

Timelines of vegetation recovery following fire in a shrub-dominated Mediterranean-type ecosystem

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Abstract

Fire is a natural disturbance in many Mediterranean-type ecosystems, but wildfires are increasing in frequency and severity in many places worldwide, including California. Vegetation recovery following wildfire is critical for landscape stability and foundational to resilience of many ecosystem processes in the years and decades that follow fire. While remote sensing tools are increasingly important for mapping changes in vegetation following fire, to date these tools have limited application in shrubland systems such as those found in parts of California, hindering assessments of vegetation recovery timelines and inferences about ecological impacts. Using a 100-year fire history dataset alongside both field vegetation surveys (2014-2025) and modeled percent vegetation cover (1986-2025), we analyzed temporal cover dynamics of dominant vegetation classes in the years leading up to, and following, major wildfire events in the Santa Monica Mountains of California. Field survey data broadly corresponded with modeled vegetation cover, particularly for shrubs and herbaceous/graminoid cover. We identified consistent patterns in vegetation cover classes among dominant vegetation communities, including reductions in shrub and tree cover following fire in chaparral and grasslands, and pulses in herbaceous and graminoid cover in chaparral and upland woodlands, in the initial 2-5 years following fire. Herbaceous and graminoid cover returned to baseline levels faster than shrubs, which in turn recovered faster than trees. These results corroborate previous field-based studies of vegetation recovery following wildfire, and point toward modeled remote sensing products as a feasible tool for tracking post-fire recovery dynamics in remote and rugged terrain.

Keywords

Chaparral, Disturbance, Post-Fire Recovery, Rangeland Analysis Platform, Remote Sensing, Wildland Fire, Wildland-Urban Interface

Main body

1. Introduction

Fire is an important process in many ecosystems and influences vegetation structure, biodiversity, and ecosystem function (He et al., 2019). Because fire maintains successional communities, fire and the interval of its return are key mediators of landscape-scale patterns of vegetation cover (Davies et al., 2012; Hanes, 1971; Turner et al., 1998). In seasonally arid environments such as Mediterranean-type ecosystems, recurrent fire and fire severity are key selective agents that shape patterns of biodiversity: plant species adapted to Mediterranean climates have evolved with fire, and plant communities associated with these climates are particularly species-rich, due in large part to the selective force of recurrent fire (Rundel et al., 2018). Thus, changing fire regimes stand to impact structure and function for ecosystems with fire as a formative element of evolutionary history.

Increasingly frequent and severe wildfires modify trajectories of post-fire successional vegetation cover (Coop et al., 2020). Plant populations can persist after fire via fire resistance, post-fire resprouting, or post-fire recruitment, but these processes are contingent upon survival of parent vegetative material or seeds (Midgley et al., 2011; Pausas and Keeley, 2014). Because plant responses to fire regimes vary by plant functional type (Grau-Andrés et al., 2024),

changing intervals and severity of fires can have important implications for plant community composition depending on species-specific persistence strategies, potentially leading to landscape-scale vegetation type conversion (Miller et al., 2019; Nolan et al., 2021; Syphard et al., 2019a, 2022). Plant species recover following fire at different rates, so increasingly frequent fire may furthermore interact with species-specific recovery timelines to shape post-fire trajectories of vegetation cover (Tepley et al., 2018).

Animal life histories and heterotrophic community processes are strongly associated with plant community composition and vegetation structure. The impacts of fire on vegetation and timeframes of recovery following fire may therefore have additional implications for higher-order community dynamics (Doherty et al., 2022), including the resilience and resistance of wildlife to fire and associated landscape changes (Calhoun et al., 2023). Foraging opportunities become limited for herbivores immediately following fire when plant material has been lost to combustion, an immediate and direct impact on primary consumers (Kreling et al., 2021; White et al., 2023). Animals furthermore rely on vegetation structural complexity for thermal refugia (Gaudenti et al., 2021), predator avoidance (Kuntze et al., 2023; Wagnon et al., 2020), and domicile construction (Gjerdrum et al., 2005; Lacroux et al., 2023; Zhang and Liu, 2024). Thus, recovery of vegetation communities likely also governs broader biotic community recovery after fire.

Given the far-reaching importance of vegetation dynamics following wildfire, there is an urgent and growing need for land managers and decisionmakers to understand timelines of fire-

associated vegetation recovery, as well as potential tipping points leading to vegetation type conversion. Post-fire vegetation succession is often monitored using in situ field surveys such as with point-intercept transects (Barker et al., 2018; Caratti, 2006). Particularly in rugged and remote regions, management decisions can benefit from proxies for vegetation recovery. For example, access into burned areas can be difficult but at the same time vegetation status in these areas may be important for understanding terrain stabilization and wildlife habitat use. Therefore, remote sensing methods have increasingly been used for landscape-scale assessments of both burn severity and vegetation recovery. For example, satellite-derived indices of primary productivity provide valuable time series leading up to and following outbreaks of fire (Veraverbeke et al., 2012; Viana-Soto et al., 2020). More recently, burgeoning applications of machine learning and artificial intelligence for computer vision have accelerated land cover mapping efforts (Allred et al., 2021), and these tools have the potential to reveal patterns and trends in vegetation response to wildfire across broad spatial extents (Anthony et al., 2023; Applestein and Germino, 2025; Li et al., 2022). Yet, it remains unclear how timelines of vegetation recovery in modeled fractional cover data correspond to in situ surveys, and vary in association among fire histories and plant communities. This is a particularly salient issue in shrubland systems where spectral variability can mask functional variability in plant species and their fractional cover (Applestein and Germino, 2021).

These monitoring needs are especially pressing in the wildland-urban interface (WUI), where dense human populations abut fire-prone vegetation and elevate ignition frequency (Syphard et al., 2019c, 2025). Mediterranean climate zones, such as that in Southern California, contain

some of the largest and fastest growing WUI extent in the United States, and human-caused ignitions here can compress fire-return intervals well below the historical range of variability for chaparral and sage scrub systems (Safford et al., 2011). Because shortened fire-return interval is itself a driver of vegetation type conversion and altered recovery trajectories, landscapes near the WUI represent a critical context for understanding the consequences of changing post-fire vegetation dynamics.

Here, we track patterns of fractional vegetation cover from the Santa Monica Mountains and Simi Hills (California, USA), a fire-prone Mediterranean-type ecosystem that is dominated by shrublands, grasslands, and occasional upland woodland vegetation communities. We combine data from a century-long spatially resolved fire perimeter history, an annual network of vegetation monitoring transects, and a satellite-derived fractional vegetation cover dataset, to explore long-term patterns of vegetation loss and recovery following fire in Mediterranean-type ecosystems. By tracking pre- and post-fire vegetation cover, we identify baseline conditions and quantify the time-to-recovery for three plant functional types (shrubs, trees, and annual and perennial herbs and grasses) across four predominant vegetation communities (coastal sage scrub, chaparral, grasslands, and upland woodlands), with the goal of evaluating successional patterns across a frequently-burned landscape and informing management decisions across the range of vegetation recovery phases.

2. Methods

2.1 Study area

The Santa Monica Mountains climb from the California Coast to nearly 1000m above sea level, stretching from the Oxnard Plains to the Hollywood Hills, California, USA (Figure 1). They are a mix of public and private lands and are managed by the US National Park Service (NPS), California State Parks, and other regional authorities. The mountain range and the Simi Hills area to the north are collectively designated as Santa Monica Mountains National Recreation Area (hereafter, SAMO) by NPS. This rugged mountain range is characterized by a Mediterranean climate, with the majority of its precipitation occurring as rain between November and March (Gillespie et al., 2018; Radtke et al., 1981). Most seasonal precipitation comes in the form of just a few winter storms, leading to considerable interannual variability in total rainfall depending on the number of atmospheric rivers that make landfall in a given winter (Mooney and Zavaleta, 2016). Dominant vegetation communities in natural areas of SAMO include chaparral (dominated by *Adenostoma fasciculatum*, *Ceanothus megacarpus*, and *Acmispon glaber*), coastal sage scrub (dominated by *Acmispon glaber*, *Encelia californica*, *Salvia leucophylla*, and *Artemisia californica*), oak woodlands (dominated by *Quercus agrifolia*), and grasslands (dominated by *Bromus diandrus*, *Avena fatua*, and *Brassica nigra*) (Kompella et al., 2026; Tiszler and Rundel, 2007). Ecosystems with Mediterranean climates are particularly fire-prone, and recent shifts in fire frequency and severity in the region have been linked to human activities and land use change, changing thermal and moisture regimes, and changing vegetation communities (McNorton et al., 2025; Swain, 2021; Syphard et al., 2025, 2017). We present a focused analysis in a case study of vegetation cover trajectories following the 2013

Springs Fire (2 May 2013, 9,814 ha), and then extend our approach to assess recovery timelines across the entire SAMO region and its varied fire history more broadly.

2.2 Datasets

Because of the extensive history of fire across SAMO, and in the interest of understanding spatiotemporal dynamics of vegetation communities following fire, a series of 315 vegetation transects was established in 2014 and is resurveyed annually as part of the National Park Service Inventory and Monitoring (I&M) program (Kompella et al., 2026). The distribution of these transects includes the full range of the Santa Monica Mountains' geography, elevation, and vegetation communities, and equates to approximately one transect per 137 hectares. At each site, plant species were identified using a point-intercept approach every 30cm along the 30m transect. Plant species detections were aggregated to the level of growth form, under umbrella taxonomies of shrubs (shrub and subshrub), trees, graminoid/herbaceous, and other (ferns, vines, and unknown plants).

