause of 'community type-conversion' in chaparral, primarily based on studies of small extents and limited time periods. However, recent sub-regional investigations based on remote sensing suggest that short-interval fire (SIF) does not have ubiquitous impact on postfire chaparral recovery. A region-wide analysis including a greater spatial extent and time period is needed to better understand SIF impact on chaparral.

This study evaluates patterns of postfire recovery across southern California, based on temporal trajectories of Normalized Difference Vegetation Index (NDVI) derived from June-solstice Landsat image series covering the period 1984–2018. High spatial resolution aerial images were used to calibrate Landsat NDVI trajectory-based estimates of change in fractional shrub cover (dFSC) for 294 stands. The objectives of this study were (1) to assess effects of time between fires and number of burns on recovery, using stand-aggregate samples ($n = 294$) and paired single- and multiple-burn sample plots ($n = 528$), and (2) to explain recovery variations among predominant single-burn locations based on shrub community type, climate, soils, and terrain. Stand-aggregate samples showed a significant but weak effect of SIF on recovery ($p < 0.001$; $R^2 = 0.003$). Results from paired sample plots showed no significant effect of SIF on dFSC among twice-burned sites, although recovery was diminished due to SIF at sites that burned three times within 25 years. Multiple linear regression showed that annual precipitation and temperature, chaparral community

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Emanuel A. Storey: Conceptualization, Investigation, Formal analysis, Writing - original draft. **Douglas A. Stow:** Supervision, Methodology, Project administration, Writing - review & editing. **John F. O'Leary:** Writing - review & editing, Validation. **Frank W. Davis:** Conceptualization, Methodology. **Dar A. Roberts:** Formal analysis, Software, Writing - original draft.

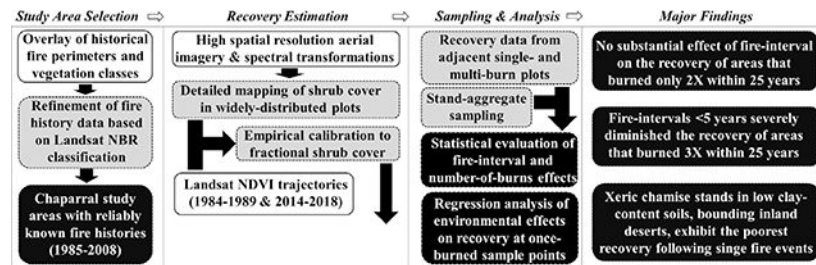
Declaration of competing interest

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type, and edaphic variables explain 28% of regional variation in recovery of once-burned sites. Many stands that exhibited poor recovery had burned only once and consist of xeric, desert-fringe chamise in soils of low clay content.

Graphical Abstract



Keywords

Fire regime; Postfire recovery; Time series; Chaparral succession; Desertification

1. Introduction

1.1. Background

The spatial structure and composition of terrestrial plant communities are shaped over long periods of time by interactions with climate, soils, topography, ecological processes, and natural disturbances (Turner, 1989). Fire disturbances in particular affect the composition, size, age, and spatial distribution of vegetation habitat patches comprising landscapes (Bormann and Likens, 2012; Prichard et al., 2017). Changes in spatial-temporal patterns (regimes) of fire have occurred in recent decades in many of regions the world; these changes are driven strongly by anthropogenic ignitions, land cover transformations, and climatic change (Bond and Keeley, 2005; Jolly et al., 2015; Balch et al., 2017). Altered disturbance regimes may shift plant communities onto abnormal successional trajectories (Turner, 2010). Structural and compositional change in vegetation can impact faunal habitat connectivity, carbon storage, important ecosystem services, and future fire behavior (Costanza et al., 1997; Prichard et al., 2017; Wohlgemuth and Lilley, 2018). Prediction of vegetation responses to shifting disturbance regimes may prove crucial for environmental conservation in many regions.

This study is concerned with fire-prone evergreen sclerophyllous shrub communities in the Mediterranean-type climate zone of southern California (hereafter: *chaparral*). The chaparral biome is a global priority in biodiversity conservation, owing to its exceptional richness of fauna and endemic vascular plants, coupled with imminent threats from human activity (Cowling et al., 1996; Rundel, 2018). These threats include destruction of habitat, propagation of exotic herbs, and abnormally frequent fires resulting from artificial ignitions, extreme föhn winds, and elevated vapor pressure deficits linked to changing climate (Syphard et al., 2007; Moritz et al., 2010; Seager et al., 2015). Potential consequences of

frequent fire in chaparral warrant scientific study to support management of fuels, watersheds, and conserved lands (Underwood et al., 2018).

Estimates of historical fire frequency in chaparral range from 25 to 65 years (Keeley, 1982; Lombardo et al., 2009). Many chaparral species establish mature canopies within 10 years after fire (Henry and Hope, 1998; McMichael et al., 2004; Hope et al., 2007). However, postfire reestablishment can decline in obligate-seeding chaparral species that are afforded insufficient time between fires (< 5–15 years) to replenish seed banks (Zedler et al., 1983; Zedler, 1995; Jacobsen et al., 2004). Recovery of obligate resprouting species can also diminish after short-interval fire due to reduction of carbohydrate storage, which inhibits vegetative regrowth and can be aggravated by climatic extrema (Pratt et al., 2014). Development of gaps and vacant areas due to limited shrub recovery within closed-canopy chaparral enables colonization by invasive grass or sage scrub species, leading to a regional continuum of canopy openness and varying states of plant community ‘type-conversion’ (Keeley et al., 2005; Jacobsen and Pratt, 2018).

Non-recovery of chaparral due to short-interval fire (SIF) is most commonly associated with *Adenostoma fasciculatum* (dominant in the widespread *chamise* community type), which regenerates facultatively from resprouts as well as seedlings (Keeley and Keeley, 1981; Vogl, 1982; Zedler et al., 1983; Keeley and Brennan, 2012; Lippitt et al., 2013). However, *A. fasciculatum* has recovered well after fire in many locations (Hanes and Jones, 1967; Hanes, 1971; Christensen and Muller, 1975; Howe and Carothers, 1980; Davis et al., 1988), and rangeland expansion studies report that chamise is highly resistant to treatments of fire, mechanical disturbance, herbicide, and grass seeding (Burcham, 1955; Bentley, 1967; Fuhrmann and Crews, 2001).

Evaluations of postfire chamise recovery were generally based on short-term field studies and may have failed to capture patterns that occur at greater spatial and temporal scales (Meng et al., 2014). Investigations conducted at sub-regional extents using remotely sensed imagery, however, arrived at differing conclusions regarding the significance of SIF in chaparral recovery (*cp.* Meng et al., 2014; Lippitt et al., 2013; Syphard et al., 2019a, 2019b). The Meng et al. (2014) study was based on Landsat imagery and found no significant effect of SIF on shrub recovery, but included only 12 large sites distributed across southern California. The Syphard et al. (2019a, 2019b) studies covered the Santa Monica Mountains and San Diego County (respectively) using aerial imagery dating back to the 1950s, and reported significant effects on recovery due to SIF as well as climatic setting and terrain. Number of burns (NOB) was also a significant control on recovery (Syphard et al., 2019b). Lippitt et al. (2013) also found that SIF impacted recovery in San Diego County by comparing recent ortho-image and field-based estimates of shrub cover, relative to historical baselines inferred from mapping criteria used in the Vegetation Type Map (VTM) project (Wieslander, 1935). Discrepant findings among the field-based and remote sensing-based evaluations of SIF impact may reflect differences in methodology or in vegetation dynamics according to location, raising two major questions: *How consistent and prevalent are impacts of SIF on postfire chaparral recovery throughout southern California? Can limited recovery occur in sites that burn only once in a period of several decades, due to other causes?* To address these questions requires estimation of change in shrub cover over several decades,

and a broad regional data sample to include diverse fire histories, plant community types, and eco-climatic settings (*cf.* Lippitt et al., 2013).

