Received: 7 April 2018 | Revised: 8 June 2018 | Accepted: 22 June 2018

DOI: 10.1111/ddi.12827

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California

Alexandra D. Syphard[1] | **Teresa J. Brennan**[2] | **Jon E. Keeley**[2,3]

[1]Conservation Biology Institute, Corvallis, Oregon

[2]USGS Western Ecological Research Center, Three Rivers, California

[3]Department of Ecology & Evolutionary Biology, University of California, Los Angeles, California

Correspondence
Alexandra D. Syphard, Conservation Biology Institute, 136 SW Washington Ave., Suite 202, Corvallis, OR 97333.
Email: asyphard@consbio.org

Editor: Tomas Vaclavik

Abstract

Aim: In Southern California, native woody shrublands known as chaparral support exceptional biodiversity. However, large-scale conversion of chaparral into largely exotic herbaceous cover is a major ecological threat and serious conservation concern. Due to substantial uncertainty regarding the causes and extent of this vegetation change, we aimed to quantify the primary drivers of and map potentially vulnerable locations for vegetation type conversion from woody into herbaceous cover.

Location: Santa Monica Mountains National Recreational Area, Southern California, USA.

Methods: We used air photograph image interpretation to quantify the extent to which chaparral shrublands transitioned to herbaceous cover from 1943 to 2014 across nearly 800 randomly located plots. Comparing plots that remained chaparral to those that converted to herbaceous cover, we performed hierarchical partitioning to quantify the independent contribution of a range of explanatory variables, and then used classification trees to explore variable interactions. We also developed a spatial model to create a seamless map delineating relative probability of type conversion.

Results: Of the original plots that were chaparral in 1943, 284 (36%) changed cover by 2014, with 79 completely converting, and 142 mostly converting to herbaceous cover. The primary mechanism behind shrubland decline and replacement was short intervals between fires (<=10 years), and type conversion was most likely to occur in arid parts of the landscape with low topographic heterogeneity and close proximity to trails and roads. Predictive maps delineated several hotspots with environmental conditions similar to those of type-converted plots.

Main conclusions: Chaparral type conversion is a widespread conservation concern, and results here suggest that short-interval fire and landscape disturbance are the most likely factors to exacerbate it, particularly in water-limited portions of the landscape where chaparral is subject to greater physiological stress and slower recovery. Reducing fire ignitions and mapping vulnerable areas may be important strategies for prevention.

KEYWORDS

disturbance, Mediterranean, site aridity, vegetation change, wildfire

1 | INTRODUCTION

The native woody chaparral of California, and similar shrubland ecosystems in other Mediterranean-climate regions, supports exceptional biodiversity and is resilient to periodic wildfire and drought (Keeley, Bond, Bradstock, Pausas, & Rundel, 2012). Despite its resilience to occasional disturbance, in many parts of California, chaparral has been invaded, and sometimes completely displaced by exotic annual forbs and grasses (Syphard, Brennan, & Keeley, 2018). This process known as vegetation type conversion is a major threat to the region's biodiversity and provision of ecosystem services, and may alter fire regimes. Although the potential for large-scale vegetation change is a widespread concern, there is ongoing uncertainty about its extent and primary drivers (Halsey & Syphard, 2015; Park, Hooper, Flegal, & Jenerette, 2018).

While much of contemporary vegetation type conversion is caused unintentionally, the initial establishment and spread of this exotic herbaceous vegetation were due to deliberate type conversion of these shrublands to herbaceous cover. For thousands of years, Native Americans living in the region burned woody vegetation at a high frequency to open the landscape (Anderson & Byrd, 1998; Anderson & Keeley, 2018; Keeley, 2002), resulting in the expansion of native grasses and forbs. When Europeans settled about 200 years ago, they brought many aggressive exotic grasses and forbs that now dominate grasslands in the state (Keeley, 1990; Seabloom et al., 2003). These settlers and their descendants continued the practice of deliberate type conversion, largely to accommodate extensive livestock grazing (Burcham, 1955; Bentley, 1967; Keeley & Fotheringham, 2003).

Although deliberate conversion of shrubland into herbaceous cover is less common now, vegetation change continues, and part of the solution to slowing it is to understand why it is happening. A range of potential factors have been proposed to explain chaparral type conversion, and many are drivers that have been documented in studies of drought-deciduous sage scrub conversion into herbaceous cover (e.g., Cox, Preston, Johnson, Minnich, & Allen, 2014; Minnich & Dezzani, 1998; Talluto & Suding, 2008). While reasonable to assume many of the factors are the same, these two shrubland vegetation types include species with differing life history traits, and they have different distributions on the landscape (Keeley & Davis, 2007).

The earliest ecological studies contended that chaparral type conversion was largely driven by high frequency of wildfires (Cooper, 1922; Wells, 1962). Despite the fact that chaparral is a fire-type vegetation, indeed even some species are fire-dependent, the natural regime is thought to have been between 30 and 130 years (Keeley & Syphard, 2018). When fire intervals are shorter, this can threaten recovery of some species, in particular, obligate seeding shrubs, which are very susceptible because they regenerate entirely from long-lived, fire-cued, soil-stored seed banks that require 15 years or more to accumulate sufficient numbers for recovery (Zedler, 1995). A number of field studies have documented obligate seeder decline or elimination after repeated fire (Haidinger & Keeley, 1993; Jacobsen, Davis, & Fabritius, 2004; Keeley & Brennan, 2012; Lippitt et al., 2012; Zedler, Gautier, & McMaster, 1983). Although resprouting species are more resilient to frequent fire than obligate seeders, even these can be reduced after burning in multiple short-interval fires (Haidinger & Keeley, 1993; Keeley & Brennan, 2012). Many sage scrub species have life history traits that allow better persistence under frequent fire, but even these have an upper limit of tolerance (Syphard, Franklin, & Keeley, 2006; Westman & O'Leary, 1986). Due to the fact that chaparral shrub species vary in their resilience to short fire intervals, often type conversion may progress in stages, first, the obligate seeding species are eliminated, and with continued short-interval fires, this chaparral /herbaceous cover mixture may continue on a trajectory of increasing grass and forb dominance.

Contributing to this trajectory is that once annual grasses and forbs establish they provide highly flammable, flashy fuels that extend the fire season, and typically result in lower-intensity fires that also favour exotic species (D'Antonio, 1992; Keeley, Baer-Keeley, & Fotheringham, 2005). Thus, grasses themselves alter the fire regime and create a positive feedback process, often referred to as the grass-fire cycle, which is recognized as a potential problem in ecosystems around the world (e.g., Balch, Bradley, D'Antonio, & Gómez-Dans, 2013; Bowman, MacDermott, Nichol, & Murphy, 2014; Brooks et al., 2004; Keeley et al., 2012; Rossiter, Setterfield, Douglas, & Hutley, 2003).

Another potential factor effecting type conversion is atmospheric nitrogen deposition. The role of nitrogen in causing conversion of sage scrub to herbaceous cover has been hypothesized and studied for more than a decade and research results suggest that a combination of nitrogen deposition, drought, and frequent fire have all contributed to this change (Allen, Padgett, Bytnerowicz, & Minnich, 1998; Padgett & Allen, 1999; Talluto & Suding, 2008). However, as mentioned above, this link has not been established in chaparral, despite attempts to associate nitrogen deposition with levels of postfire alien invasion (Keeley, Baer-Keeley et al., 2005).