The Rangeland Analysis Platform (RAP) provides annual fractional cover estimates for four plant functional types: shrubs, trees, annual herbs/graminoids, and perennial herbs/graminoids at 30m pixel resolution across the western US (Allred et al., 2021). RAP data are useful for tracking trends in vegetation cover (Rigge et al., 2021) in the context of wildlife conservation (Berger et al., 2022; Pilliod et al., 2022), and have been used in conjunction with gridded weather data to generate fire risk forecasts (Smith et al., 2023). RAP fractional cover estimates are highly correlated with in-situ data in relevant ecosystems (e.g., $r = 0.91$ for herbaceous cover in San

Diego County; (Lee West et al., 2025)). Previous work with this product shows that across the western US, fractional cover decreases following fire immediately for herbs and graminoids, but is progressively more delayed for shrubs and trees (Li et al., 2022). Accuracy does vary across topography, model versions, and year (Applestein and Germino, 2023, 2022), so caution must be taken in interpreting analyses of long-term change in RAP data. For this study, we downloaded annual percent cover RAP data for herbaceous/graminoids, shrubs, and trees from 1986-2025 via Google Earth Engine (Gorelick et al., 2017). Because our interest was motivated by structural characteristics of plant community regeneration following fire with the aim of informing wildlife ecology, annual and perennial herbaceous/graminoids were combined into a single class. Across the SAMO study area, RAP vegetation cover data indicate that approximately 60% of the region is shrub-dominated, 35% of the region is herbaceous/graminoid dominated, and an additional 5% is tree-dominated (Figure 1).

Fire history for SAMO was generated from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program and an internal US National Parks Service database, to include fires within SAMO that were larger than 30 acres, and which initiated after 3 March 1925 and before 9 January 2025 (FRAP, 2026). Approximately 70% of the study area has burned since 2010, mostly from the catastrophic Springs (2013; 98km²), Woolsey (2018; 392km²) and Palisades (2025; 95km²) fires, which collectively accounted for 585km² of fire impacts in SAMO (Figure 1). Historical fire frequency was summarized using the number of fires at a given point in the 50 years leading up to a focal fire, and fire interval was calculated as the number of years between a focal fire and the most recent previous fire. Subsequent fire

frequency was summarized using the number of fires at a given point in the 10 years following a focal fire.

Elevation was taken from the Shuttle Radar Topography Mission Digital Elevation Model (Farr et al., 2007). Terrain characteristics were calculated using the 8-neighbor rule with the terra package v1.9.11 in R (Hijmans et al., 2026). Rugged, remote canyons make accessing much of SAMO difficult: nearly a third of the park area (32.9%) rests on slopes in excess of 20°, including over 40km² of terrain steeper than 30°. Vegetation community was defined using land cover classes from (Benson et al., 2016) and we focused on areas of chaparral, coastal sage scrub, grasslands, and upland woodlands.

2.3 Remote sensing validation with in situ data

To validate RAP percent cover data, annual fractional cover for shrubs, trees, and herbaceous/graminoid were extracted from the location of each NPS I&M transect during the time period of in situ vegetation monitoring (2014-2025). We used mixed effects linear regression to assess the extent to which RAP percent cover predicts in situ vegetation recovery. Recovery concordance between RAP and I&M was assessed using the trajectory of percent cover following fire, hierarchically within the level of transect (thereby tracking percent cover across time). In-situ percent cover was used as the response variable, and RAP percent cover was used as a predictor, in addition to broad-scale vegetation community identity (i.e. coastal sage, chaparral, grassland, and upland woodland), plant growth form (i.e. shrub, tree, and

herbaceous/graminoid), and their interaction. The slope between RAP and I&M cover was allowed to vary according to transect identity.

2.4 Chronosequence generation and temporal dynamics of fractional vegetation cover

To explore timelines of vegetation recovery following fire, we combined the spatially resolved fire history dataset with vegetation fractional cover from RAP. For a given point, the fire history was extracted as well as percent cover of trees, shrubs, and herbaceous/graminoids from RAP (Allred et al., 2021) in each year. Then, for every year, the time since the most recent fire, and the time to the next fire, was calculated. RAP time series were filtered to only include point/times that were within 10 years prior to a fire and 30 years following a fire, and centered on 0 as the year of a given fire (hereafter, “chronosequence”). For each cover type in each chronosequence, the percent cover time series was normalized so that the pre-fire cover was scaled to 100%, in order to standardize chronosequences across initial cover percentages and cover types (hereafter the normalized values are referred to as “relative cover”). In this way, for a RAP pixel that began with 50% shrub cover prior to a fire, fell to 25% shrub cover immediately after the fire, and recovered to 48% several years later, the relative cover would run from 100% to 50% to 96%. Accordingly, increases in fractional cover after fire are indicated by relative cover values >100%. We removed chronosequences with starting fractional cover less than 10% in order to avoid radical changes in relative cover associated with minute initial values.

We used the Springs Fire (extent: 98 km²), which burned the western third of the Santa Monica Mountains in May 2013, as a case study to examine RAP-derived relative cover reductions and

subsequent recoveries following fire. Multispectral surface reflectance imagery from Landsat-8 was used to contextualize the fire in the broader mosaic of urban landscapes, agricultural plains, and montane chaparral of our study area. Relative cover was calculated, as described above, for every pixel in the RAP time series leading up to and following the Springs Fire. The density distribution of relative cover was plotted by vegetation cover class each year from 2009-2024, and relative cover was projected for each pixel in a segmented time series leading up to and following the fire (2012-2015, 2020, and 2025, corresponding to the year before, year of, and two years following the fire; and two 5-year intervals thereafter).

To investigate timelines of recovery more broadly across SAMO's history, annual percent cover data from RAP were collated across the SAMO region from 1986-2025. A spatially random sample of 1000 points was created within the intersection of SAMO and each of four dominant vegetation communities: chaparral, coastal sage scrub, grassland, and woodland (Benson et al., 2016). Relative cover was calculated for each point as above, and vegetation loss and recovery were visualized using loess curves along the chronosequences.

2.5 Assessing timelines of recovery

To estimate timelines of vegetation recovery following fire, vegetation cover was reclassified by identifying the first year in which 4 consecutive years demonstrated recovery in the time series. For shrubs and trees, 80% of pre-fire cover was used as a minimum benchmark for recovery. Because we found that herbaceous cover initially increases following fire in SAMO (see Results section 3.3), 120% of pre-fire cover was used as a maximum benchmark for recovery in annual +

perennial herbaceous/graminoids. The number of years between each fire and vegetation recovery (or, in the event recovery was not detected, the number of years between the fire and the end of the chronosequence) were used in a survival analysis with time-to-recovery or time-to-end as response variables (with time-to-end treated as censorship). Kaplan-Meier plots were used to visualize differences in recovery timelines by vegetation growth form, and a Cox Proportional Hazards model was used to investigate direct effects of fire year, historical and subsequent fire frequency, vegetation community, and plant growth form on recovery timelines using the R package survival v3.8-6 (Therneau, 2026). Because “recovery” is the focal event of the analysis, positive log-hazards ratios indicate that recovery is accelerated, and negative log-hazards ratios indicate that recovery is slowed.

3. Results

3.1 Remote sensing validation with in situ data

Across the full I&M dataset (2014-2025), RAP was highly effective for predicting temporal variability in observed fractional vegetation cover, particularly for shrubs and herbaceous/graminoids (Figure 2 and Table 1). By allowing the slope between I&M and RAP data to vary by transect location, our mixed-effects linear model revealed consistently positive associations between the two datasets across time. RAP percent cover data were also a strong predictor of observed in-situ variability across space (though again, less so for trees; Supplementary materials S1). After accounting for plant growth form, vegetation community, and their interaction, RAP fractional cover data predicted 73.6% of the interannual variation in

vegetation cover data from the I&M transects. With transect identity (the hierarchical effect in our model) included, the model explained 76.8% of in situ variability.

3.2 Outcomes of the Springs Fire

The Springs Fire burned during early May 2013 in western SAMO near Camarillo, CA, with widespread effects on vegetation cover across the region (Figure 3). Both I&M and RAP datasets correspond in showing that the fire led to dramatic losses of shrub cover, but simultaneous increases in graminoid cover, in the first 2-5 years following the fire (Supplementary materials S2). Thereafter, shrub and tree cover began increasing, and graminoid cover began decreasing, in a return toward baseline cover conditions. Notably, the frequency of cases where relative cover dropped to nearly 0 ($\leq 1\%$ of pre-fire cover) increased substantially for woody species during the subsequent decade but not for herbs and graminoids (Supplementary materials S3).

3.3 Chronosequences of cover and recovery

Across the full RAP dataset (1986-2025), relative cover chronosequences indicate that the fractional cover of both shrubs and trees initially dropped, particularly in chaparral, coastal sage scrub, and grasslands of SAMO (Figure 4). Conversely, herbaceous and graminoid cover initially increased following fire in chaparral, coastal sage scrub, and upland woodland, but remained consistent in grasslands where they were already dominant under the pre-fire baseline. After several years, relative cover of all three plant growth forms returned to pre-fire levels, although recovery rates varied across growth forms and habitat classes (Figure 4).

319

320 *3.4 Assessing timelines for recovery*

321 Survival analysis revealed that the median timeline of recovery (estimated as the timepoint at
322 which the risk of recovery crosses 50%) shown with 95% lower and upper confidence limits in
323 brackets) was 6 [5,6] years for herbaceous/graminoid cover, 9 [8,9] years for shrub cover, and
324 16 [14,21] years for tree cover (Figure 5). In addition to plant growth form and vegetation
325 community, fire year, fire interval, and subsequent fire during recovery, were all important
326 determinants of recovery timelines (Table 2). In particular, fires that occurred more recently
327 had longer recovery periods and fires with increased subsequent fire frequency had longer
328 recovery periods. Fires with a longer preceding fire interval had longer recovery periods,
329 although this effect was driven by the rapid recovery of herbaceous and graminoid cover
330 compared to woody plant types (Supplementary materials S4). Grasslands recovered faster
331 than chaparral and coastal sage scrub. Upland woodlands also recovered faster than either of
332 the shrublands, but shrubs in this community did not face apparent losses (Figure 4) and their
333 “recovery” was therefore immediate.

334

335 **4. Discussion**

336 Our work quantifies timelines of vegetation recovery following wildfire in a shrub-dominated
337 Mediterranean-type ecosystem in the wildland-urban interface by combining percent cover
338 data from in-situ vegetation surveys and a fine-scale, modeled remote sensing product. We
339 found that recovery time varied by plant growth form, vegetation community, and local fire
340 history. Whereas percent cover of herbs and graminoids increased immediately after fire and

then decreased over 5-6 years after fire, that of woody plants initially dropped and then progressively recovered toward higher cover over longer timelines.