Techniques to infer postfire recovery of large areas include: (1) comparison of plant community maps constructed at different times, (2) use of concurrent data sampled from sites in different phases of maturation (*i.e.*, space-for-time substitution or chrono-sequencing), (3) analysis of multi-temporal aerial frame imagery, and (4) use of archived satellite imagery to track past changes in vegetation at moderate spatial resolution. Errors in map comparison often stem from spatial cross-tabulation artefacts or differences in cartographic method (Foody, 2007). Postfire recovery assessments based on historical aerial imagery are subject to discrepancies of image quality, illumination, and seasonality (Wing et al., 2014). Recovery assessments based on chrono-sequence sampling are inherently uncertain due to high inter-site variability in chaparral (Peterson and Stow, 2003). Therefore, tracking change in a spatially explicit manner using satellite remote sensing may be most suitable to study postfire shrub recovery (Shoshany, 2000).

The Landsat (4, 5, 7, and 8) archive consists of 30-m spatial resolution images collected at 16-day intervals since 1984, providing multispectral data which are commonly used to study fire-related land cover dynamics (Shoshany, 2000; Masek et al., 2013). Transformation of Landsat imagery to surface reflectance by the United States Geologic Survey (USGS) facilitates vegetation monitoring by reducing artefacts of atmospheric scattering and solar irradiance variation (Masek et al., 2006; Vermote et al., 2016). The Landsat-derived Normalized Vegetation Index (NDVI) (Rouse Jr et al., 1974) reliably estimates fractional shrub cover (FSC) in semi-arid shrublands, and has been shown to outperform other spectral vegetation indices (Vila and Barbosa, 2010; Chen et al., 2011; Storey et al., 2016; Storey et al., 2019). Previous research also shows utility in deriving best-fit pixel trajectories from anniversary image series in order to reduce phenological artefacts (Hope et al., 2007). Arithmetical metrics based on pixel trajectories are useful to compare plant abundance in prefire *versus* postfire phases (Díaz-Delgado et al., 1998; Röder et al., 2008; van Leeuwen et al., 2010). Landsat-derived trajectories that are calibrated to units of FSC are especially useful for ecological interpretation (Fraser et al., 2011).

Ecological inferences drawn from remotely-sensed data are greatly contingent on sampling and statistical analysis procedures (Chuvieco, 1999). A paired sampling approach using adjacent sites with similar terrain characteristics was shown by Meng et al. (2014) to effectively control for environmental variations when assessing influences of burn frequency on postfire chaparral recovery. In the present study of postfire chaparral recovery, we utilized Landsat NDVI imagery based on a similar sampling technique as Meng et al. (2014), but included a substantially greater number of twice-burned areas, and a maximal extent of areas that burned only once in recent decades. This region-wide approach allowed us to assess postfire vegetation decline in areas subjected either to singular fires or to recurrent, variable-interval fires.

1.2. Research objectives

The main objective of this study was to characterize and explain patterns of postfire chaparral recovery across southern California (116°25′–119°25′ W; 32°30′–34°40′ N)

based on the multi-decadal Landsat image record. This broad regional analysis of recovery was undertaken in order to provide a synoptic perspective of postfire chaparral recovery, and of the variables controlling it. We focused on SIF as a potential inhibitor of recovery in chaparral sites that burned in the period 1985–2008. Large fires of 2002, 2003, and 2007 overlapped with many other fires that occurred after 1984, providing a diversity of potential study sites having variable environmental characteristics and time between fires (TBF) within a 25-year period. Our study area included chamise, mixed, and montane shrub community types (Schoenherr, 1992; Sawyer et al., 1995), and addressed the following Research Questions:

1. How prevalent is decline in chaparral cover associated with limited postfire recovery?
2. How do the number of burns and time between fires affect postfire chaparral recovery?
3. How is chaparral recovery affected by environmental variables (climate, soils, and terrain) after singular fire events?

2. Material and methods

2.1. Overview

In this study we identified a set of potential study areas based on overlay of publically available fire history and plant community type maps (Fig. 1). Maps of fire history in chaparral areas that burned in the period 1985–2008 were refined using Landsat-derived burn severity data in order to improve sample positioning. Recovery estimation was based on near-anniversary (June-solstice) Landsat surface reflectance image series covering the period 1984–2018. We utilized high spatial resolution aerial imagery to empirically calibrate Landsat NDVI to estimates of FSC, corresponding to the periods 1984–1988 and 2014–2018. Changes in shrub cover were evaluated for multiple-burn areas in relation to TBF and NOB using (1) stand-averages samples ($n = 256$) and (2) paired sample plots ($n = 528$) representing similar, proximal locations within adjacent single- and multiple-burn stands. Sample points ($n = 491$) distributed randomly within single-burn areas were used to evaluate the influences of climate setting, shrub community type, terrain, and edaphic variables on recovery. These analyses were conducted using multiple linear regressions, probability testing, and visual interpretation of map and graphical data. The workflow of this study is summarized in Fig. 1.

2.2. Preliminary selection of study areas

We considered all *chamise*, *mixed*, and *montane* chaparral as potential study area within southern California. Other chaparral and sage scrub community types were excluded from the study due to their limited extents. Shrub community types were identified using digitized CALVEG maps (frap.fire.ca.gov/mapping/gis-data) (Matyas and Parker, 1980), which represent vegetation distributions prior to the study period. More recent and detailed FVEG maps (fs.usda.gov/detail/r5/landmanagement) depict the same chaparral community types as more extensive in some areas. Thus, we utilized a spatial union of the FVEG and CALVEG

maps – favoring the antecedent CALVEG maps in areas of conflict between vegetation classes.

Fire history within the chaparral areas of interest was evaluated using historical perimeter data from the California Fire and Resource Assessment Program (FRAP) (frap.fire.ca.gov/mapping/gis-data). Potential study areas included those that burned at least once since the first Landsat-4 Thematic Mapper (TM) imagery from 1984. Because chaparral requires ~10 years to regrow after fire, we excluded areas that burned more recently than 2008 (as mature-stage recovery could not be evaluated in such areas using data that spanned to 2018). We also excluded areas that had burned in the period 1974–1984, because these contained immature chaparral at the beginning of the study period. A minimum-size criterion of 1 km² was applied to the single-burn and multi-burn (overlap) areas. We masked out all areas containing built features and human land cover transformations, through manual digitization in reference to high spatial resolution (0.6-m), color-infrared ortho-imagery collected by the National Agriculture Imagery Program (NAIP) in 2016 (earthexplorer.usgs.gov).

2.3. Landsat image data

We utilized imagery from Landsat (4–8) covering World Reference System (WRS) paths 40–36, 40–37, and 41–36. These images were processed by the USGS Land Surface Reflectance Climate Data Record (LSRCDR) to directional surface reflectance (espa.cr.usgs.gov). Landsat NDVI images used to estimate shrub cover were selected annually from the period 10 June to 15 July. This period is characterized by high solar illumination and senescence in understory herbs, which can strongly influence NDVI prior to late May (*cf.* Hope et al., 2007; Park et al., 2018). Landsat surface reflectance images taken in various years and seasons within the study period were used to generate maps of burned area. Maps of cloud-covered and cloud-shadowed pixels based on *Fmask* (Zhu and Woodcock, 2012) were used in quality control. In the four Landsat images obstructed by clouds within the areas of interest, pixels of images from proximal dates were substituted for the cloud-affected pixels.

2.4. Refinement of fire history and final study area selection

In order to prevent invalid sampling due to inaccuracy in the FRAP data (*cf.* Syphard and Keeley, 2017), we produced refined maps of fire history in the prospective study areas using Landsat imagery. Refined maps of burned area were derived from prefire-to-postfire relative differences in Normalized Burn Ratio (RdNBR) (García and Caselles, 1991; Key and Benson, 1999; Miller and Thode, 2007). To classify burned areas, we applied exceedance thresholds that were deemed to reflect fully-burned conditions by visual inspection of the RdNBR images, supplemented by comparison with the FRAP fire perimeter data. Multiple-burn areas were defined as areas that burned fully in multiple years (as illustrated in Supplementary Material 1).