Proximity to direct habitat disturbance via anthropogenic activities could also facilitate conversion of shrubs to grass. Residential and urban land development and road construction provide conduits for grass expansion into undisturbed woody vegetation (Gavier-Pizarro, Radeloff, Stewart, Cynthia, & Keuler, 2010), and recreational trails and mechanical fuel treatments for fire management may also facilitate their spread (Merriam, Keeley, & Beyers, 2006). Recent investigation into the impacts of masticated fuel treatments on vegetation structure and composition (Brennan & Keeley, 2017) revealed a significant increase in non-native grasses after treatment, which was consistent with other findings in chaparral by Potts and Stephens (2009) and Coulter, Southworth, and Hosten (2010).

Finally, it is possible that vegetation change is more or less likely depending on the biophysical characteristics of a site. This is because some areas may be more suitable for invasion than others based on species' different physiological limitations. A number of studies have shown that chaparral species' composition and postfire recovery rates vary according to factors such as elevation, slope, climate or soil. These act as environmental filters determining composition (Keeley, Fotheringham, & Baer-Keeley, 2005), and these factors also affect alien success (Keeley, Baer-Keeley et al., 2005). In their study of apparent cover change, Meng, Dennison, D'Antonio, and Moritz (2014) found that, while climatic factors were not significantly associated with vegetation change, elevation was a significant correlate, and that reduction in woody cover was more likely in lower elevations. On the other hand, Park et al. (2018) determined that precipitation and soil moisture were the most significant factors in explaining where fire or other anthropogenic disturbances are most likely to affect type conversion.

Given that there appears to be an acceleration of type conversion from native shrublands to exotic herbaceous cover throughout the 20th and 21st centuries (Syphard et al., 2018), there is a critical need to understand why and where type conversion is occurring, or is likely to occur, so that strategies can be identified to prevent further loss. Also, if the environmental correlates of type conversion can be modelled, maps can be made based on this information to identify other areas on the landscape that share the same characteristics. In this study, we used spatial analysis and air photograph image interpretation to identify how and why woody chaparral transitioned to herbaceous cover from 1943 to 2014 across nearly 800 randomly located plots in the Santa Monica Mountains of Southern California. In addition to analysing the drivers of change, we also developed probabilistic maps highlighting other areas in the landscape that may potentially be vulnerable.

2 | METHODS

2.1 | Study area

We conducted our study within the Santa Monica Mountain National Recreation Area, an administrative unit encompassing approximately 60,000 ha of relatively undeveloped coastal mountains bordered by the Pacific Ocean and the Los Angeles metropolitan area (Figure 1). Approximately half of the land is publicly owned and protected, and of the privately owned land, about 25% is developed (ranging from sparsely distributed rural communities to densely populated subdivisions). The Santa Monica Mountains are a rugged east–west trending range with a Mediterranean climate of cool, wet winters and hot, dry summers. Chaparral is the most extensive vegetation type, but it is intermixed with sage scrub, oak woodland, riparian woodland, and grasslands (Radtke, Arndt, & Wakimoto, 1982). The Santa Monica Mountains are highly fire-prone, with the majority of landscape having burned at least once and some areas having burned up to 14 times since record keeping began in the early 20th century. The areas of highest fire frequency tend to occur within canyons prone to Santa Ana winds. The park contains some of the largest remaining areas of intact chaparral in Southern California, as much of the vegetation in other parts of the region has been developed. The study area is highly representative of the region's plant community and topographic diversity, and also experiences a wide variation in fire frequency, development, and other landscape disturbance such as trails and roads.

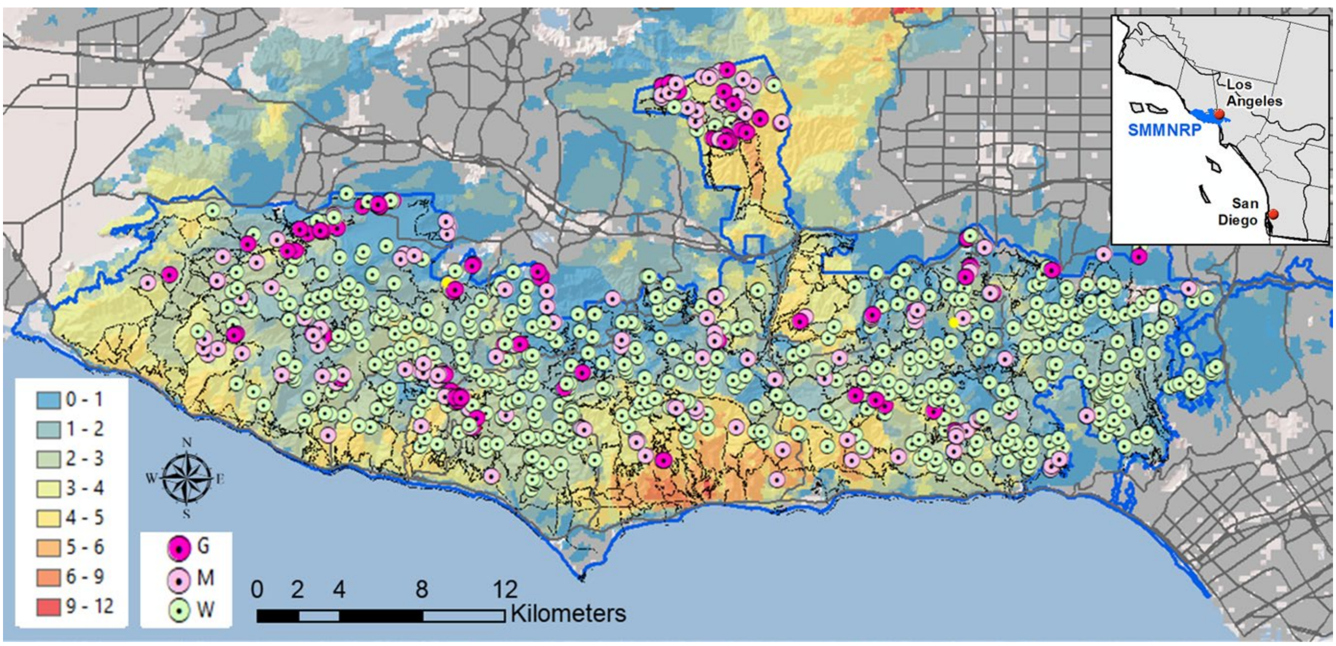

FIGURE 1 Vegetation type (G = grass; M = mixed; W = woody) in 2014 overlaid on historical fire count in the Santa Monica Mountains National Recreation Area, CA study area. Small black lines within the study area show locations of trails, and thick grey lines show the distribution of primary and secondary roads. Insert shows location of study area within the Southern California region

2.2 | Generation of random points

Because our objective was to compare the differences between areas that had converted from chaparral to grass to those that remained chaparral, we used vegetation maps to guide our sampling design. We overlaid a vegetation type map from the 1930s (Kelly, Allen-Diaz, & Kobzina, 2005) with a recent (2007) vegetation map of the study area, created a common vegetation type classification scheme, and delineated mapped areas where chaparral remained chaparral and where chaparral became grass during that time. Within each of these mapped areas, we placed as many randomly located points as possible that were at least 30 m apart to minimize the potential for plots to overlap. We designed this process of random point selection to obtain adequate samples of both converted and unchanged vegetation. After generating the points, we pooled them together into one dataset for air photograph image interpretation. We also created 30-m buffers around all random sample points to ensure we were evaluating areas at least as large as the spatial resolution of our explanatory variables. Thus, we refer to these 0.28 ha buffers as plots from here on out.

2.3 | Image interpretation

Our historical imagery dated back to 1947, and we tracked each plot through time according to years of later available imagery, which included 1976/1977, 1989, 1995, 2005 and 2014. The earliest air-photographs (up through 1995) were available through prior research (Syphard, Clarke, & Franklin, 2005), and the more contemporary photographs were provided by staff at the National Park Service.