In general, fractional cover estimated using the modeled remote sensing product corresponded with in situ vegetation survey data over space and time. In both datasets, initial pulses of graminoid cover that followed fire decreased through time, while initial declines in woody cover increased over a longer time period. Across all vegetation communities except grasslands, fractional cover of shrubs corresponded strongly between the in-situ and remote sensing data products. However, fractional cover of trees only showed relationships between in-situ and RAP data in the upland woodland, a finding that stands in contrast to other work demonstrating RAP's strong efficacy at predicting fractional cover of trees across western US rangelands (Harrison et al., 2025; Savage and Slyder, 2022). This suggests that the utility of some modeled remote sensing products may be limited under changing environmental conditions or vegetation communities, such as cases of wildfire and recovery thereafter, and particularly if modeled products are prone to intraclass confusion, which can happen with woody species in RAP fractional cover (Allred et al., 2025). However, the strong association between RAP and in-situ measurements of shrubs and herbaceous/graminoid cover indicate its promise for understanding post-fire vegetation dynamics in open landscapes such as grasslands and shrub/scrublands. This approach could be particularly useful for guiding management decisions in rugged and remote terrain where site accessibility limits decisionmakers' understanding of changes taking place on the ground.

Within the boundary of the 2013 Springs Fire, we identified consistent reductions in shrub cover and increases in graminoid cover following the fire in both the RAP and I&M datasets. Notably, woody cover decreased substantially in many areas after the Springs Fire, with fractional cover often dropping below 10% of pre-fire cover during the first 3-4 years after fire for shrubs and across a much longer timeframe for trees (Figure 3). Such dramatic losses in woody cover can precipitate landscape-scale shifts in ecosystem function, including carbon sequestration (Moghli et al., 2022; Roche et al., 2024), soil retention (Malkinson et al., 2011), and water runoff regulation (Soulis et al., 2021). Thus, understanding timelines of recovery after loss of woody cover may be critical for management decisions not just regarding the retention of the local species pool but also for broader processes that govern functioning of the ecosystem as a whole.

Ecosystem structural characteristics such as vegetation cover are also important determinants of wildlife habitat selection (Riley et al., 2021; Smith et al., 2019), migration tactics (Berger et al., 2022; Deppe and Rotenberry, 2008), and hunting behavior (Blake and Gese, 2016; Dickie et al., 2017). Fire alters the spatial and temporal configuration of vegetation structure, forcing wildlife into dynamic decision-making in post-fire landscapes. Some animals demonstrate behavioral plasticity in navigating complex fire histories, as seen by mule deer (*Odocoileus hemionus*) in Washington, USA, that seasonally alter use of burned landscapes in response to changing forage and predation risk (Ganz et al., 2022). Yet, increasingly frequent and severe wildfires reshape vegetation communities and upset dominance of plant functional types in novel ways that persist for years following fire (Linley et al., 2022). By validating RAP data for

assessing fire recovery in Mediterranean-type ecosystems, our approach allows for insights into how fire will affect wildlife communities by reliably predicting timelines of vegetation recovery.

Timelines of vegetation recovery following fire in Mediterranean-type systems relate to fire history, pre-fire plant community composition, and post-fire climatic conditions (Blanco-Rodríguez et al., 2023; Ermitão et al., 2024; Storey et al., 2020). However, the frequency of fires is rising exponentially due to increasing fuel aridity (Abatzoglou and Williams, 2016; Cunningham et al., 2024) and an increase in housing density at the wildland-urban interface (Syphard et al., 2019b). Short-interval fire decreases resilience of some shrub species and delays ecosystem recovery (Turner et al., 2019), and plant reproduction and recruitment are particularly impacted in cases of recurrent short-interval fires (Nolan et al., 2021). Chaparral systems in California historically experienced fire every 30-100 years, but reductions in fire intervals in Coastal California shrublands have led to increases in non-native grasses that rapidly take advantage of burned landscapes and in turn reduce native woody vegetation (D'Antonio and Vitousek, 1992; Grunehoff and Safford, 2024). Similarly, at SAMO, an added interaction between time since fire and plant growth form (Supplementary materials S4) reveals that shrubs recover significantly more slowly than grasses when fire interval becomes shorter, suggesting that the faint but significant pattern of faster recovery with shorter fire intervals we found in our base model was driven by the rapid recovery of graminoids. SAMO is representative of the broader wildland-urban interface (WUI) of southern California, where dense human populations elevate ignition frequency independent of climate driven fire weather thereby compressing fire return intervals that may accelerate type conversion.

Understanding recovery timelines in this system through novel remote sensing techniques is vital for protection of both human and natural resources, and has a direct relevance to fire management across the Mediterranean climate zone.

Validation of remote sensing techniques for tracking landscape-scale vegetation recovery after wildfire is critical for understanding how ecosystems recover and designing management strategies that anticipate differences among plant growth forms and account for spatial heterogeneity in burn severity. Critically, in rugged and remote ecosystems where site accessibility limits immediate management response to wildfire, remote sensing tools provide opportunities to understand where fire impacts are most severe. Creative management approaches leading up to and following outbreaks of wildfire stand to not only mitigate its costs (Strabo et al., 2026) but also accelerate recovery of plant communities that burn (Beschta et al., 2004; Carrari et al., 2022). As intervals between wildfire shrink and intensity of wildfire increases, it is imperative we develop a clear picture of vegetation recovery timelines and the factors that influence variation therein.

Data and code availability

Remote sensing data for this publication are publicly available. NPS I&M data are stored on the Integrated Resource Management Applications portal (<https://irma.nps.gov/DataStore/Reference/Profile/2318437>), however access to data is restricted due to the sensitive nature of species and location data. Non-NPS users can apply to obtain the data by contacting the author of the dataset (MM), or nps-pwr-medn@doimsp.onmicrosoft.com. Code to reproduce analyses will be made available at [placeholder***] upon acceptance of this manuscript for publication.

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Author contributions

Conceptualization: CJ, ECB, and JAS. Data curation: CJ, ECB, MM, and JA. Formal analysis: CJ and ECB. Investigation: All authors. Methodology: CJ, ECB, MM, and JA. Supervision: CJ and JAS. Visualization: CJ and ECB. Writing – original draft: All authors. Writing – review and editing: All authors.

443 **References**

- 444 Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire
445 across western US forests. *Proc. Natl. Acad. Sci.* 113, 11770–11775.
446 <https://doi.org/10.1073/pnas.1607171113>
- 447 Allred, B.W., Bestelmeyer, B.T., Boyd, C.S., Brown, C., Davies, K.W., Duniway, M.C., Ellsworth,
448 L.M., Erickson, T.A., Fuhlendorf, S.D., Griffiths, T.V., Jansen, V., Jones, M.O., Karl, J.,
449 Knight, A., Maestas, J.D., Maynard, J.J., McCord, S.E., Naugle, D.E., Starns, H.D.,
450 Twidwell, D., Uden, D.R., 2021. Improving Landsat predictions of rangeland fractional
451 cover with multitask learning and uncertainty. *Methods Ecol. Evol.* 12, 841–849.
452 <https://doi.org/https://doi.org/10.1111/2041-210X.13564>
- 453 Allred, B.W., McCord, S.E., Assal, T.J., Bestelmeyer, B.T., Boyd, C.S., Brooks, A.C., Cady, S.M.,
454 Duniway, M.C., Fuhlendorf, S.D., Green, S.A., Harrison, G.R., Jensen, E.R., Kachergis, E.J.,
455 Knight, A.C., Mattilio, C.M., Meador, B.A., Naugle, D.E., O’Leary, D., Olsoy, P.J., Peirce,
456 E.S., Reinhardt, J.R., Shriver, R.K., Smith, J.T., Tack, J.D., Tanner, A.M., Tanner, E.P.,
457 Twidwell, D., Webb, N.P., Morford, S.L., 2025. Sentinel-2 based estimates of rangeland
458 fractional cover and canopy gap class for the western United States. *Sci. Data* 12, 1889.
459 <https://doi.org/10.1038/s41597-025-06160-9>
- 460 Anthony, C.R., Applestein, C.V., Germino, M.J., 2023. Satellite-derived prefire vegetation
461 predicts variation in field-based invasive annual grass cover after fire. *Appl. Veg. Sci.* 26,
462 e12759. <https://doi.org/10.1111/avsc.12759>
- 463 Applestein, C., Germino, M.J., 2023. Satellite-derived plant cover maps vary in performance
464 depending on version and product. *Ecol. Indic.* 155, 110950.
465 <https://doi.org/10.1016/j.ecolind.2023.110950>
- 466 Applestein, C., Germino, M.J., 2022. How do accuracy and model agreement vary with
467 versioning, scale, and landscape heterogeneity for satellite-derived vegetation maps in
468 sagebrush steppe? *Ecol. Indic.* 139, 108935.
469 <https://doi.org/10.1016/j.ecolind.2022.108935>
- 470 Applestein, C., Germino, M.J., 2021. Detecting shrub recovery in sagebrush steppe: comparing
471 Landsat-derived maps with field data on historical wildfires. *Fire Ecol.* 17, 5.
472 <https://doi.org/10.1186/s42408-021-00091-7>
- 473 Applestein, C.V., Germino, M.J., 2025. Post-fire recovery of sagebrush-steppe communities is
474 better explained by elevation than climate-derived indicators of resistance and
475 resilience. *J. Appl. Ecol.* 62, 689–700. <https://doi.org/10.1111/1365-2664.14876>
- 476 Barker, B.S., Pilliod, D.S., Welty, J.L., Arkle, R.S., “Sherm” Karl, M.G., Toevs, G.R., 2018. An
477 Introduction and Practical Guide to Use of the Soil-Vegetation Inventory Method (SVIM)
478 Data. *Rangel. Ecol. Manag.* 71, 671–680. <https://doi.org/10.1016/j.rama.2018.06.003>
- 479 Benson, J.F., Sikich, J.A., Riley, S.P.D., 2016. Individual and Population Level Resource Selection
480 Patterns of Mountain Lions Preying on Mule Deer along an Urban-Wildland Gradient.
481 *PLOS ONE* 11, e0158006. <https://doi.org/10.1371/journal.pone.0158006>
- 482 Berger, D., German, D., John, C., Hart, R., Stephenson, T., Avgar, T., 2022. Seeing Is Be-Leaving:
483 Perception Informs Migratory Decisions in Sierra Nevada Bighorn Sheep (*Ovis*
484 *canadensis sierrae*). *Front. Ecol. Evol.* 10. <https://doi.org/10.3389/fevo.2022.742275>