Landsat-based mapping and overlay of 177 fire perimeters resulted in a set of 294 study areas (hereafter referred to as *stands*) which represent contiguous areas of chaparral with internally-uniform fire history during the study period. In many cases, several stands with identical fire histories were distinguished only by non-contiguity. The stands range in area

from 1 to 557 (19 ± 44 , $\bar{x} \pm \text{SD}$) km² and comprise a total area of 6775 km². A total of 495 km² within the study region (88 of the stands) burned twice, whereas only 75 km² (nine stands) burned three times within the study period (Fig. 2). A total of 362 km² (54 stands) burned at intervals shorter than 10 years, including stands that burned twice or three times within the study period.

2.5. Landsat NDVI time-series aggregation

We evaluated postfire recovery on the basis of change in shrub cover between two periods, deemed as *prefire* (1984–1988) and *postfire* (2014–2018). Aggregation into these 5-year periods served to reduce uncertainty due to inter-annual variation in precipitation and contingent growth response, to which single-year observations are more subject (Storey et al., 2016). Landsat NDVI trajectories were characterized using 5-year mean values for the prefire period, during which vegetation abundance was assumed stable. Postfire trajectories were characterized differently, using linear best-fit functions in order to capture ongoing regrowth for the study sites that burned within ten years prior to 2014 (*i.e.*, between 2004 and 2008). Postfire NDVI trajectory values were based on termini of the 5-year trajectories, which coincide with 21 June 2018.

The Landsat NDVI trajectories enabled assessment of recovery in stands that burned in 1989–2008. In a *post-hoc* procedure to maximize the extent of study area, we included several areas that re-burned in 2017 or 2018; this was accomplished by removing the 2017 and 2018 data points from the time series of pixels within these stands. We also included stands that burned in 1985, 1986, 1987, or 1988 – by including only the data points from years preceding fire into the prefire trajectories, beginning with 1984. A total of 13 stands were included in these *post-hoc* procedures.

In previous studies, Landsat NDVI trajectories were normalized for precipitation effects using synchronous NDVI values from unburned control sites (*cf.* Riaño et al., 2002; Hope et al., 2007; Lhermitte et al., 2011). We elected not to utilize this normalization for the following reasons: (1) sites in southern California that were unburned in the study period are remarkably sparse (*cf.* Storey et al., 2016); (2) substantial error can stem from inter-site differences in phenology (Lhermitte et al., 2011); and (3) no substantial improvement in accuracy of chaparral change detection was shown to result from this normalization (Storey et al., 2019). Deriving multi-annual trajectories from time periods that were consistent for the entire study region helped to control for temporal variations in precipitation. Only minor inter-annual variation in NDVI was observed in trajectories covering the prefire period. Drought caused substantial reduction of NDVI in 2014–2016, but NDVI levels rebounded in 2017 and 2018.

2.6. Estimation of shrub cover change

We utilized the high spatial resolution NAIP imagery from 2016 to derive maps of shrub cover, which supported calibration (or retrieval) of fractional cover change estimates based on changes in Landsat NDVI. Shrub cover maps were derived by applying a knowledge-based, exceedance threshold classifier to spectral transforms of the ortho-imagery including NDVI, brightness intensity, and red-to-intensity ratio (Supplementary Material 2) using

ERDAS IMAGINE™ (Hexagon Geospatial, 2018). This same approach led to a classification accuracy of 87–95% in chaparral environments in a prior study by Storey et al. (2016). Thresholds were estimated through pixel queries and adjusted based on iterative classification trials. Map classes included green shrub, soil, and non-shrub vegetation consisting mainly of herbs.

The calibration procedure involved 73 widely-distributed plots having 3-km × 3-km dimensions. Plot locations were selected interactively based on the following criteria: (1) absence of fire during the period 2008–2016; (2) high internal variation in shrub cover (dense to sparse); and (3) visual similarity to chaparral in surrounding areas. A total of 58 calibration plots were located within or adjacent to stands of interest, and 15 plots had not burned since 1974.

Fractional shrub cover was tabulated using 90-m × 90-m sub-plots (located within the 3-km × 3-km calibration plots) which we aligned to boundaries of ground resolution elements associated with Landsat image pixels. Randomly distributed samples consisting of 30 sub-plots were extracted from each calibration plot in order to relate Landsat NDVI to FSC based on ordinary-least-squares (OLS) regressions. The OLS regressions based on each calibration plot resulted in linear slope, intercept, and R^2 values indicating goodness-of-fit. The aggregate-mean R^2 value resulting from all of the regressions combined ($n = 73$) was 0.83 (max = 0.95, min = 0.56, $\sigma = 0.13$).

The slopes and intercepts characterizing FSC-NDVI relations within the unburned calibration plots were consistent between prefire and postfire periods, whereas FSC-NDVI relations within the burned calibration plots were slightly altered due to vegetation change during the study period. Therefore, we elected to use only the postfire FSC-NDVI relations for the purpose of calibration.

The FSC-NDVI relations obtained from plots were then extended to surrounding areas based on a custom regional map consisting of 49 calibration zones (Supplementary Material 3). The calibration zone map was constructed manually in reference to the 2016 ortho-imagery, and the zones were defined as having internally-consistent shrub community composition, as determined from visual assessment of infrared and visible brightness radiance patterns. Outer boundaries of the CALVEG community types coincide in many places with those of the calibration zones, although the calibration zones represent finer spatial units than the CALVEG plant community polygons. Estimates of prefire and postfire FSC were differenced to produce a regional map representing change in shrub cover (hereafter: $dFSC$).

2.7. Spatial sampling to analyze shrub cover change

Three separate data samples based on the $dFSC$ map supported different aspects of the analysis. These samples included (1) *stand-aggregates* used to evaluate the frequency-probability of shrub cover change (among 1-burn, 2-burn, and 3-burn stands) and the potential effects of TBF and NOB on recovery, using linear regression analysis and Welch's t -tests ($\alpha_E = 0.05$); (2) proximal *paired plots*, used to evaluate effects of TBF and NOB on postfire recovery (using linear regressions and Welch's t -tests) at a finer scale, with advantageous control for environmental variations and consistency in areal sample

dimensions; and (3) *random points*, distributed across all once-burned study areas to support linear multiple regressions evaluating the relationship between postfire recovery and environmental variables. All statistical analyses were conducted using SPSS™ (IBM Corp, 2019).

Most of the paired samples (416 plots, 208 pairs) compared recovery in one-burn *versus* two-burn stands and were used only to assess the significance of TBF in recovery variation. Paired samples used to evaluate compound effects of TBF *and* NOB were arranged in neighboring two-burn and three-burn stands (112 plots, 56 pairs). We selected the locations of these 0.5-km × 0.5-km plot pairs, within corresponding vegetation community types and terrain aspects (Supplementary Material 4), as determined from a 30-m digital elevation model (ned.usgs.gov) processed in ArcMap™ (Environmental Systems Research Institute (ESRI), 2018). Landscape variations within the stands limited the number of possible locations for the paired plots. Plot pairs were placed in the closest possible proximities (2.2 ± 1.3 km, $\bar{x} \pm$ SD) at a mean density of one plot per 2 km², covering approximately 12.5% of the collective multi-burn area. Comparison of mean dFSC values between the paired plots enabled us to distinguish the potential effects of TBF and NOB from environmental effects.