We first overlaid the random plots on the 1947 imagery and calculated the percentage of woody (shrubland) vegetation in each buffer. Any plots that did not begin with 100% woody cover were then eliminated, in addition to plots for which there was no available imagery in 1977. We overlaid the remaining buffered plots on all years of the imagery, and for each one, we calculated the percentage land cover of woody shrubland vegetation; grass/bare ground; and developed area on a scale of 1 – 4, where 1 = 0%–25% cover; 2 = 26%–50%; 3 = 51%–75%; and 4 = 76%–100%. In other words, each plot was assigned a value of 1–4 for woody (W), grass (G), and developed (D) land cover type. We also assigned each plot with one class representing the dominant land cover type for each year. For these, W—Woody veg >50% with <25% grass & <50% developed area; G—Grass >50% with <25% woody & <50% developed area; D—Developed areas = or >50% with <50% woody & grass; We also created a mixed class, where M—woody/grass/dev. mix where veg >50% and dev. is <50%.

2.4 | Explanatory variables

Given the potential for soil characteristics to mediate plant development and productivity (Franklin, 1995), we evaluated and compared

TABLE 1 Description and scale of variables used in modelling type conversion in the Santa Monica Mountains, CA

Variable	Description and source	Scale
Vegetation change (dependent variables)		
Full conversion	Plot that was fully chaparral in 1943 and fully grass in 2014, compared to no vegetation change	30-m buffers around points (0.28 ha), binary
Majority conversion	Plot that was fully chaparral in 1943 and more than 50% grass in 2014, compared to no vegetation change	30-m buffers around points (0.28 ha), binary
Explanatory variables		
Nitrogen deposition	Annual deposition or reduced and oxidized nitrogen (Tonnesen et al., 2007)	4-km, kilogram of nitrogen per hectare
Number of fires	Total number of fires that occurred since 1933, Cal Fire perimeter database	30 m, calculated at plot location
Minimum fire interval	Shortest number of years between any two fires from 1933 to 2014	30 m, calculated at plot location
Available water holding capacity	The amount of available water in the soil that can be absorbed by a plant (Shirazi et al., 2001)	1-km, inches of water available in soil profile
Elevation	US Geological Survey digital elevation model	30-m
Slope	Derived from elevation	30-m
Topographic heterogeneity	Range of elevation values within 270-m radius of centre cell	90-m, index from 0 to 1
Winter solar insolation	Daily insolation for winter solstice, derived from elevation model (Syphard & Franklin, 2010)	30-m
Distance to all roads	TIGER line, Exclude 4WD and OHV roads; Combine others, including RRs. TIGER Roads 2015, US Department of Commerce, US Census Bureau	Euclidean distance, 30-m
Distance to primary-secondary roads	Exclude all but primary and secondary roads from all roads	Euclidean distance, 30-m
Distance to trails	Digitized by the National Park Service	Euclidean distance, 30-m

several soil maps that were derived from the California State Soil Geographic Database (STATSGO) at 1-km resolution (Shirazi, Boersma, Haggerty, & Johnson, 2001). These included the following: soil depth (DEPL), depth to water-table (WTDL), soil available water capacity (AWCL), salinity (SALL) and pH (PHL). Preliminary results indicated that DEPL, WTDL, SALL and PHL had virtually no association with vegetation change, so we only considered AWCL through the rest of the analysis (Table 1).

We also explored the potential for atmospheric nitrogen deposition to facilitate type conversion using a 2002 map representing total annual deposition of reduced and oxidized nitrogen (kilograms of nitrogen per hectare per year) for the most polluted parts of California (Tonnesen, Wang, Omary, & Chien, 2007). This map was produced at 4-km resolution.

In addition to edaphic factors, topographic variables have also been predictive of plant species' distributions due to their effect on energy and moisture balance (Franklin, 1995). Therefore, we explored potential associations between vegetation type conversion and several topographically derived variables. These included elevation and slope derived from a 30-m US Geological Survey digital elevation model (DEM), a 90-m topographic heterogeneity layer (https://databasin.org/datasets/1f86100938b544a3b6361eee6ac05945), and a 30-m grid of daily insolation for the winter solstice (from Syphard & Franklin, 2010). Topo-heterogeneity is an index ranging from 0 to 1 indicating the range in elevation values within a 270-m radius from any given cell.

To evaluate the effect of fire frequency on vegetation change, we created a 30-m grid in which each pixel represented the number of fires that had occurred historically from 1933 to 2014 using the Cal Fire perimeter database (http://frap.fire.ca.gov/data/frapgisdata-sw-fireperimeters_download). In addition, using attribute data that recorded the year of fires and prescribed fires, we calculated the minimum interval between any two fires during the period of record. For those plots in which no fires had occurred, we estimated the minimum interval to be 10 years older than the first date of the imagery through 2014, which is 77 years.

We explored three types of anthropogenic variables, including distance to trails, distance to all roads, and distance to primary and secondary roads. We additionally evaluated a map of historical fuel breaks and treatments, but this map was highly correlated with the trails map, so we only used the trails map as it was more spatially extensive. The trails map was provided by the National Park Service, and roads came from the 2015 Topographically Integrated Geographic Encoding and Referencing System TIGER/Line files from the US Census. We also considered evaluating the distance to development; however, because the Santa Monica Mountains are surrounded by the high-density development of Los Angeles, the variation in distance did not capture the finer-scale variation in landscape disturbance as did the roads and trails features.

Many of the explanatory variables were provided with different native resolutions (Table 1), which captured the differences in spatial variation and heterogeneity of each variable. To ensure that this heterogeneity was preserved across variables, we resampled all maps to the resolution of the finest-scale variable, which was 30 m.

2.5 | Analysis and mapping of vegetation type conversion

Because vegetation type conversion typically occurs as a gradual transition, we compared two different binary dependent variables, one representing full conversion of shrubland into herbaceous ("complete conversion"), and the other representing a later transitional stage in which the plot had mostly converted to herbaceous, but still contained mixed woody cover ("majority conversion"). To create the first variable, we selected all plots where grass had a cover class of 4 in 2014, that is they fully type converted, to compare to plots that were woody class 4 in both 1947 and 2014 (i.e., unchanged vegetation, or "absence"). We removed those that had become developed or converted to agriculture for this analysis because our focus was vegetation type change. The second dependent variable added grass of cover type 3 to plots with grass of cover type 4 (that is, some plots had at least 51% conversion from 1947 to 2014). We performed this comparison to determine whether the drivers of partial vegetation change were representative of those explaining full type conversion.

To best understand the reasons for vegetation type conversion, we used three different analysis techniques that allowed us to (a) identify the independent contribution of each explanatory variable; (b) assess how interactions among multiple variables drive type conversion, and identify important thresholds; and (c) map the potential for vegetation change across the study area.

To quantify relative variable importance, we performed a hierarchical partitioning analysis using the HIER.PART package in R, version 3.2.3. Based on a hierarchy of regression models using all combinations of explanatory variables, this algorithm produces a measure of every variables' independent influence on the response (MacNally & Walsh, 2004; R Core Team 2016). Because we had two binary dependent variables, we ran the algorithm using logistic regression with a "binomial" response and log likelihood as a measure of goodness-of-fit.