- Beschta, R.L., Rhodes, J.J., Kauffman, J.B., Gresswell, R.E., Minshall, G.W., Karr, J.R., Perry, D.A., Hauer, F.R., Frissell, C.A., 2004. Postfire Management on Forested Public Lands of the Western United States. *Conserv. Biol.* 18, 957–967. <https://doi.org/10.1111/j.1523-1739.2004.00495.x>
- Blake, L.W., Gese, E.M., 2016. Resource selection by cougars: Influence of behavioral state and season. *J. Wildl. Manag.* 80, 1205–1217. <https://doi.org/10.1002/jwmg.21123>
- Blanco-Rodríguez, M.Á., Ameztegui, A., Gelabert, P., Rodrigues, M., Coll, L., 2023. Short-term recovery of post-fire vegetation is primarily limited by drought in Mediterranean forest ecosystems. *Fire Ecol.* 19, 68. <https://doi.org/10.1186/s42408-023-00228-w>
- Calhoun, K.L., Goldstein, B.R., Gaynor, K.M., McInturff, A., Solorio, L., Brashares, J.S., 2023. Mammalian resistance to megafire in western U.S. woodland savannas. *Ecosphere* 14, e4613. <https://doi.org/10.1002/ecs2.4613>
- Caratti, J.F., 2006. Point intercept (PO). Lutes Duncan C Keane Robert E Caratti John F Key Carl H Benson Nathan C Sutherl. Steve Gangi Larry J 2006 FIREMON Fire Eff. Monit. Inventory Syst. Gen Tech Rep RMRS-GTR-164-CD Fort Collins CO US Dep. Agric. For. Serv. Rocky Mt. Res. Stn. P PO-1-17 164.
- Carrari, E., Biagini, P., Selvi, F., 2022. Early vegetation recovery of a burned Mediterranean forest in relation to post-fire management strategies. *For. Int. J. For. Res.* 95, 548–561. <https://doi.org/10.1093/forestry/cpab057>
- Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S.D., Higuera, P.E., Hurteau, M.D., Tepley, A., Whitman, E., Assal, T., Collins, B.M., Davis, K.T., Dobrowski, S., Falk, D.A., Fornwalt, P.J., Fulé, P.Z., Harvey, B.J., Kane, V.R., Littlefield, C.E., Margolis, E.Q., North, M., Parisien, M.-A., Prichard, S., Rodman, K.C., 2020. Wildfire-Driven Forest Conversion in Western North American Landscapes. *BioScience* 70, 659–673. <https://doi.org/10.1093/biosci/biaa061>
- Cunningham, C.X., Williamson, G.J., Bowman, D.M.J.S., 2024. Increasing frequency and intensity of the most extreme wildfires on Earth. *Nat. Ecol. Evol.* 8, 1420–1425. <https://doi.org/10.1038/s41559-024-02452-2>
- D’Antonio, C.M., Vitousek, P.M., 1992. Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change. *Annu. Rev. Ecol. Syst.* 23, 63–87.
- Davies, G.M., Bakker, J.D., Dettweiler-Robinson, E., Dunwiddie, P.W., Hall, S.A., Downs, J., Evans, J., 2012. Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. *Ecol. Appl.* 22, 1562–1577. <https://doi.org/10.1890/10-2089.1>
- Deppe, J.L., Rotenberry, J.T., 2008. Scale-Dependent Habitat Use by Fall Migratory Birds: Vegetation Structure, Floristics, and Geography. *Ecol. Monogr.* 78, 461–487. <https://doi.org/10.1890/07-0163.1>
- Dickie, M., Serrouya, R., McNay, R.S., Boutin, S., 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *J. Appl. Ecol.* 54, 253–263. <https://doi.org/10.1111/1365-2664.12732>
- Doherty, T.S., Geary, W.L., Jolly, C.J., Macdonald, K.J., Miritis, V., Watchorn, D.J., Cherry, M.J., Conner, L.M., González, T.M., Legge, S.M., Ritchie, E.G., Stawski, C., Dickman, C.R., 2022. Fire as a driver and mediator of predator–prey interactions. *Biol. Rev.* 97, 1539–1558. <https://doi.org/10.1111/brv.12853>

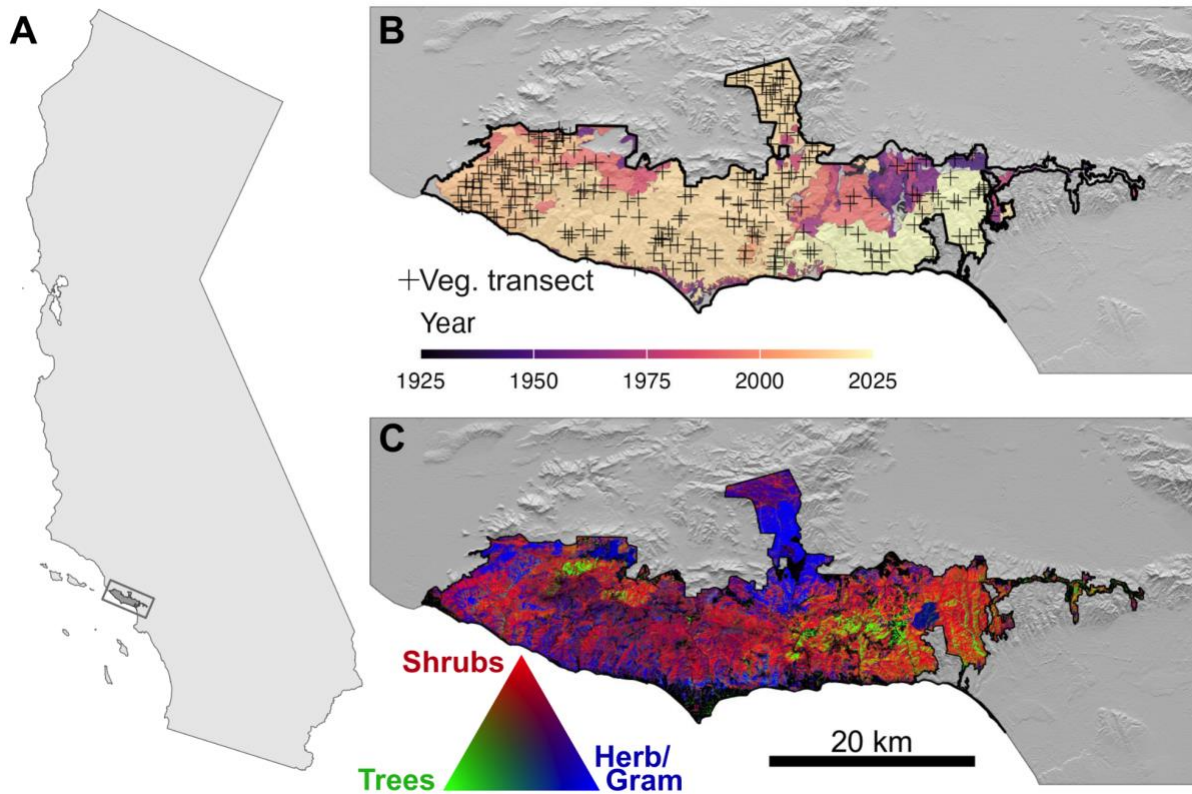
529 Ermitão, T., Gouveia, C.M., Bastos, A., Russo, A.C., 2024. Recovery Following Recurrent Fires
 530 Across Mediterranean Ecosystems. *Glob. Change Biol.* 30, e70013.
 531 <https://doi.org/10.1111/gcb.70013>
 532 Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M.,
 533 Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin,
 534 M., Burbank, D., Alsdorf, D., 2007. The Shuttle Radar Topography Mission. *Rev.*
 535 *Geophys.* 45. <https://doi.org/10.1029/2005RG000183>
 536 FRAP, 2026. FRAP Fire Perimeters Product Metadata.
 537 Ganz, T.R., DeVivo, M.T., Kertson, B.N., Roussin, T., Satterfield, L., Wirsing, A.J., Prugh, L.R.,
 538 2022. Interactive effects of wildfires, season and predator activity shape mule deer
 539 movements. *J. Anim. Ecol.* 91, 2273–2288. <https://doi.org/10.1111/1365-2656.13810>
 540 Gaudenti, N., Nix, E., Maier, P., Westphal, M.F., Taylor, E.N., 2021. Habitat heterogeneity affects
 541 the thermal ecology of an endangered lizard. *Ecol. Evol.* 11, 14843–14856.
 542 <https://doi.org/10.1002/ece3.8170>
 543 Gillespie, T.W., Ostermann-Kelm, S., Dong, C., Willis, K.S., Okin, G.S., MacDonald, G.M., 2018.
 544 Monitoring changes of NDVI in protected areas of southern California. *Ecol. Indic.* 88,
 545 485–494. <https://doi.org/10.1016/j.ecolind.2018.01.031>
 546 Gjerdrum, C., Elphick, C.S., Rubega, M., 2005. Nest Site Selection and Nesting Success in
 547 Saltmarsh Breeding Sparrows: The Importance of Nest Habitat, Timing, and Study Site
 548 Differences. *Condor Ornithol. Appl.* 107, 849–862.
 549 <https://doi.org/10.1093/condor/107.4.849>
 550 Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth
 551 Engine: Planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.*, Big
 552 Remotely Sensed Data: tools, applications and experiences 202, 18–27.
 553 <https://doi.org/10.1016/j.rse.2017.06.031>
 554 Grau-Andrés, R., Moreira, B., Pausas, J.G., 2024. Global plant responses to intensified fire
 555 regimes. *Glob. Ecol. Biogeogr.* 33, e13858. <https://doi.org/10.1111/geb.13858>
 556 Grunehoff, A.R., Safford, H.D., 2024. High fire frequency in California chaparral reduces
 557 postfire shrub regeneration and native plant diversity. *Ecosphere* 15, e70128.
 558 <https://doi.org/10.1002/ecs2.70128>
 559 Hanes, T.L., 1971. Succession after Fire in the Chaparral of Southern California. *Ecol. Monogr.*
 560 41, 27–52. <https://doi.org/10.2307/1942434>
 561 Harrison, G.R., Rigge, M., Assal, T.J., Applestein, C., James, D.K., McCord, S.E., 2025. An accuracy
 562 assessment of satellite-derived rangeland fractional cover. *Ecol. Indic.* 172, 113267.
 563 <https://doi.org/10.1016/j.ecolind.2025.113267>
 564 He, T., Lamont, B.B., Pausas, J.G., 2019. Fire as a key driver of Earth’s biodiversity. *Biol. Rev.* 94,
 565 1983–2010. <https://doi.org/10.1111/brv.12544>
 566 Hijmans, R.J., Brown, A., Barbosa, A.M., Cordano, E., Dyba, K., Bivand, R., Chirico, M., Pebesma,
 567 E., Rowlingson, B., Sumner, M.D., 2026. terra: Spatial Data Analysis.
 568 Kompella, M., Pandori, L., Weisenborn, K., Mendelsohn, M., Ostermann-Kelm, S., 2026.
 569 Vegetation Monitoring at Santa Monica Mountains National Recreation Area (SAMO) by
 570 the Mediterranean Coast Inventory and Monitoring Network (MEDN) 2014-2025: Data
 571 Package. <https://doi.org/10.57830/2318437>