Geospatial variables attributed to the random points ($n = 491$) included distance to the Pacific coastline and to annual grassland (based on recent FVEG maps); 30-year mean climate parameters including precipitation, temperature, and vapor pressure deficit (VPD) (prism.oregonstate.edu); time since the most recent fire (also evaluated in the stand-aggregate analysis); a suite of edaphic variables from the State Soil Geographic (STATSGO) (available water capacity, clay content, organic matter content, permeability, thickness, erodibility, hydrologic group, drainage class, slope, hydric condition, water content at cohesion-failure point, and flood frequency), most of which are hydrologically related (www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey/geo); terrain slope, aspect, flow accumulation, growth-season irradiance, and terrain complexity (7×7 pixel-kernel standard deviation) derived from the 30-m elevation data (ned.usgs.gov); and chaparral community type. Given the close relationship between annual precipitation and biomass in semi-arid shrub communities (Shoshany, 2012), we treated chaparral community type as an ordinal variable on the basis of ascending precipitation receipt (chamise = 1, mixed = 2, montane = 3). We conducted linear multiple regressions to evaluate these variables as controls on postfire recovery according to the dFSC map. In the OLS multiple regressions we used an automated stepwise variable selection procedure ($\alpha_E = 0.05$, $\alpha_R = 0.10$). Burn severity was not used as a variable in our analysis because it could not be reliably estimated from Landsat imagery with varied seasonality and postfire lag timing, and is not a significant correlate of postfire recovery in chaparral (Keeley et al., 2008).

3. Results

3.1. Stand-level analysis

Substantial variation in postfire recovery was observed among the chaparral study areas. Mean changes in shrub cover within the 294 stands exhibit the frequency distribution shown in Fig. 7. Approximately 65% of the stands exhibited strong recovery, based on a mean shrub cover decline of less than 5%. A few of the stands exhibited minor increases in shrub

cover (0–5%) and were considered as fully recovered. Moderate declines in mean shrub cover (5–15%) were observed in 32% of the stands. More severe declines in mean shrub cover (15–25%) occurred in only 3% of the stands. Shrub cover decline exceeding 25% was not observed at the stand-aggregate level (Fig. 3), although some locations within the stands exhibited 25–75% decline in FSC.

Comparison of dFSC frequency distributions suggests that the central tendency and variance in shrub cover change are similar between the once- and twice-burned stands (Fig. 4). Furthermore, a one-tailed Welch's *t*-test indicated no significant difference between the twice-burned *versus* once-burned stand-aggregate dFSC samples ($p = 0.11$). In contrast, the stands that burned three times during the study period exhibit a significant ($p < 0.001$) mean difference of approximately 4% in shrub cover decline, as compared to the once- and twice-burned stands (Fig. 4).

Values of dFSC indicating strong recovery are distributed evenly across the range of TBF values associated with multiple-burn stands (Fig. 5). Shrub cover reductions of 5–15% were somewhat more prevalent in stands associated with TBF values of 1–9 years, although equivalent reductions in shrub cover were also observed in stands with TBF values of 10–20 years (Fig. 5-a). Linear regressions indicated that the correlation between dFSC and TBF is significant, but weak ($p < 0.001$, $R^2 = 0.003$) based on the stand-aggregate data. This was also true of the relationship between dFSC and time since fire ($p = 0.017$, $R^2 = 0.020$) (Fig. 5-b).

3.2. Paired sample analysis

We found no statistically significant difference in the mean dFSC values of the once- *versus* twice-burned 0.25-km² plots (based on a paired, one-tailed Welch's *t*-test; $p = 0.23$). However, a data subset including only the plots that declined in FSC by more than 5% exhibited a significant difference between once- and twice-burned samples (based on a paired, one-tailed Welch *t*-test; $p = 0.01$). The latter statistical result is also reflected in Fig. 6, which depicts the majority of the data points grouped in the range of 0 to –5% shrub cover change on both axes, and substantially greater recovery in the once-burned *versus* twice-burned locations in which dFSC was lower than –5%. These results suggest that: (1) declines in FSC were more severe in the twice-burned plots when all recovered plots were ignored; and (2) propensity to recovery was not significantly different in once-burned *versus* twice-burned plots when considering the entire data set.

Relative differences in dFSC between the paired once- and twice-burned plots (*i.e.*, change in the twice-burned plots minus change in their once-burned counterparts) generally range from +10 to –10% (Fig. 7). The TBF exhibits no statistically significant effect on recovery ($p = 0.79$), according to a linear regression test applied these plot-based, relative-difference dFSC values (Fig. 7).

Recovery was significantly lower in three-burn plots than in the paired two-burn plots ($p = 0.001$) (Fig. 8-a). Values of dFSC in the three-burn plots are depicted in Fig. 8-b as a function of shortest TBF (*i.e.*, the least of two intervals in each sequence of three fires). Reduction of shrub cover in the three-burn plots was on average 11.9% greater at TBF

values of 3 years or less (12.2%), as compared to those that burned at 4-, 8-, and 14-year intervals (0.3%) (Fig. 8–b).

3.3. Regional and random-points analyses

The vast majority of burned study area recovered to within 5% of prefire FSC (Fig. 9). Stands exhibiting the most severely limited recovery are in the eastern part of the study region. Recovery was generally higher in areas near to the Pacific Ocean and along the Transverse Range (northern part of the study region), in comparison to the Peninsular Range (eastern and southern parts of the study region). The leeward, north-western portion of the Transverse Range also exhibits limited recovery in some areas. Small zones of limited recovery are prevalent in the south-western part of the study region (San Diego County and environs).

Non-significant variables in the multiple linear regression included time since fire, growth-season cumulative irradiance, slope angle, slope aspect, flow accumulation, and terrain complexity (*cp.* Syphard et al., 2019a), distance to annual grassland per the recent FVEG dataset, distance to coast, mean temperature maxima, mean VPD maxima, and most of the edaphic (STATSGO) variables. Collinearity tests led to removal of elevation (collinear to precipitation) and soil hydraulic permeability (collinear to soil available water content). The final linear multiple regression model produced an Adjusted R^2 of 0.28 (Table 1).

Mean annual precipitation and temperature explain the greatest portions of observed variance in recovery, based on standardized β coefficients (Table 1). Chaparral community type was also a significant explanatory variable, albeit with a low β coefficient value (Table 1). The positive slope coefficient (α) (Table 1) signifies that recovery was most limited in chamise chaparral (the vast majority of sample points were located in either chamise or mixed chaparral). The soil characteristic variables yielded β coefficients of -0.15 to 0.21 . Positive slope coefficients indicate that precipitation, soil clay content, and soil organic matter were positively associated with recovery (Table 1). In summary, climatic and edaphic variables explained more variation in recovery within the spatial-temporal domain of this study than did TBF, although most of the total variation was unexplained.

4. Discussion

This study represents the most spatially and temporally extensive analysis yet conducted on postfire recovery in southern Californian chaparral. A 34-year series of Landsat images enabled estimation of recovery in 294 stands, which represent a wide variety of fire history and environmental characteristics. Our primary objectives were: (1) to evaluate the prevalence of shrub cover reduction associated with limited postfire recovery; (2) to assess potential effects of TBF and NOB on recovery, by comparing single-burn and multiple-burn areas; and (3) to evaluate recovery of once-burned locations based on terrain, shrub community type, climate, and soil characteristics.

Limited postfire recovery was more prevalent among stands that burned at intervals shorter than 10 years (Fig. 5–a). However, our statistical tests based on the data from paired 0.25- km^2 plots suggest that TBF was not a significant predictor of recovery, owing to strong

recovery in most areas with TBF values shorter than 10 years. Plots that burned three times within 25 years exhibited significantly lower recovery in cases where fire intervals were shorter than four years; this result most likely reflects a compound influence of SIF and NOB. Based on refined maps of fire history we also find that the probability of SIF in southern California was low during the period 1984–2008: multiple fires occurred in only 7% of the collective study area (Fig. 2), whereas only 5% of the collective study area burned at intervals shorter than 10 years (3% of all chaparral in the region). Notably, the period of this study cannot fully represent the regional fire regime or its ecological consequences, which ideally should be analyzed at centennial time scales (Lombardo et al., 2009; Moritz et al., 2009).