To visualize data structure and potential interactions among the different drivers of vegetation change, we developed classification trees using the RPART and RPART.PLOT packages in R, version 3.2.3, with full or majority conversion as the binary dependent variable and unchanged vegetation plots for the absence data. Classification trees (Breiman, Friedman, Olshen, & Stone, 1984) are nonparametric tools that facilitate interpretation of complex relationships via an iterative partitioning algorithm that separates data into a series of homogenous classes that divide across different thresholds. The resulting tree represents a hierarchy with those variables that best differentiate between classes at the top, and lower-importance variables fall to the bottom. To avoid overfitting, we pruned the tree using the complexity parameter that resulted in the smallest cross-validated error. We quantified the performance of the classification tree models using the area under the curve (AUC) for receiver operating characteristic (ROC) plots (Hanley & McNeil, 1982). The AUC ranges from 0.5 to 1.0 and represents the probability that for a randomly selected pair of observations, the model's prediction for the presence results in a higher value than the prediction for the absence. Interpretation of the value can be subjective, but a good model is often assumed to have an AUC of 0.70 or higher, and an excellent model is assumed to have an AUC of 0.85 or higher.

Finally, we used the MaxEnt statistical software program (Phillips, Anderson, & Schapire, 2006) to build probabilistic models and maps representing suitable environmental conditions for full or majority type conversion based on our explanatory variables. MaxEnt uses a machine-learning algorithm to iteratively evaluate environmental contrasts between locations of the dependent variable (full or majority type-converted points) and the locations of a random sample of 10,000 background points distributed across the landscape. Among the large number of probability distributions that potentially meet the constraints of the presence data, the algorithm selects the one with the maximum entropy (i.e., most uniform) as the best. The model outputs a map in which each grid cell represents the suitability for the modelled condition (i.e., type conversion) to occur, ranging from 0 to 1. In addition to its most common application, species distribution modelling (Franklin, 2010), this modelling approach has been successfully used to map the distribution of fire probability (e.g., Davis, Yang, Yost, Belongie, & Cohen, 2017), structure risk to wildfire (e.g., Syphard, Keeley, Massada, Brennan, & Radeloff, 2012), and ignition probability (e.g., Syphard & Keeley, 2015).

Instead of using an absence dataset (e.g., vegetation that remained unchanged), we allowed the model to generate a random sample distribution of background points across the landscape. However, because we initially drew our own random sample from areas that were mapped to be chaparral vegetation in the 1930s, we used this same map as a mask to guide sample selection here. Therefore, the output of the model can be interpreted as the probability of type conversion relative to all areas mapped as chaparral. The primary distinction is that, for the "absence" data, we have confirmed that these points remained woody through airphotograph interpretation.

We used MaxEnt version 3.3.3k with the default settings, except we excluded hinge features and used a regularization multiplier of 1.5 to minimize overfitting. We ran the model with five cross-validated replicates to get a mean fivefold calculation of the AUC on test data.

3 | RESULTS

Of the original 1,400 plots we sampled from the 1930s map, 788 were identified as entirely chaparral (woody 4) in 1947, and these were the plots we used for the rest of the analysis. Of these 788 plots, 534 (64%) were also woody 4 in 2014. For all plots across the five dates of historical imagery, the top 10 change classes, included: 64% no change at all; 18% a combination of woody and mixed cover oscillations over time; 14% continued to decline with no period of recovery; 3% some recovery after full conversion into grass. In 2014, 79 plots were completely grass (grass 4) and 142 plots were mostly (>51%) grass (grass 3). The mean number of years it took for a plot to transition from full woody to full grass was 49.8 (minimum 30, maximum 67).

The analysis of independent contribution of explanatory variables showed multiple important drivers explaining complete and majority vegetation type conversion, with soil moisture, terrain, fire frequency and landscape disturbance all making substantial contributions (Figure 2). Available soil water capacity contributed the largest independent contribution, with type-converted plots occurring more frequently on drier sites. Type conversion was also more likely to occur on flatter slopes with lower topographic heterogeneity; and at close proximity to major roads, primary/secondary roads and trails. There was a positive association with historical fire frequency and negative association with intervals between fires. There was relatively little difference in variable importance depending on whether there was complete or majority type conversion.

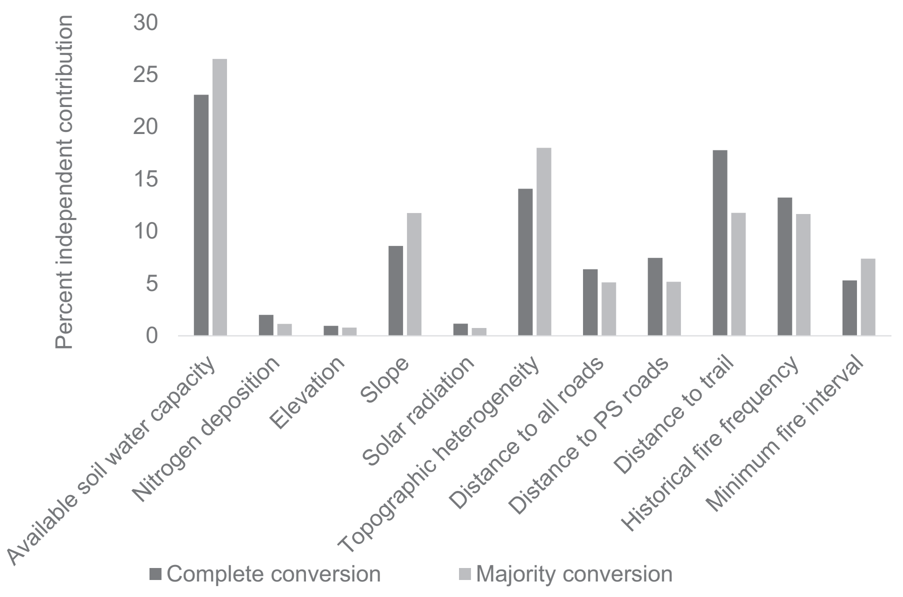

FIGURE 2 Per cent independent contribution of variables in hierarchical partitioning analysis explaining complete and majority type conversion of woody shrublands to herbaceous cover

The classification tree analysis that revealed variable interactions for both complete and majority-converted plots showed that the variable that best differentiated type converted from unchanged vegetation was AWCL, followed by the minimum yearly interval between fires, and distance to trail (complete conversion) or topographic heterogeneity (majority conversion) (Figure 3). The