- Kreling, S.E.S., Gaynor, K.M., McInturff, A., Calhoun, K.L., Brashares, J.S., 2021. Site fidelity and behavioral plasticity regulate an ungulate's response to extreme disturbance. *Ecol. Evol.* 11, 15683–15694. <https://doi.org/10.1002/ece3.8221>
- Kuntze, C.C., Pauli, J.N., Zulla, C.J., Keane, J.J., Roberts, K.N., Dotters, B.P., Sawyer, S.C., Peery, M.Z., 2023. Landscape heterogeneity provides co-benefits to predator and prey. *Ecol. Appl.* 33, e2908. <https://doi.org/10.1002/eap.2908>
- Lacroux, C., Krief, S., Douady, S., Cornette, R., Durand, S., Aleeje, A., Asalu, E., Pouydebat, E., 2023. Chimpanzees select comfortable nesting tree species. *Sci. Rep.* 13, 16943. <https://doi.org/10.1038/s41598-023-44192-6>
- Lee West, K.R., Stow, D.A., Sousa, D.J., Roberts, D.A., O'Leary, J.F., 2025. Landsat spectral unmixing analysis for mapping herbaceous fractional cover in wildfire-prone Mediterranean-type ecosystems. *Int. J. Remote Sens.* 46, 4079–4106. <https://doi.org/10.1080/01431161.2025.2486321>
- Li, Z., Angerer, J.P., Wu, X.B., 2022. The impacts of wildfires of different burn severities on vegetation structure across the western United States rangelands. *Sci. Total Environ.* 845, 157214. <https://doi.org/10.1016/j.scitotenv.2022.157214>
- Linley, G.D., Jolly, C.J., Doherty, T.S., Geary, W.L., Armenteras, D., Belcher, C.M., Bliege Bird, R., Duane, A., Fletcher, M.-S., Giorgis, M.A., Haslem, A., Jones, G.M., Kelly, L.T., Lee, C.K.F., Nolan, R.H., Parr, C.L., Pausas, J.G., Price, J.N., Regos, A., Ritchie, E.G., Ruffault, J., Williamson, G.J., Wu, Q., Nimmo, D.G., 2022. What do you mean, 'megafire'? *Glob. Ecol. Biogeogr.* 31, 1906–1922. <https://doi.org/10.1111/geb.13499>
- Malkinson, D., Wittenberg, L., Beerli, O., Barzilai, R., 2011. Effects of Repeated Fires on the Structure, Composition, and Dynamics of Mediterranean Maquis: Short- and Long-Term Perspectives. *Ecosystems* 14, 478–488. <https://doi.org/10.1007/s10021-011-9424-z>
- McNorton, J., Moreno, A., Turco, M., Keune, J., Giuseppe, F.D., 2025. Hydroclimatic Rebound Drives Extreme Fire in California's Non-Forested Ecosystems. *Glob. Change Biol.* 31. <https://doi.org/10.1111/gcb.70481>
- Midgley, J.J., Kruger, L.M., Skelton, R., 2011. How do fires kill plants? The hydraulic death hypothesis and Cape Proteaceae "fire-resisters." *South Afr. J. Bot.* 77, 381–386. <https://doi.org/10.1016/j.sajb.2010.10.001>
- Miller, A.D., Thompson, J.R., Tepley, A.J., Anderson-Teixeira, K.J., 2019. Alternative stable equilibria and critical thresholds created by fire regimes and plant responses in a fire-prone community. *Ecography* 42, 55–66. <https://doi.org/10.1111/ecog.03491>
- Moghli, A., Santana, V.M., Baeza, M.J., Pastor, E., Soliveres, S., 2022. Fire Recurrence and Time Since Last Fire Interact to Determine the Supply of Multiple Ecosystem Services by Mediterranean Forests. *Ecosystems* 25, 1358–1370. <https://doi.org/10.1007/s10021-021-00720-x>
- Mooney, H., Zavaleta, E., 2016. *Ecosystems of California*. Univ of California Press.
- Nolan, R.H., Collins, L., Leigh, A., Ooi, M.K.J., Curran, T.J., Fairman, T.A., Resco de Dios, V., Bradstock, R., 2021. Limits to post-fire vegetation recovery under climate change. *Plant Cell Environ.* 44, 3471–3489. <https://doi.org/10.1111/pce.14176>
- Pausas, J.G., Keeley, J.E., 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytol.* 204, 55–65. <https://doi.org/10.1111/nph.12921>

- Pilliod, D.S., Beck, J.L., Duchardt, C.J., Rachlow, J.L., Veblen, K.E., 2022. Leveraging Rangeland Monitoring Data for Wildlife: From Concept to Practice. *Rangelands* 44, 87–98. <https://doi.org/10.1016/j.rala.2021.09.005>
- Radtke, K.W.-H., Arndt, A.M., Wakimoto, R.H., 1981. Fire History of the Santa Monica Mountains, in: *Dynamics and Management of Mediterranean-Type Ecosystems*. San Diego, CA, USA.
- Rigge, M., Homer, C., Shi, H., Meyer, D., Bunde, B., Granneman, B., Postma, K., Danielson, P., Case, A., Xian, G., 2021. Rangeland Fractional Components Across the Western United States from 1985 to 2018. *Remote Sens.* 13, 813. <https://doi.org/10.3390/rs13040813>
- Riley, S.P.D., Sikich, J.A., Benson, J.F., 2021. Big Cats in the Big City: Spatial Ecology of Mountain Lions in Greater Los Angeles. *J. Wildl. Manag.* 85, 1527–1542. <https://doi.org/10.1002/jwmg.22127>
- Roche, P.K., Campagne, C.S., Ganteaume, A., 2024. Post-fire Recovery Dynamics and Resilience of Ecosystem Services Capacity in Mediterranean-Type Ecosystems. *Ecosystems* 27, 833–847. <https://doi.org/10.1007/s10021-024-00924-x>
- Rundel, P.W., Arroyo, M.T.K., Cowling, R.M., Keeley, J.E., Lamont, B.B., Pausas, J.G., Vargas, P., 2018. Fire and Plant Diversification in Mediterranean-Climate Regions. *Front. Plant Sci.* 9. <https://doi.org/10.3389/fpls.2018.00851>
- Safford, H.D., van de Water, K., Schmidt, D., 2011. California Fire Return Interval Departure (FRID) Map Metadata: Description of Purpose, Data Sources, Database Fields, and their Calculations.
- Savage, S., Slyder, J., 2022. Evaluation of Fractional Vegetation Cover Products (No. Technical Note 456). U.S. Department of the Interior, Bureau of Land Management, Denver, CO.
- Smith, J.A., Donadio, E., Pauli, J.N., Sheriff, M.J., Bidder, O.R., Middleton, A.D., 2019. Habitat complexity mediates the predator–prey space race. *Ecology* 100, e02724. <https://doi.org/10.1002/ecy.2724>
- Smith, J.T., Allred, B.W., Boyd, C.S., Davies, K.W., Kleinhesselink, A.R., Morford, S.L., Naugle, D.E., 2023. Fire needs annual grasses more than annual grasses need fire. *Biol. Conserv.* 286, 110299. <https://doi.org/10.1016/j.biocon.2023.110299>
- Soulis, K.X., Generali, K.A., Papadaki, C., Theodoropoulos, C., Psomiadis, E., 2021. Hydrological Response of Natural Mediterranean Watersheds to Forest Fires. *Hydrology* 8, 15. <https://doi.org/10.3390/hydrology8010015>
- Storey, E.A., Stow, D.A., Roberts, D.A., O’Leary, J.F., Davis, F.W., 2020. Evaluating Drought Impact on Postfire Recovery of Chaparral Across Southern California. *Ecosyst. N. Y.* N 2020, 10.1007/s10021-020-00551–2. <https://doi.org/10.1007/s10021-020-00551-2>
- Strabo, F., Bryan, C., Reimer, M.N., 2026. Wildfire damages and the cost-effective role of forest fuel treatments. *Science* 392, 629–635. <https://doi.org/10.1126/science.aea6463>
- Swain, D.L., 2021. A Shorter, Sharper Rainy Season Amplifies California Wildfire Risk. *Geophys. Res. Lett.* 48, e2021GL092843. <https://doi.org/10.1029/2021GL092843>
- Syphard, A.D., Brennan, T.J., Keeley, J.E., 2019a. Extent and drivers of vegetation type conversion in Southern California chaparral. *Ecosphere* 10, e02796. <https://doi.org/10.1002/ecs2.2796>