In agreement with the Meng et al. (2014) study, we found that TBF was not a strong control on postfire recovery. This result stems from additional methodological components than the Meng et al. (2014) study, including: (1) use of NDVI, which is more reliable than NBR as a basis for FSC estimation (Storey et al., 2019); (2) use of small-scale paired sample plots, located in consistent terrain positions; (3) use of more reliable maps of burned area, derived from Landsat NBR; and (4) assessment of a substantially greater number of once- and twice-burned stands. Differences in our findings relative to other research on SIF impact may reflect differences in geographic scale, observational timing, or technique of vegetation change estimation. Results of the Lippitt et al. (2013) study were potentially affected by the consistency and precision with which the prefire 1935 VTM mapping criteria were applied (*cf.* Foody, 2007). The Lippitt et al. (2013) study was also limited to sites that burned at intervals of 10 years or less and – similar to the Meng et al. (2014) and Syphard et al. (2019b) studies – evaluated recovery of immature chaparral sites that had burned only 3–6 years prior.

In the present study, we observe a minor discrepancy between the plot-based and stand-aggregate samples with regard to the significance of TBF as a control on postfire recovery. The paired sampling technique associated with the plot-based results provides control for environmental variations, and is based upon sample areas of uniform size. Therefore, we place more confidence in the plot-based than stand-aggregate results. We observed a substantial difference in median size among the stands in which shrub cover decline exceeded 10% ($\bar{x} = 1.7 \text{ km}^2$) *versus* the entire set of sampled stands ($\bar{x} = 19.1 \text{ km}^2$). Our visual assessment of the regional dFSC map generated in this study suggests that some of the relatively large stands contain acute zones of limited recovery, but these low-recovery anomalies were obscured through spatial aggregation. Inconsistency in extent among data samples appears problematic for postfire recovery assessment in the southern California region. Finally, the correspondence between dFSC and TBF at the stand-aggregate level was significant yet weak ($R^2 = 0.003$).

We observed a stronger effect on shrub cover reduction from NOB than from TBF, which was also noted in the Syphard et al. (2019b) study. The major discrepancies between our results *versus* those of Syphard et al. (2019b) concern (1) the significance of TBF in recovery variation, and (2) the severity and prevalence of shrub cover decline, reported as substantially higher by the latter study. These discrepancies most likely stem from differences in methodology. The aerial imagery used by Syphard et al. (2019b) for prefire

assessment is panchromatic and has 5-m nominal spatial resolution; a lack of near-infrared data and coarse spatial resolution (as compared to the 0.6-m NAIP imagery used for postfire assessment) may have led to overestimation of prefire shrub cover. Another difference is that Syphard et al. (2019b) selected only the sites that had prefire FSC greater than 75%, whereas we included samples from a full range of prefire FSC. Also, as the Syphard et al. (2019b) study spans the long time period 1953–2016, it is possible that the observed SIF impacts occurred in 1954–1983 – prior to our study period. Notably, TBF independently contributed to only 12–23% of the recovery variation that was explained by the Syphard et al. (2019a, 2019b) studies – both of which describe either climatic setting, terrain, or soil variations as comparably strong controls on recovery.

Results of the present study do not supersede those of field-based studies that recorded plant species abundances in prefire and postfire periods (Zedler et al., 1983; Haidinger and Keeley, 1993; Zedler, 1995; Keeley and Brennan, 2012). While clearly showing decline of chaparral species and ascent of exotic plants in some areas subjected to SIF, these field-based studies did not evaluate mature-stage recovery at large spatial extents. Exotic herb incursion associated with type-conversion is prevalent in low-elevation sites prone to anthropogenic disturbance (Lippitt et al., 2013; Meng et al., 2014). Therefore, possible sample bias due to differential accessibility of montane *versus* low-elevation areas should warrant caution in extending conclusions from small field-studies to the greater chaparral bioregion. In regard to the present study, we recognize the possibility that vulnerable chaparral species were already extinguished from some (but not all) of our study areas due to fires preceding 1985, thus contributing to unexplained variation in postfire recovery (*cf.* Meng et al., 2014). Nonetheless, it seems clear from our results and from Syphard et al. (2019b) that reduction of shrub cover has occurred in a substantial fraction of southern Californian chaparral that burned in recent decades, and that shifts in fire frequency combined with other environmental stressors may cause some areas to undergo community type-conversion in the long term.

A major insight gained through this study is that limited recovery was common in once-burned areas. Postfire recovery in once-burned stands was limited most extensively and severely in transmontane areas bounding the Colorado Desert (-116.5° to -117.0° W) (Fig. 9, Table 1). These vulnerable stands consist of mid- to high-elevation chamise and receive relatively little precipitation ($350\text{--}550\text{ mm yr}^{-1}$). Therefore, climatic and edaphic characteristics of the eastern Peninsular Range may partly explain the limited recovery from singular fires observed there. Desert-fringe areas consisting of chamise and having low edaphic clay content were especially limited in recovery. The observed non-recovery in chaparral may reflect failure of resprouting or of seedling regeneration. Resprouting in chamise becomes more prevalent than seedling recruitment as elevation increases (Keeley and Soderstrom, 1986). As the desert-fringe locations represent the mid- to high-elevation domain of our study region, limited recoveries there seem most attributable to diminished resprouting (*cf.* Pratt et al., 2014). Aridification and temperature extrema associated with climatic change may expand the geographic domain in which the recovery of chamise is limited, although a substantive evaluation such climatic change impact was beyond the scope of this study. Nonetheless, the acute sensitivity to single fire events may warrant caution against prescribed burning of xeric chamise stands.

Visual analysis of ortho-imagery suggested that limited recovery within the cismontane, southern region (characterized by mild climate) occurred in areas having shrub compositions that differ from surrounding areas, implying differential impacts according to shrub species. Landscape restoration by propagation of native shrub seedlings is advisable for degraded sites of relatively high ecological significance, including connective habitat and conserved lands (Allen et al., 2018; Jennings, 2018). Chaparral managers would collectively benefit from standardized practice of postfire recovery monitoring, based upon field surveys and aerial images of sufficient resolution to track compositional change in relation to fire and other stressors.

A major limitation of this study was reliance on generalized plant community maps, because shrub responses are highly specific (Schwilk and Keeley, 2012). Although recovery of chamise can be associated closely with *A. fasciculatum*, specific recoveries within *mixed* and *montane* chaparral community types are tenuous to infer. The spatial distribution of obligate seeding chaparral (*e.g.*, *Ceanothus* spp.) – which are likely to be most impacted by short-interval fire due to the limited seed production characteristic of immature stands – is currently not well documented. Specific responses to fire or climatic change are perhaps best understood using laboratory or field experiments combined with long-term monitoring based on field-site networks. Nonetheless, Landsat image series enabled this assessment of the regional pattern and statistical correlates of postfire chaparral recovery.

5. Conclusions

This work provides new insights into the fire ecology of southern Californian chaparral, addressing our Research Questions (Section 1.2) as follows: (1) Moderate decline in chaparral cover (5–15%) associated with limited postfire recovery was widespread (occurred in 32% of stands), although severe declines in mean shrub cover (>15%) occurred in only 3% of the stands; (2) Short time between fires (<4 years) diminished recovery at sites that burned three times within 25 years, but time between fires had no substantial effect on recovery at sites that burned only twice within 25 years; (3) Soil characteristics and shrub community types influenced recovery, although mean climate parameters (temperature and precipitation) were most influential on postfire recovery variation.