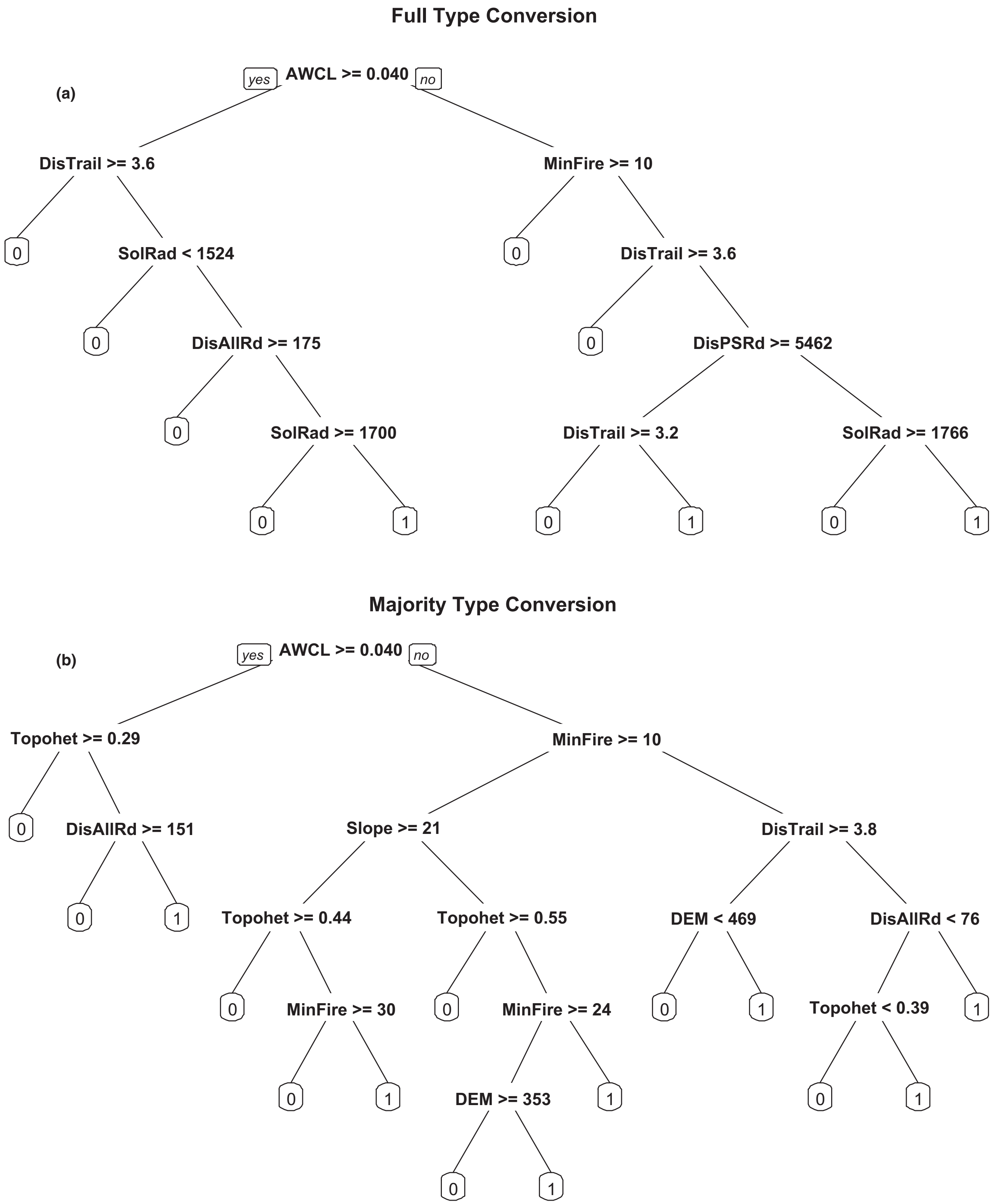

FIGURE 3 Classification tree plots showing the relationship among (a) full and (b) majority vegetation type conversion and explanatory variables

thresholds identified as most important for type conversion were to have a low AWCL (<0.04) and fewer than 10 years of minimal interval between fires; or to have high AWCL (>=0.04) and short distance to a trail (<3.6 m, complete conversion), or high topo-heterogeneity (>=0.29, majority conversion). The AUC for the classification tree was 0.78 for complete conversion and 0.85 for majority conversion.

The probabilistic distribution maps of environmental suitability for vegetation change were similar for complete and majority type conversion (Figure 4). There are clear hotspots in the middle of the study area where fires tend to be frequent and there is substantial density of roads and trails. There are also hotspots along the northern edge of the study area, closest to the 101 freeway, and at the northernmost tip where fires and prescribed fires have historically been very frequent. The AUC for the test data of the cross-validated model replicates was 0.77 for complete conversion and 0.75 for majority type conversion.

4 | DISCUSSION

It is clear from studies discussed in the introduction that type conversion of native shrublands to non-native annual grasslands has transformed a substantial portion of the California landscape (Park et al., 2018; Syphard et al., 2018). Investigators have long suggested that this process began with anomalously high fire frequency (Cooper, 1922; Keeley, 1990; Wells, 1962); however, Jacobsen et al. (2004) provided a needed perspective that frequent fires are not

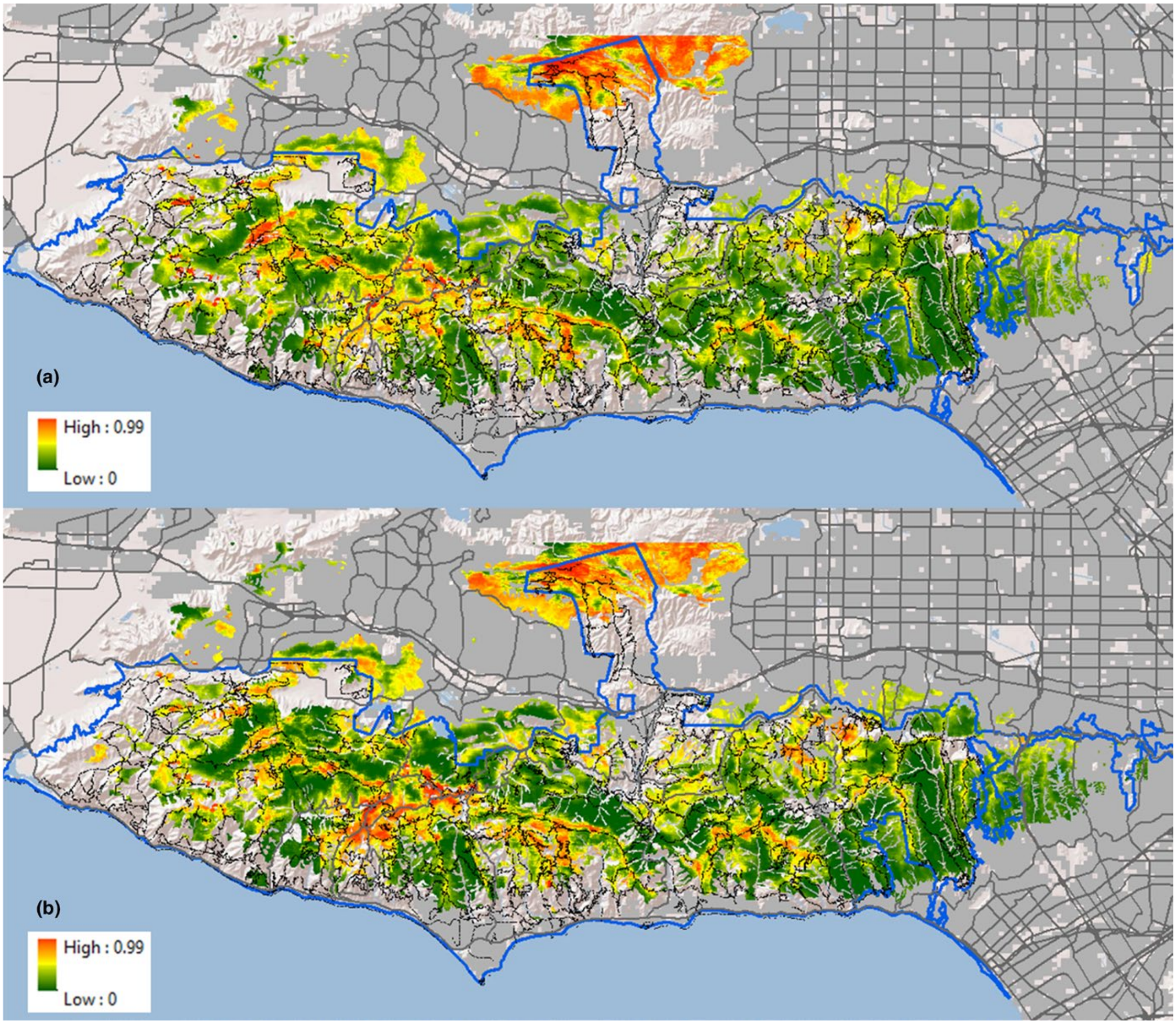

FIGURE 4 Probabilistic maps representing areas potentially suitable for vegetation type conversion using locations of (a) full and (b) majority conversion of chaparral to herbaceous vegetation. Map extent reflects areas with full data coverage for all variables. Small black lines within the study area show locations of trails, and thick grey lines show the distribution of primary and secondary roads

necessarily the key to type conversion; rather, it is occurrence of short intervals between fires, which of course are more likely to occur when fire overall is more frequent. The mechanism behind this effect is that many shrub species, particularly those with an obligate seeding life history, require one to two decades to replenish the soil seed bank after a fire. The results from the classification tree analysis here support this explanation, suggesting a threshold of <=10 years between fires as a critical splitting point in the data.