- Syphard, A.D., Brennan, T.J., Keeley, J.E., 2019b. Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California. *Divers. Distrib.* 25, 90–101. <https://doi.org/10.1111/ddi.12827>
- Syphard, A.D., Brennan, T.J., Rustigian-Romsos, H., Keeley, J.E., 2022. Fire-driven vegetation type conversion in Southern California. *Ecol. Appl.* 32, e2626. <https://doi.org/10.1002/eap.2626>
- Syphard, A.D., Keeley, J.E., Conlisk, E., Gough, M., 2025. Regional patterns in U.S. wildfire activity: the critical role of ignition sources. *Environ. Res. Lett.* 20, 054046. <https://doi.org/10.1088/1748-9326/adc9c8>
- Syphard, A.D., Keeley, J.E., Pfaff, A.H., Ferschweiler, K., 2017. Human presence diminishes the importance of climate in driving fire activity across the United States. *Proc. Natl. Acad. Sci.* 114, 13750–13755. <https://doi.org/10.1073/pnas.1713885114>
- Syphard, A.D., Rustigian-Romsos, H., Mann, M., Conlisk, E., Moritz, M.A., Ackerly, D., 2019c. The relative influence of climate and housing development on current and projected future fire patterns and structure loss across three California landscapes. *Glob. Environ. Change* 56, 41–55. <https://doi.org/10.1016/j.gloenvcha.2019.03.007>
- Tepley, A.J., Thomann, E., Veblen, T.T., Perry, G.L.W., Holz, A., Paritsis, J., Kitzberger, T., Anderson-Teixeira, K.J., 2018. Influences of fire–vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes. *J. Ecol.* 106, 1925–1940. <https://doi.org/10.1111/1365-2745.12950>
- Therneau, T.M., 2026. A Package for Survival Analysis in R.
- Tizler, J., Rundel, P.W., 2007. Santa Monica Mountains: Biogeography and cultural history, in: Knapp, D.A. (Ed.), *Flora and Ecology of the Santa Monica Mountains: Proceedings of the 32nd Annual Southern California Botanists Symposium*. Fullerton, CA, pp. 1–17.
- Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. *Ecosystems* 1, 511–523. <https://doi.org/10.1007/s100219900047>
- Turner, M.G., Braziunas, K.H., Hansen, W.D., Harvey, B.J., 2019. Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proc. Natl. Acad. Sci.* 116, 11319–11328. <https://doi.org/10.1073/pnas.1902841116>
- Veraverbeke, S., Verstraeten, W.W., Lhermitte, S., Van De Kerchove, R., Goossens, R., 2012. Assessment of post-fire changes in land surface temperature and surface albedo, and their relation with fire–burn severity using multitemporal MODIS imagery. *Int. J. Wildland Fire* 21, 243–256. <https://doi.org/10.1071/WF10075>
- Viana-Soto, A., Aguado, I., Salas, J., García, M., 2020. Identifying Post-Fire Recovery Trajectories and Driving Factors Using Landsat Time Series in Fire-Prone Mediterranean Pine Forests. *Remote Sens.* 12, 1499. <https://doi.org/10.3390/rs12091499>
- Wagnon, C.J., Schooley, R.L., Cosentino, B.J., 2020. Shrub encroachment creates a dynamic landscape of fear for desert lagomorphs via multiple pathways. *Ecosphere* 11, e03240. <https://doi.org/10.1002/ecs2.3240>
- White, C.Q., Bush, J.P., Sacks, B.N., 2023. Deer dietary responses to wildfire: Optimal foraging, individual specialization, or opportunism? *Mol. Ecol.* 32, 6953–6968. <https://doi.org/10.1111/mec.17185>

700 Zhang, R., Liu, W., 2024. Preference for ground cover when selecting burrow entrances in
701 plateau pikas. *Ecol. Evol.* 14, e11564. <https://doi.org/10.1002/ece3.11564>
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706 *Figure 1*

707 Santa Monica Mountain National Recreation Area (SAMO) is located along the coast in southern
 708 California (A). SAMO fire history shows that most of the region has burned within the last
 709 decade, but some areas have not burned for over a century (B). Overall mean fractional cover
 710 of trees, shrubs, and herbs/graminoids mapped to RGB values reveals spatial variability in
 711 predominant vegetation cover classes across the region (C).

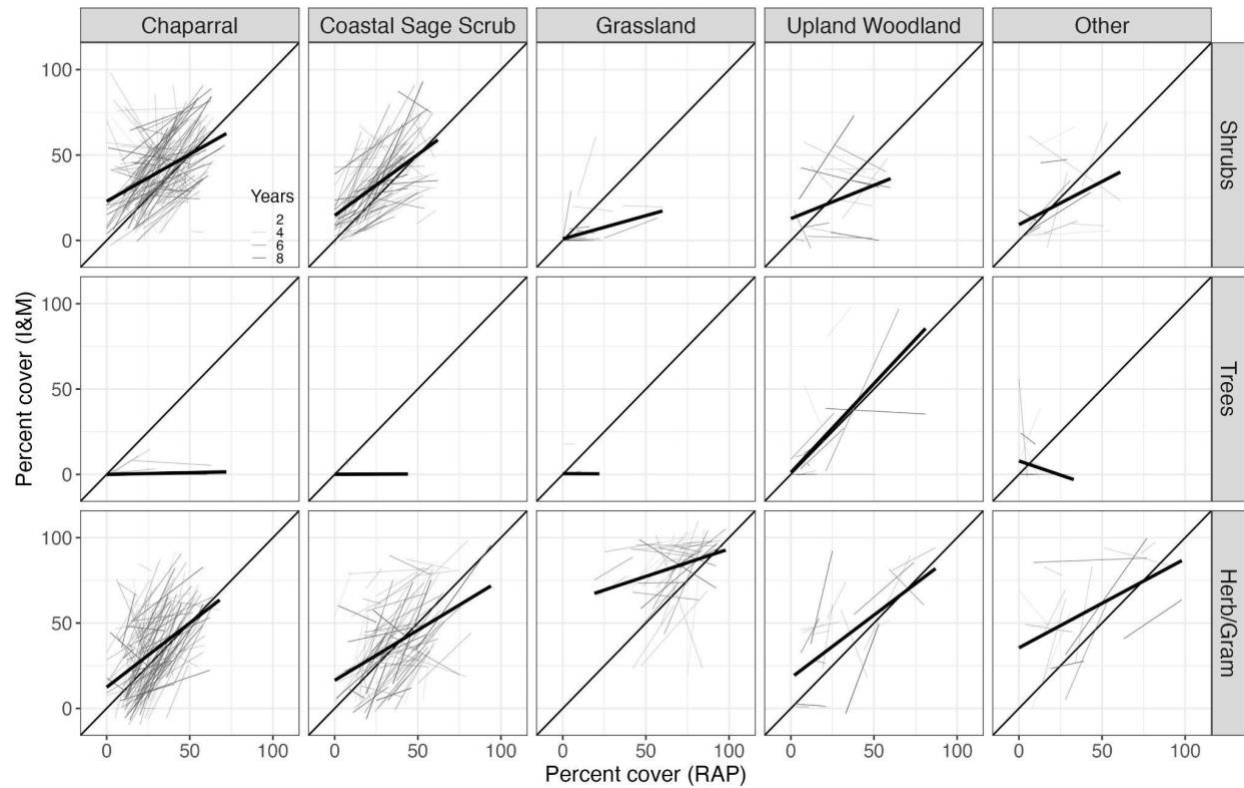


Figure 2

Regressions linking RAP to I&M data in the three plant growth forms by transect over time, across the full SAMO study area in the four main vegetation communities. In each panel, fine lines are linear regressions for individual transects over the full time series for which in-situ point-intercept data were collected. Fine lines are drawn with an intensity corresponding to the number of years of data available in that transect's time series. Bold lines show the overall linear relationship between RAP and I&M percent cover. The diagonal is a 1:1 line.