The regional pattern of postfire recovery elucidated in this study implies a contraction in geographic range of chamise chaparral (accompanied by westward expansion of the Colorado Desert), driven by even single fire events and influenced by climatic setting. Whereas this study emphasizes change in shrub cover, further research is needed in order to evaluate the regional process of exotic grass incursion, which represents another key aspect of type-conversion in chaparral. Closer integration of time-sequential satellite remote sensing with finer-scale botanical data would improve evaluations of postfire recovery for chaparral and other Mediterranean-type shrublands.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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HIGHLIGHTS

- Regional postfire recovery of chaparral was evaluated using Landsat series.
- Short-interval (<10 year) fires did not impede recovery of twice-burned sites.
- Sites that burned 3 times in 25 years were impacted by short-interval fire.
- Desertic ecotones showed limited recovery after singular fire events.

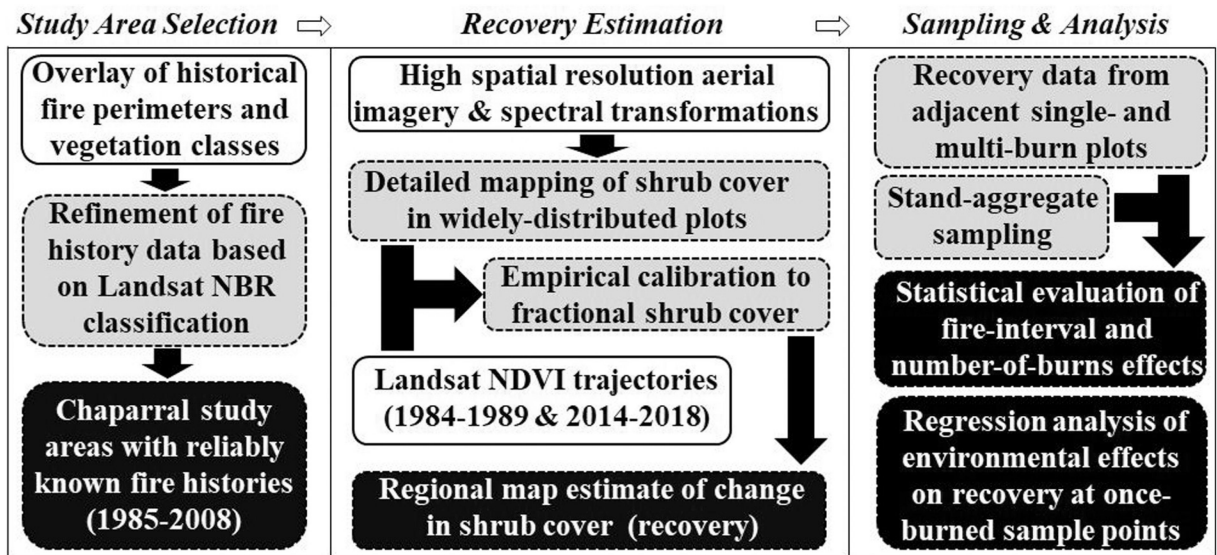


Fig. 1. Methodological flowchart showing key data sources (light boxes), major procedural steps (shaded in grey), and key information produced in this study (dark boxes with light text) in order to evaluate shrub recovery across southern California. Separate flowcharts depict the major, sequential phases of the study (study area selection, recovery estimation, sampling and analysis).

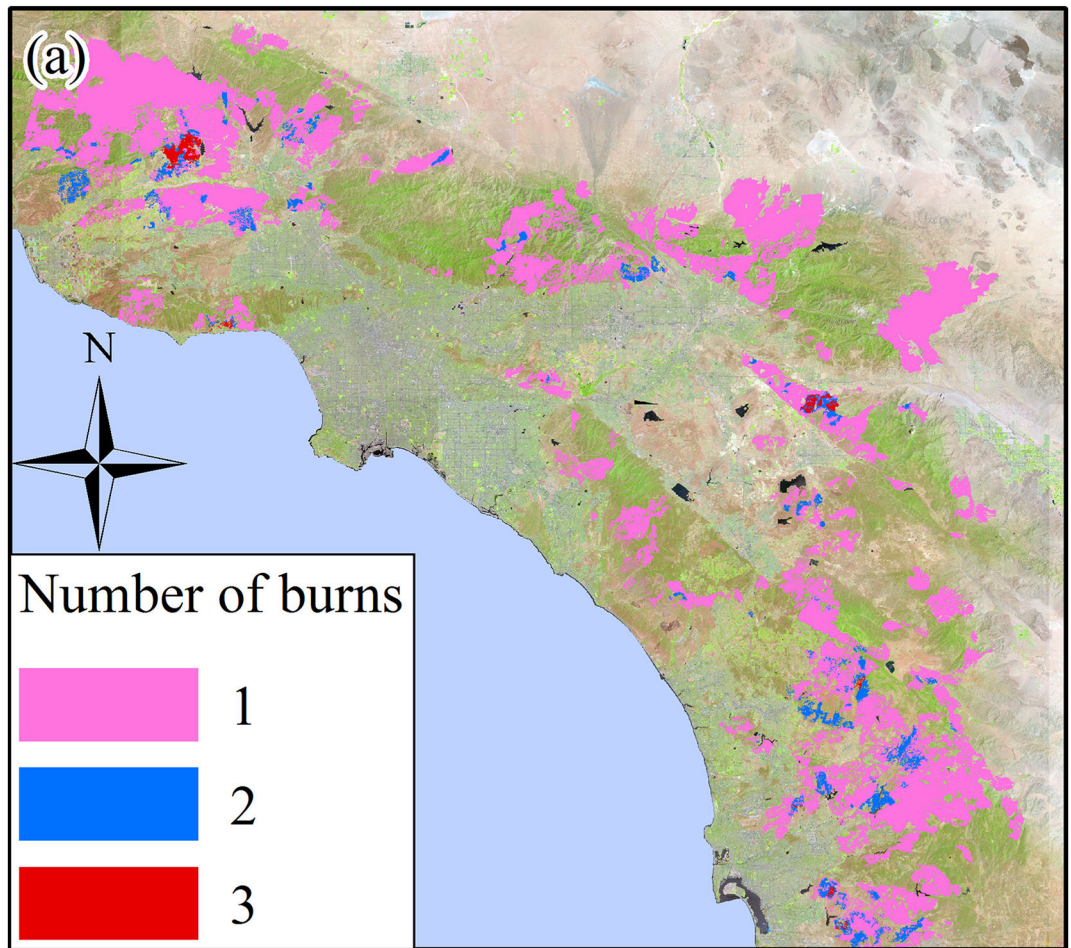


Fig. 2. Burned areas of interest throughout southern California, color-coded by number of burns during the period 1985 to 2008. Background is a true-color Landsat image mosaic from June 2013.

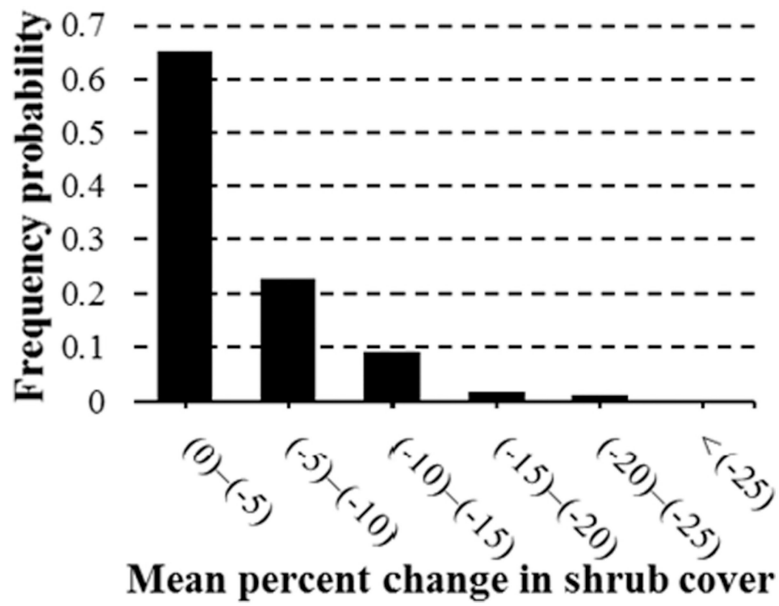


Fig. 3. Frequency probabilities of mean percentage change in shrub cover among 296 chaparral stands included in this study.