Given this distinction between minimum fire interval and average fire interval or frequency, other studies may not have adequately captured the mechanism behind the effect of fire (e.g., Park et al., 2018; Talluto & Suding, 2008). In field studies, however, the detrimental effect of short-interval fires has been documented in post-fire chaparral communities, where native shrub species have been extirpated and replaced with extensive establishment of non-native grasses(e.g., Haidinger & Keeley, 1993; Keeley & Brennan, 2012; Lippitt et al., 2013; Zedler et al., 1983).

While short-interval fire is a primary mechanism that leads to shrubland extirpation and replacement, this study also shows that the relative probability of this outcome is a function of the underlying environmental variation in the landscape, that is factors that govern water–energy balance and plant physiological limitations, including available soil water capacity, slope, and topographic heterogeneity. This is consistent with recent work showing that moisture availability was the strongest spatial correlate with herbaceous-dominated areas in the nearby Angeles National Forest (Park et al., 2018).

The role of soil moisture in facilitating type conversion is likely due as much as or more to its influence on chaparral than its favourability for herbaceous vegetation. This is because highly arid conditions can limit postfire recovery in chaparral and result in the thinning of young shrublands (Keeley, Fotheringham, & Baer-Keeley, 2005). Postfire drought may also promote higher cover and richness of herbaceous species at the expense of shrublands, particularly for obligate seeding species that are most sensitive to repeat fires (Parra & Moreno, 2018). Furthermore, the most fire-sensitive obligate seeding species are generally most abundant in xeric environments, on hot dry slopes (Meentemeyer, Moody, & Franklin, 2001), so the explanation for this relationship is also one of spatial correlation.

To the extent that site aridity is especially prone to dieback and mortality under prolonged drought, another complicating issue with type conversion is that long drought periods in Southern California may cause extensive dieback and mortality of chaparral (Davis et al., 2002). This dead biomass may in turn facilitate rapid spread and growth of large wildfires due to more effective ignition following ember production in severe, wind-driven fire weather (Keeley & Zedler, 2009). This increase in site flammability, along with the high flammability of senescent grassland, may interact to drive the type of feedbacks inherent to a fire-grass cycle (Bowman et al., 2014; Brooks et al., 2004; D'Antonio, 1992).

In addition to site conditions, close proximity to trails, and to a lesser extent roads, was one of the most important correlates of type conversion in this study. Given the extensive parkland in the study area, there is an extensive trail network for recreational activities. Often these trails double as, or are spatially aligned with, fuel breaks on the landscape, which are linear strips of vegetation modification where shrublands are often purposefully converted to grasslands in efforts to control wildfire behaviour. These trails and fuelbreaks therefore provide a source and means for herbaceous species to enter and disperse throughout an otherwise undisturbed landscape.

Landscape disturbance has long been associated with the invasion of exotic species, as it provides openings in the landscape that are available for colonization (Gavier-Pizarro et al., 2010). Linear landscape features in particular, such as roads and fuel breaks, provide effective conduits for exotic species dispersal and spread (Gelbard & Belnap, 2003; Merriam et al., 2006). In California, the ability for exotic annuals to disperse widely and rapidly colonize disturbed areas has been proposed as the primary reason these grasslands have so extensively replaced dispersal-limited native grasses (Seabloom et al., 2003).

In terms of chaparral displacement, if herbaceous species successfully colonize a burned area where shrub species have been extirpated, grasslands are likely to persist. This is because, in addition to the flammability and reproductive success of grasslands, recolonization of chaparral species is difficult and slow due to short dispersal distances and infrequent recruitment between fires (Keeley, Baer-Keeley et al., 2005; Keeley, Fotheringham et al., 2005). In fact, the trajectory is more likely to move in the opposite direction in that, after multiple short-interval fires, chaparral slowly disappears from a site that is increasingly invaded by herbaceous cover. In this study, the time for chaparral to completely convert to herbaceous cover was approximately 50 years. That there were such similar model results for complete conversion vs. conversion from woody to a mix of woody and herbaceous suggests that this slow trajectory of type conversion may be occurring extensively.

Given that short-interval fires are such a critical driver of chaparral type conversion, some may argue that fuel breaks and other types of vegetation treatment are a needed resource sacrifice to control wildfire. Fires are so frequent now in Southern California that the region is burning far beyond what historical return intervals used to be (Safford & Van de Water, 2014). However, recent studies have documented lower cover and density of shrubs and higher cover and density of exotic herbaceous plants in areas treated for fire management (Brennan & Keeley, 2017). These results, and the strength of the relationship documented here, suggest that the negative ecological impact of these treatments may exceed whatever benefit they may provide in areas where they do not serve to benefit the protection of residential communities. In undeveloped wildland areas, fuel breaks have limited effectiveness in stopping fires when firefighters are not present (Syphard, Keeley, & Brennan, 2011).

One variable that has been hypothesized to be important for shrubland type conversion is nitrogen deposition (Allen et al., 1998; Padgett & Allen, 1999), which was not supported in this study. Many prior studies have shown that nitrogen favours annual plants, but the extent to which this drives type conversion of shrublands has not been documented in the field. In one field study, conclusions regarding the importance of nitrogen (Talluto & Suding, 2008) were partly based on the fact that they could not show fire as an important factor. However, the database of fire they used has been shown to miss fire events (Syphard & Keeley, 2015). We believe the evidence is clear that nitrogen deposition can enhance non-native herbaceous growth in woody vegetation when it is in an open community such as desert communities (Syphard, Keeley, & Abatzoglou, 2017). However, there is no evidence that nitrogen deposition alone can convert closed canopy chaparral or sage scrub to invasive cover. Evidence to date indicates that for nitrogen deposition to alter the balance between native shrublands and non-native herbaceous communities, there is a need for prior disturbance that diminishes shrub recovery (Keeley & Davis, 2007).

In conclusion, replacement of woody shrublands with annual herbaceous cover is becoming a widespread and serious concern in Southern California and other Mediterranean-climate and non-forested ecosystems (Balch et al., 2013; Park et al., 2018; Syphard, Radeloff, Hawbaker, & Stewart, 2009). The model results here suggest that short-interval fire is a critical mechanism contributing to shrubland extirpation; and landscape disturbances, such as trail construction, provide the means for herbaceous species to colonize open areas. Furthermore, the likelihood of these processes effecting change is strongly dependent upon environmental characteristics. The AUCs for the classification trees and MaxEnt analysis were fair to good, but also indicate that the models contain some degree of uncertainty. This may in part be due to potential inaccuracies of the mapped predictor variables; or it may suggest that additional variables may be important in describing the changes. Further studies in other parts of the region could illuminate these uncertainties.