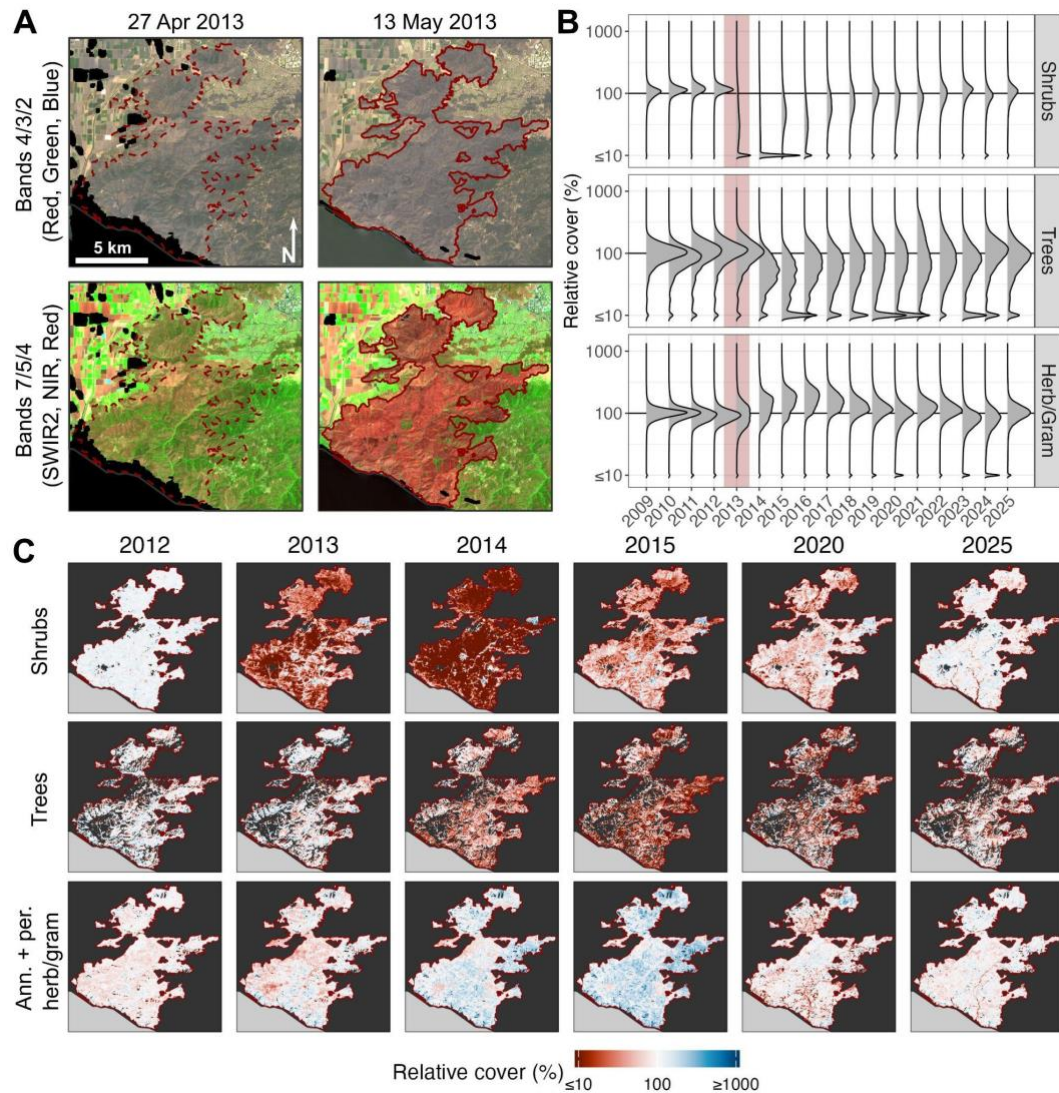


Figure 3

The Springs Fire burned from May 2-11, 2013 in the western Santa Monica Mountains near Camarillo, CA. Pre-fire and post-fire imagery from Landsat-8 shows a clear burn scar in RGB and multispectral bands; the hashed and solid red line denotes the fire perimeter (A; Landsat-8 images courtesy of the U.S. Geological Survey). Fractional tree and shrub cover, normalized to pre-fire baseline, dipped in the years following the fire, whereas herbaceous and graminoid fractional cover increased following the Springs Fire before tapering back (density plots in B with Springs Fire emphasized in red shaded bar, and shown spatially in C).

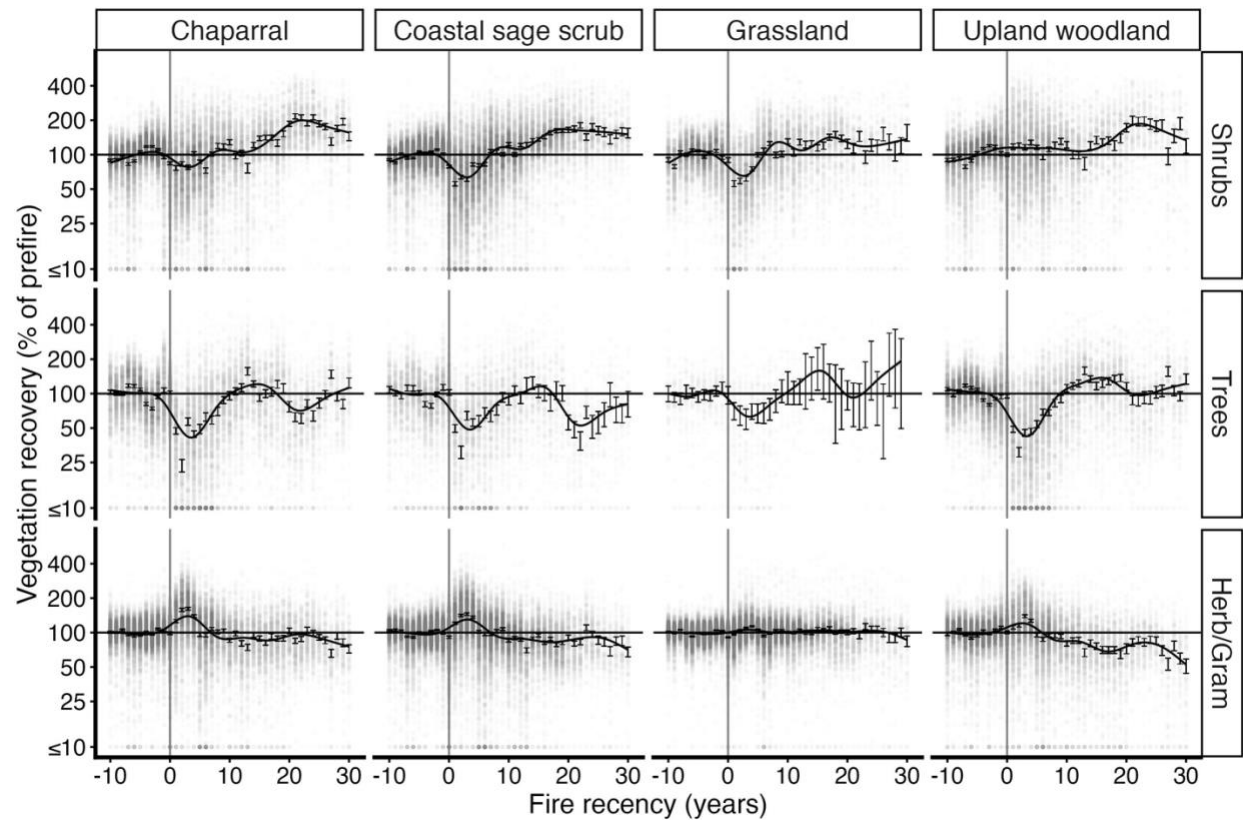


Figure 4

Chronograms of vegetation recovery across SAMO, with mean $\pm$ 2 standard errors illustrated as whiskers, and loess curve showing recovery scaled to pre-fire cover by vegetation community and plant growth form.

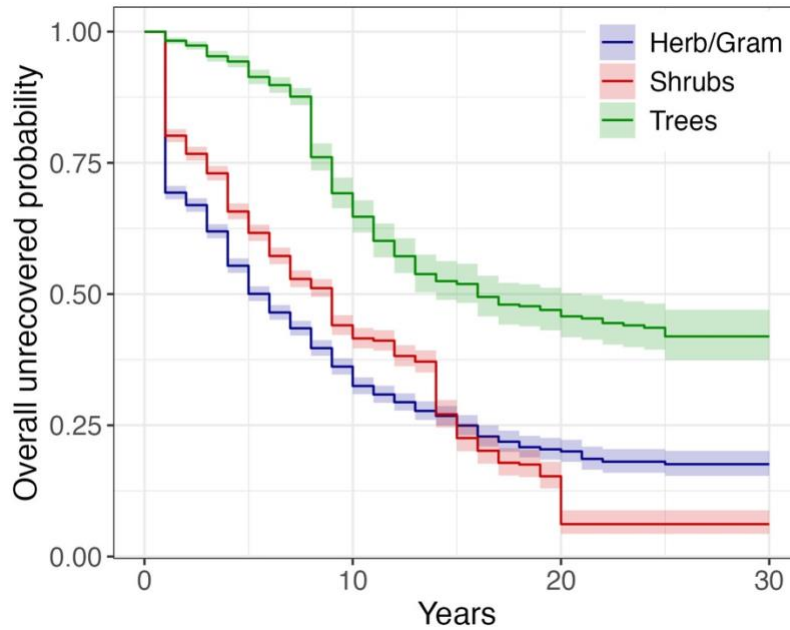


Figure 5

Kaplan-Meier plot illustrating timelines of recovery following fire, including censoring of points that did not recover before the end of the analysis. Recovery is indexed using the first year in which 4 consecutive years had relative cover > 80% pre-fire levels for Shrubs and Trees, or relative cover < 120% pre-fire levels for Herbaceous/Graminoids (see Methods section 2.5). Early in chronosequences, no points have achieved recovery (unrecovered probability is 100%), and over time vegetation progressively recovers following fire (unrecovered probability goes down). Herbaceous/Graminoid cover returns to baseline first, with a median recovery time of 6 years, followed by Shrubs (9 years), and finally Trees (16 years).

744 *Table 1*

745 Summary of main effects from the mixed-effects linear regression model fit with NPS I&M
 746 transect data as a response to RAP percent cover (both log+1 transformed), plant community ,
 747 plant growth form, and their interaction. The model was fit with a random slope between I&M
 748 and RAP cover for each transect (see Fig 4 for visualization of transect-specific slopes).

Predictor	Beta	95% CI	p-value
RAP	0.39	0.34, 0.43	<0.001
Vegetation community			
Chaparral	—	—	
Coastal sage scrub	0.17	0.05, 0.28	0.004
Grassland	1.1	0.94, 1.3	<0.001
Upland woodland	0.23	0.03, 0.43	0.025
Other	0.75	0.53, 0.98	<0.001
Plant growth form			
Herb/Gram	—	—	
Shrubs	0.51	0.41, 0.61	<0.001
Trees	-2.4	-2.6, -2.3	<0.001
Vegetation community × Plant growth form			
Coastal sage scrub × Shrubs	-0.32	-0.48, -0.17	<0.001
Grassland × Shrubs	-3.4	-3.6, -3.1	<0.001
Upland woodland × Shrubs	-0.96	-1.2, -0.68	<0.001
Other × Shrubs	-1.5	-1.8, -1.2	<0.001
Coastal sage scrub × Trees	-0.05	-0.22, 0.12	0.6
Grassland × Trees	-0.85	-1.1, -0.59	<0.001
Upland woodland × Trees	1.6	1.3, 1.8	<0.001
Other × Trees	0.11	-0.24, 0.46	0.5

Abbreviation: CI = Confidence Interval

Marginal R²: 0.736 | Conditional R²: 0.768

750 *Table 2*

751 Summary of Cox Proportional Hazards model relating fire history, plant growth form, and
 752 vegetation community to timelines of vegetation recovery following fire, indexed using hazards
 753 ratios (HR). Because HR here is based on the “risk” of vegetation recovering after fire, $\log(\text{HR}) >$
 754 0 indicates the variable hastens recovery timelines relative to the intercept, and $\log(\text{HR}) < 0$
 755 indicates the variable delays recovery timelines.