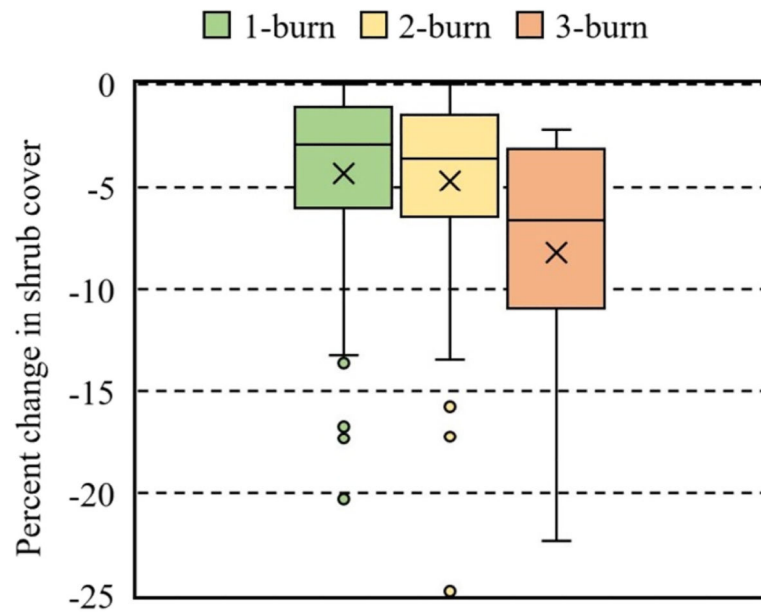


Fig. 4. Box-and-whisker plot showing distributions of change in shrub cover for 1-burn, 2-burn, and 3-burn stand-aggregate samples. Chart elements signify sample statistics as follow: X = mean, horizontal box division = median, vertical and horizontal error bars = positive and negative standard deviations, bottom and top of box = first and third quartiles, open circles = outlier values.

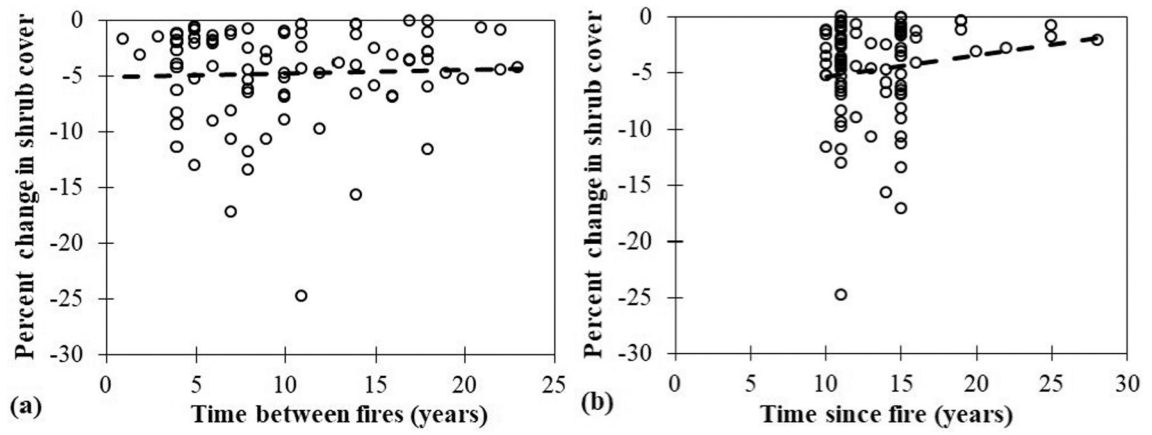


Fig. 5. Scatter plot depicting percent change in shrub cover as a function of (a) time between fires and (b) time since fire, based on mean values of 88 stands that burned twice in the period 1985 to 2008. Dashed lines represent best-fit relationships based on linear regressions.

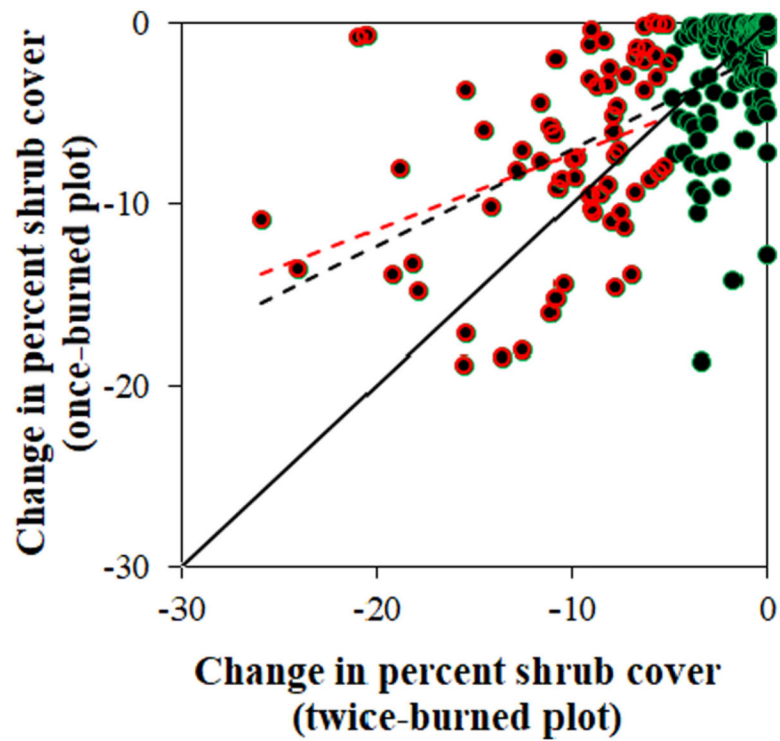


Fig. 6. Scatter plot of shrub cover change estimates derived from paired sets of 0.5-km \times 0.5-km plots located in adjacent portions of once- and twice-burned sites. Red symbols indicate a subset of the data sample, in which shrub cover declined by more than 5% in the twice-burned plots; green symbols indicate data points in which cover declined by less than 5%. The red best-fit line is associated with the red data points. The black, dashed best-fit line represents the entire data sample (red and green symbols together). The solid diagonal line indicates 1:1 relationship. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

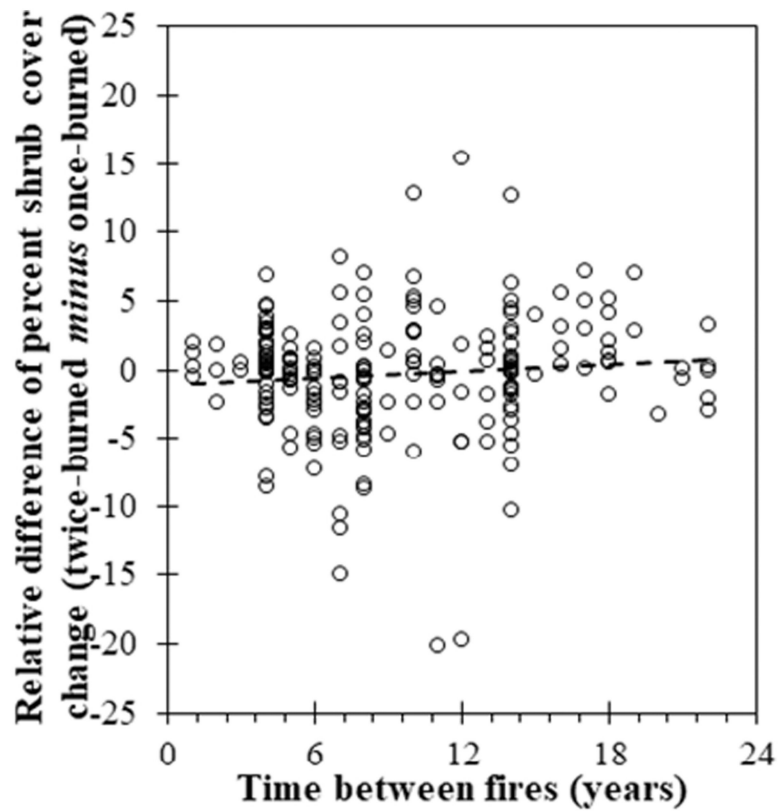


Fig. 7. Scatter plot depicting differences in shrub cover change between once- and twice-burned paired plots (0.25 km²), as a function of time between fires. Relative difference in shrub cover change (y-axis) is calculated as: (percent change in twice-burned plot) – (percent change in once burned plot). Negative values signify greater reduction of shrub cover in the twice-burned plots. The dashed line represents a best-fit linear regression trend.