Although the true extent or rate of chaparral vegetation type conversion has not been completely mapped or quantified, Meng et al. (2014) questioned how extensive type conversion could be due to repeat fires, but this conclusion may have resulted from factors not accounted for in that study (Halsey & Syphard, 2015). Because we deliberately sampled the landscape to identify areas where chaparral type conversion occurred, we cannot provide true estimates of the extent to which shrubland decline has occurred over the last 60 years. Nevertheless, more than 30% of the woody plots in 1943 had either partly or completely converted to herbaceous cover by 2014, which is a substantial amount of vegetation change over a relatively short time period. Recent work by Park et al. (2018) and Syphard et al. (2018) also suggests that widespread vegetation change has already occurred. To reduce further landscape degradation, preventive steps should be taken now to conserve the regions' natural heritage and biodiversity. In addition to steps that may be effective in reducing fire ignitions (Syphard & Keeley, 2015), conservation decision-makers may benefit from the type of map produced here, delineating the areas on a landscape that have the most similar conditions as those that are known to have already type converted. These maps could guide management priorities or could even by overlaid with ignition maps developed using a similar methodology (e.g., Syphard et al., 2008; Syphard & Keeley, 2015).

ACKNOWLEDGEMENTS

The US government does not endorse any product mentioned in this manuscript.

DATA ACCESSIBILITY

Geographical plot data and related attributes generated for this study will be available at a US Geological Survey data repository.

ORCID

Alexandra D. Syphard http://orcid.org/0000-0003-3070-0596

REFERENCES

Allen, E. B., Padgett, P. E., Bytnerowicz, A., & Minnich, R. (1998). Nitrogen deposition effects on coastal sage vegetation of southern California. In Proceedings of the international symposium on air pollution and climate change effects on forest ecosystems (pp. 131–140). Riverside, CA: US Department of Agriculture Forest Service, Pacific Southwest Research Station Riverside.

Anderson, R. S., & Byrd, B. F. (1998). Late-Holocene vegetation changes from the Las Flores Creek coastal lowlands, San Diego County, California. *Madroño*, *45*(2), 171–182.

Anderson, M.. K., & Keeley, J. E. (2018). Native peoples' relationship to the California chaparral. In E. C. Underwood, H. D. Safford, J. E. Keeley, N. Molinari & J. J. Hooper (Eds.), *Valuing chaparral. Ecological, socio-economic, and management perspectives* (pp. 73–114). New York, NY: Springer.

Balch, J. K., Bradley, B. A., D'Antonio, C. M., & Gómez-Dans, J. (2013). Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology*, *19*(1), 173–183. https://doi.org/10.1111/gcb.12046

Bentley, J. R. (1967). *Conversion of chaparral to grassland: techniques used in California*. Washington, DC: U.S. Department of Agriculture, Forest Service, Agricultural Handbook No. 328, 35.

Bowman, D. M. J. S., MacDermott, H. J., Nichol, S. C., & Murphy, B. P. (2014). A grass–fire cycle eliminates an obligate-seeding tree in a tropical savanna. *Ecology and Evolution*, *4*(21), 4185–4194. https://doi.org/10.1002/ece3.1285

Breiman, L., Friedman, J., Olshen, R., & Stone, C. (1984). *Classification and regression trees*. Belmont, CA: Wadsworth.

Brennan, T. J., & Keeley, J. E. (2017). Impacts of mastication fuel treatments on California, USA, chaparral vegetation structure and composition. *Fire Ecology*, *13*(2), 120–138. https://doi.org/10.4996/fireecology

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., … Pyke, D. (2004). Effects of invasive alien plants on fire regimes. *BioScience*, *54*(7), 677–688. https://doi.org/10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2

Burcham, L. T. (1955). Recent trends in range improvement on California foothill ranges. *Journal of Range Management*, *8*, 121–125. https://doi.org/10.2307/3893999

Cooper, W. S. (1922). *The broad-sclerophyll vegetation of California. An ecological study of the chaparral and its related communities*. Washington, DC: Carnegie Institution of Washington. https://doi.org/10.5962/bhl.title.20836

Coulter, C. T., Southworth, D., & Hosten, P. E. (2010). Prescribed fire and post-fire seeding in brush masticated oak-chaparral: Consequences for native and nonnative plants. *Fire Ecology*, *6*(2), 60–75. https://doi.org/10.4996/fireecology

Cox, R. D., Preston, K. L., Johnson, R. F., Minnich, R. A., & Allen, E. B. (2014). Influence of landscape-scale variables on vegetation conversion to exotic annual grassland in southern California, USA. *Global Ecology and Conservation*, *2*, 190–203. https://doi.org/10.1016/j.gecco.2014.09.008

D'Antonio, C. (1992). Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics*, *23*(1), 63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Davis, S. D., Ewers, F. W., Sperry, J. S., Portwood, K. A., Crocker, M. C., & Adams, G. C. (2002). Shoot dieback during prolonged drought in Ceanothus (Rhamnaceae) chaparral of California: A possible case of hydraulic failure. *American Journal of Botany*, *89*(5), 820–828. https://doi.org/10.3732/ajb.89.5.820

Davis, R., Yang, Z., Yost, A., Belongie, C., & Cohen, W. (2017). The normal fire environment—Modeling environmental suitability for large forest wildfires using past, present, and future climate normals. *Forest Ecology and Management*, *390*, 173–186. https://doi.org/10.1016/j.foreco.2017.01.027

Franklin, J. (1995). Predictive vegetation mapping: Geographic modeling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, *19*, 474–499. https://doi.org/10.1177/030913339501900403

Franklin, J. (2010). *Mapping species distributions: Spatial inference and prediction*. New York: Cambridge University Press. https://doi.org/10.1017/CBO9780511810602

Gavier-Pizarro, A. G. I., Radeloff, V. C., Stewart, S. I., Cynthia, D., & Keuler, N. S. (2010). Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecological Applications*, *20*(7), 1913–1925. https://doi.org/10.1890/09-2168.1

Gelbard, J. L., & Belnap, J. (2003). Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology*, *17*, 420–432. https://doi.org/10.1046/j.1523-1739.2003.01408.x

Haidinger, T. L., & Keeley, J. E. (1993). Role of high fire frequency in destruction of mixed chaparral. *Madroño*, *40*, 141–147.

Halsey, R. W., & Syphard, A. D. (2015). *High-severity fire in chaparral: Cognitive dissonance in the shrublands*. *The ecological importance of mixed-severity fires: nature's phoenix*.

Hanley, J. A., & McNeil, B. J. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, *143*(1), 29–36. https://doi.org/10.1148/radiology.143.1.7063747

Jacobsen, A. L., Davis, S. D., & Fabritius, S. L. (2004). Fire frequency impacts non-sprouting chaparral shrubs in the Santa Monica Mountains of southern California. In M. Arianoutsou & V. Papanastasis, (Eds.), *Ecology, conservation and management of mediterranean climate ecosystems* (pp. 1–6). Rotterdam, The Netherlands: Millpress.

Keeley, J. E. (1990). The California valley grassland. In A. A. Schoenherr (Ed.), *Endangered plant communities of southern California* (Special Publication No. 3., pp. 2–23). Fullerton, CA: Southern California Botanists.

Keeley, J. E. (2002). Native American impacts on fire regimes of the California coastal ranges. *Journal of Biogeography*, *29*, 303–320. https://doi.org/10.1046/j.1365-2699.2002.00676.x

Keeley, J. E., Baer-Keeley, M., & Fotheringham, C. J. (2005). Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecological Applications*, *15*(6), 2109–2125. https://doi.org/10.1890/04-1222

Keeley, J. E., Bond, W. J., Bradstock, R. A., Pausas, J. G., & Rundel, P. W. (2012). *Fire in Mediterranean ecosystems ecology, evolution and management*. Cambridge, UK: Cambridge University Press.