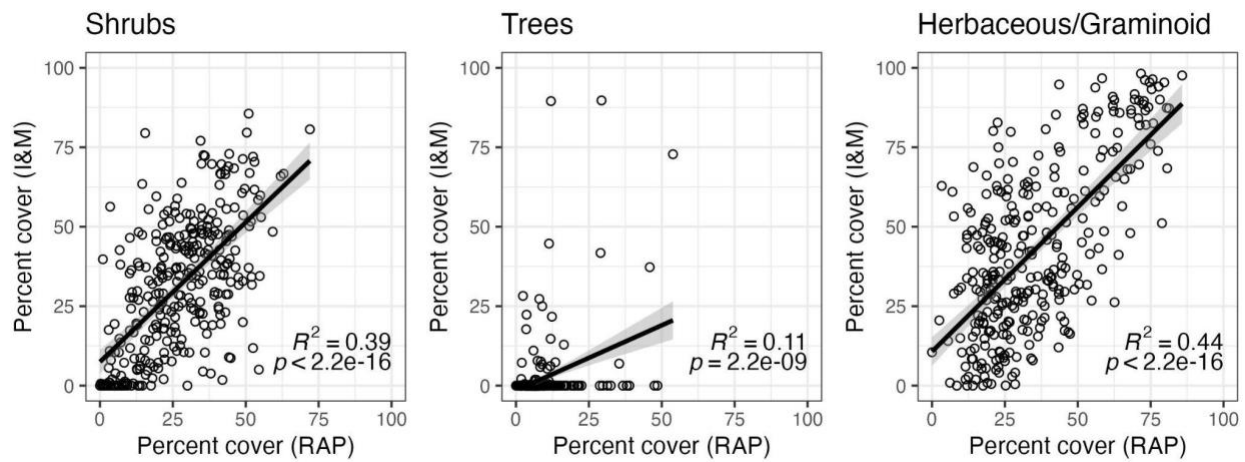
Predictor	$\log(\text{HR})$	95% CI	p-value
Focal fire year	-0.03	-0.04, -0.03	<0.001
Fire interval	-0.01	-0.01, -0.01	<0.001
Number of upcoming fires	-1.3	-1.6, -1.1	<0.001
Vegetation community			
Chaparral	—	—	
Coastal sage scrub	0.08	-0.04, 0.19	0.2
Grassland	0.84	0.73, 0.95	<0.001
Upland woodland	0.37	0.24, 0.50	<0.001
Plant growth form			
Herb/Gram	—	—	
Shrub	0.17	0.05, 0.29	0.007
Tree	-0.91	-1.1, -0.73	<0.001
Vegetation community × Plant growth form			
Coastal sage scrub × Shrub	-0.28	-0.43, -0.12	<0.001
Grassland × Shrub	-1.1	-1.3, -0.95	<0.001
Upland woodland × Shrub	0.22	0.04, 0.40	0.014
Coastal sage scrub × Tree	-0.42	-0.72, -0.11	0.007
Grassland × Tree	-0.74	-1.3, -0.17	0.011
Upland woodland × Tree	-0.19	-0.43, 0.05	0.12

Abbreviations: CI = Confidence Interval, HR = Hazard Ratio

R²: 0.737

1 Supplementary materials

2 Supplementary materials S1



3

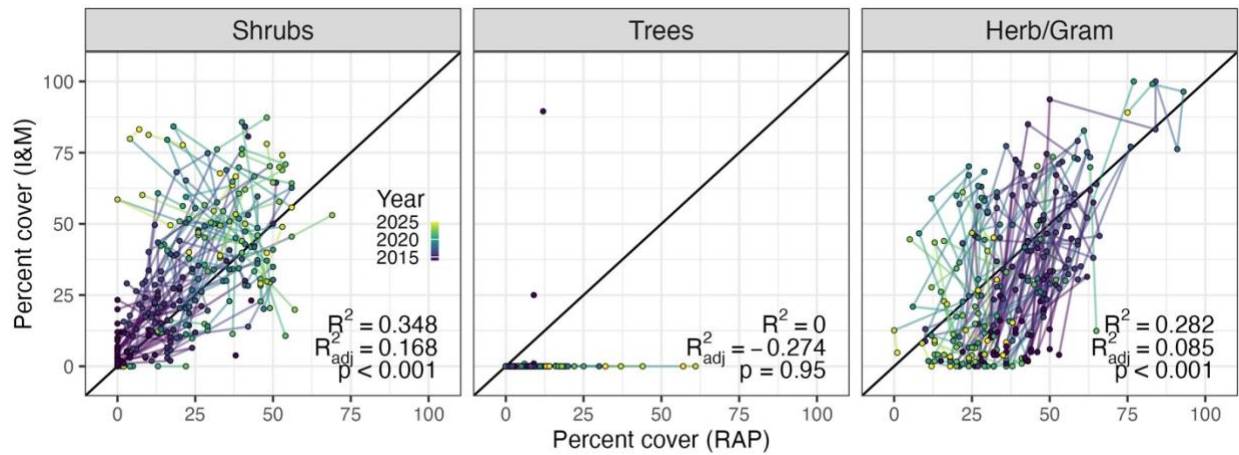
4 Spatial comparison of in-situ measurements (Inventory and Monitoring; I&M) and RAP

5 predictions of fractional cover of shrubs, trees, and herbaceous/graminoids. Here, percent

6 cover of each transect is averaged across time to generate a single overarching estimate of

7 tree, shrub, and graminoid cover for each location.

8 Supplementary materials S2



9

10 Comparison of in-situ measurements (Inventory and Monitoring; I&M) and RAP predictions of

11 fractional cover of trees, shrubs, and herbaceous/graminoids following the Springs Fire of 2013.

12 Point fill color and line color is based on year of sampling (2014-2025), and paths follow the

13 temporal trajectory of individual transects. While percent cover from I&M data do not

14 correspond with RAP for trees, they are highly correlated for shrubs and

15 herbaceous/graminoids. Notably, fractional cover of shrubs is initially low in the early years

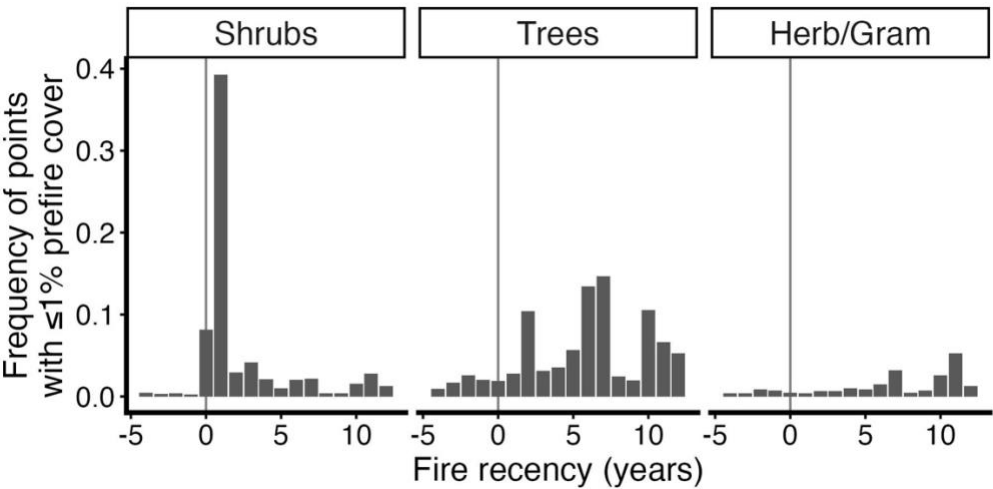
16 following the fire, and increases across time; whereas fractional cover of

17 herbaceous/graminoids is initially high in the early years following the fire, and decreases

18 across time. Inset statistics show R^2 , adjusted R^2 , and p values for panel data estimators fit with

19 transects as individuals and years as time using the plm package v2.6-7.

20 **Supplementary materials S3**



21

22 Frequency of percent cover falling below 1% of the baseline pre-fire cover following the Springs

23 Fire of 2013, revealing a stronger catastrophic response in woody plant cover than in

24 herbaceous/graminoid cover.

25 Supplementary materials S4

Predictor	log(HR)	95% CI	p-value
Focal fire year	-0.03	-0.04, -0.03	<0.001
Fire interval	-0.02	-0.03, -0.02	<0.001
Number of upcoming fires	-1.3	-1.6, -1.1	<0.001
Vegetation community			
Chaparral	—	—	
Coastal sage scrub	-0.23	-0.49, 0.03	0.079
Grassland	0.06	-0.18, 0.30	0.6
Upland woodland	-0.01	-0.31, 0.28	>0.9
Plant Growth Form			
Herb/Gram	—	—	
Shrub	-0.15	-0.45, 0.15	0.3
Tree	-1.7	-2.2, -1.2	<0.001
Fire interval × Vegetation community			
Fire interval × Coastal sage scrub	0.01	0.00, 0.02	0.072
Fire interval × Grassland	0.03	0.02, 0.04	<0.001
Fire interval × Upland woodland	0.01	0.00, 0.02	0.007
Vegetation community × Plant growth form			
Coastal sage scrub × Shrub	0.12	-0.24, 0.48	0.5
Grassland × Shrub	-0.50	-0.91, -0.10	0.015
Upland woodland × Shrub	0.25	-0.15, 0.65	0.2
Coastal sage scrub × Tree	0.51	-0.25, 1.3	0.2
Grassland × Tree	0.79	-0.64, 2.2	0.3
Upland woodland × Tree	0.67	0.03, 1.3	0.041
Fire interval × Plant Growth Form			
Fire interval × Shrub	0.01	0.00, 0.02	0.022
Fire interval × Tree	0.03	0.01, 0.04	<0.001
Fire interval × Vegetation community × Plant Growth Form			
Fire interval × Coastal sage scrub × Shrub	-0.01	-0.03, 0.00	0.034
Fire interval × Grassland × Shrub	-0.03	-0.04, -0.01	<0.001
Fire interval × Upland woodland × Shrub	0.00	-0.01, 0.01	>0.9
Fire interval × Coastal sage scrub × Tree	-0.03	-0.06, 0.00	0.026
Fire interval × Grassland × Tree	-0.06	-0.12, 0.00	0.038
Fire interval × Upland woodland × Tree	-0.03	-0.05, -0.01	0.005

Abbreviations: CI = Confidence Interval, HR = Hazard Ratio

R²: 0.742

26

27 Summary results of coxph model fit with an interactive term for fire interval, revealing a
 28 significant effect in which a shorter recent fire interval slows the recovery timeline of shrubs
 29 and trees compared to herbaceous/graminoids (note that VIF > 4 so multicollinearity may
 30 impact modeling results).