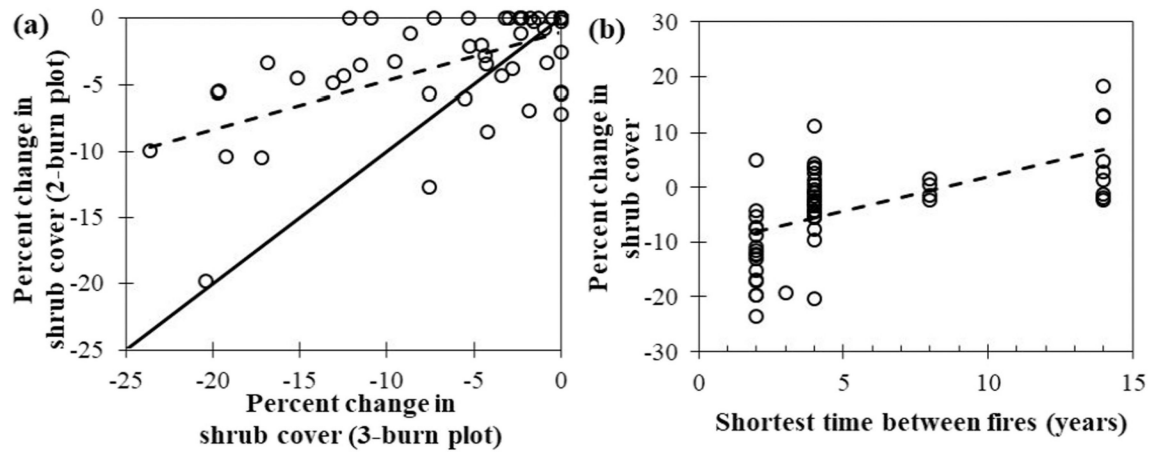


Fig. 8.

(a) Scatter plot of shrub cover change estimates derived from paired sets of 0.25-km² plots located in adjacent portions of two-burn and three-burn sites. Solid diagonal line indicates 1:1 relationship; best-fit line is dashed. (b) Shrub cover change as a function of least time between fires, in plots that burned three times during the period (1985 to 2008). Dashed lines represent best-fit relationships based on linear regressions.

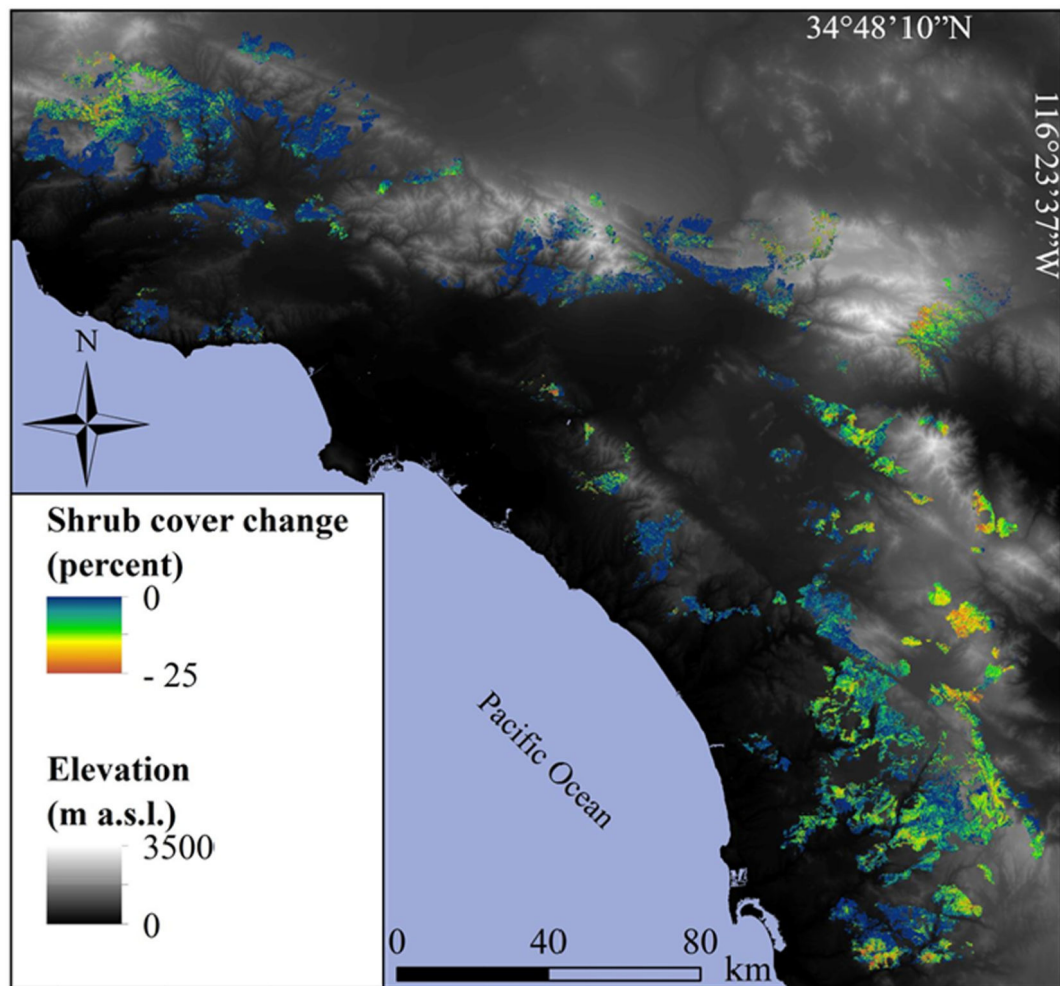


Fig. 9. Raster map illustrating Landsat-derived patterns of postfire recovery (in units of percent shrub cover change) among the chaparral areas included in this study. Background shows terrain relief based on a digital elevation model of 30 m spatial resolution. Spectrum color scale is based on a true-value, min-max display; a small fraction of observations is lower than -25% shrub cover change.

Table 1

Results of multiple linear regression model in which change in shrub cover is the dependent variable. Adj. $R^2 = 0.28$; SE = 7.39; $df_1 = 8$; $df_2 = 536$; $F_{value} = 28.0$; $F_{sig} < 0.001$.

Independent variable	Slope (α) coefficient	Standard error	β coefficient	t-Value	p-Value	Collinearity tolerance	VIF
Mean annual precipitation	0.03	0.00	0.45	10.49	0.000	0.712	1.405
Mean annual temperature	2.45	0.24	0.51	10.11	0.000	0.519	1.928
Chaparral community type	1.83	0.63	0.12	2.92	0.004	0.783	1.277
Soil hydrologic group	-3.04	1.31	-0.17	-2.33	0.020	0.257	3.895
Soil organic matter	3.59	1.31	0.12	2.74	0.006	0.694	1.440
Soil thickness	-0.15	0.05	-0.18	-3.04	0.002	0.391	2.558
Soil available water content	-53.60	23.26	-0.15	-2.31	0.022	0.324	3.084
Soil clay content	0.33	0.10	0.21	3.31	0.001	0.339	2.954