Keeley, J. E., & Brennan, T. J. (2012). Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia*, *169*(4), 1043–1052. https://doi.org/10.1007/s00442-012-2253-8

Keeley, J. E., & Davis, F. W. (2007). Chaparral. In M. G. Barbour, T. Keeler-Wolf, & A. A. Schoenherr (Eds.), *Terrestrial vegetation of California* (3rd ed., pp. 339–366). Los Angeles, CA: University of California Press. https://doi.org/10.1525/california/9780520249554.001.0001

Keeley, J. E., & Fotheringham, C. J. (2003). Impact of past, present, and future fire regimes on North American mediterranean shrublands. In T. T. Veblen, et al. (Eds.), *Fire and climate change in temperate ecosystems of the western Americas* (pp. 218–262). New York, NY: Springer. https://doi.org/10.1007/b97443

Keeley, J. E., Fotheringham, C. J., & Baer-Keeley, M. (2005). Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. *Ecological Applications*, *15*(5), 1515–1534. https://doi.org/10.1890/04-1005

Keeley, J. E., & Syphard, A. D. (2018). South coast bioregion. In N. G. Sugihari, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, & A. E. Thode (Eds.), *Fire in California's ecosystems*(pp. 319–351). Berkeley, CA: University of California Press.

Keeley, J. E., & Zedler, P. A. (2009). Large, high intensity fire events in southern California shrublands: Debunking the fine-grained age-patch model. *Ecological Applications*, *19*, 69–94. https://doi.org/10.1890/08-0281.1

Kelly, M., Allen-Diaz, B., & Kobzina, N. (2005). Digitization of a historic dataset: The Wieslander California vegetation type mapping project. *Madroño*, *52*(3), 191–201.

Lippitt, C. L., Stow, D. A., O'Leary, J. F., & Franklin, J. (2012). Influence of short-interval fire occurrence on post-fire recovery of fire-prone shrublands in California, USA. *International Journal of Wildland Fire*, *22*(2), 184–193. https://doi.org/10.1071/WF10099

MacNally, R., & Walsh, C. J. (2004). Hierarchical partitioning public-domain software. *Biodiversity and Conservation*, *13*(3), 659–660.

Meentemeyer, R. K., Moody, A., & Franklin, J. (2001). Landscape-scale patterns of shrub-species abundance in California chaparral–the role of topographically mediated resource gradients. *Plant Ecology*, *156*(1), 19–41. https://doi.org/10.1023/A:1011944805738

Meng, R., Dennison, P. E., D'Antonio, C. M., & Moritz, M. A. (2014). Remote sensing analysis of vegetation recovery following short-interval fires in southern California shrublands. *PLoS ONE*, *9*(10), e110637. https://doi.org/10.1371/journal.pone.0110637

Merriam, K. E., Keeley, J. E., & Beyers, J. L. (2006). Fuel breaks affect nonnative species abundance in Californian plant communities. *Ecological Applications*, *16*(2), 515–527. https://doi.org/10.1890/1051-0761(2006)016[0515:FBANSA]2.0.CO;2

Minnich, R. A., & Dezzani, R. J. (1998). Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. *Western Birds*, *29*, 366–391.

Padgett, P. E., & Allen, E. B. (1999). Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. *Plant Ecology*, *144*(1), 93–101. https://doi.org/10.1023/A:1009895720067

Park, I. W., Hooper, J., Flegal, J. M., & Jenerette, G. D. (2018). Impacts of climate, disturbance and topography on distribution of herbaceous cover in Southern California chaparral: Insights from a remote-sensing method. *Diversity and Distributions*, *24*(4), 497–508. https://doi.org/10.1111/ddi.12693

Parra, A., & Moreno, J. M. (2018). Drought differentially affects the post-fire dynamics of seeders and resprouters in a Mediterranean shrubland. *Science of the Total Environment*, *626*, 1219–1229. https://doi.org/10.1016/j.scitotenv.2018.01.174

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*(3–4), 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Potts, J. B., & Stephens, S. L. (2009). Invasive and native plant responses to shrubland fuel reduction: Comparing prescribed fire, mastication, and treatment season. *Biological Conservation*, *142*(8), 1657–1664. https://doi.org/10.1016/j.biocon.2009.03.001

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project. org/

Radtke, K. W. H., Arndt, A. M., & Wakimoto, R. H. (1982). Fire history of the Santa Monica Mountains. In C. E. Conrad & W. C. Oechel (Eds.), *Proceedings of the symposium on dynamics and management of Mediterranean-type ecosystems* (pp. 438–443). Berkeley: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station.

Rossiter, N. A., Setterfield, S. A., Douglas, M. M., & Hutley, L. B. (2003). Testing the grass-fire cycle: Alien grass invasion in the tropical savannas of northern Australia. *Diversity & Distributions*, *9*(3), 169–176. https://doi.org/10.1046/j.1472-4642.2003.00020.x

Safford, H. D., & Van de Water, K. M. (2014). *Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on national forest lands in California*. Albany, CA. Retrieved from https://doi.org/res Pap. PSW-RP-266

Seabloom, E. W., Borer, E. T., Boucher, V. L., Burton, R. S., Cottingham, K. L., Goldwasser, L., … Micheli, F. (2003). Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. *Ecological Applications*, *13*(3), 575–592. https://doi.org/10.1890/1051-0761(2003)013[0575:CSLDAR]2.0.CO;2

Shirazi, M. A., Boersma, L., Haggerty, P. K., & Johnson, C. B. (2001). Spatial extrapolation of soil characteristics using whole-soil particle size distributions. *Journal of Environmental Quality*, *30*(1), 101–111. https://doi.org/10.2134/jeq2001.301101x

Syphard, A. D., Brennan, T. J., & Keeley, J. E. (2018). The ecological chaparral landscape conversion in Southern California. In E. Underwood, H. Safford, N. Molinari & J. E. Keeley (Eds.), *Value of ecosystem services and resource management* (pp. 323–346). Chaparral Landscapes: Springer.

Syphard, A. D., Radeloff, V. C., Keuler, N. S., Taylor, R. S., Hawbaker, T. J., Stewart, S. I., & Clayton, M. K. (2008). Predicting spatial patterns of fire on a southern California landscape. *International Journal of Wildland Fire*, *17*(5), 602. http://www.publish.csiro.au/?paper=WF07087

Syphard, A. D., Clarke, K. C., & Franklin, J. (2005). Using cellular automaton model to forecast the effects of alternative scenarios of urban growth on habitat fragmentation in southern California. *Ecological Complexity*, *2*, 185–203. https://doi.org/10.1016/j.ecocom.2004.11.003

Syphard, A. D., & Franklin, J. (2010). Species' traits affect the performance of species' distribution models for plants in southern California. *Journal of Vegetation Science*, *21*(1), 177–189. https://doi.org/10.1111/j.1654-1103.2009.01133.x

Syphard, A. D., Franklin, J., & Keeley, J. E. (2006). Simulating the effects of frequent fire on southern California coastal shrublands. *Ecological Applications*, *16*(5), 1744–1756. https://doi.org/10.1890/1051-0761(2006)016[1744:STEOFF]2.0.CO;2

Syphard, A. D., & Keeley, J. E. (2015). Location, timing, and extent of wildfire varies by cause of ignition. *International Journal of Wildland Fire*, *24*(1), 37–47. https://doi.org/10.1071/WF14024

Syphard, A. D., Keeley, J. E., & Abatzoglou, J. T. (2017). Trends and drivers of fire activity vary across California aridland ecosystems. *Journal of Arid Environments*, *144*(2017), 110–122. https://doi.org/10.1016/j.jaridenv.2017.03.017

Syphard, A. D., Keeley, J. E., & Brennan, T. J. (2011). Comparing the role of fuel breaks across southern California national forests. *Forest Ecology and Management*, *261*(11), 2038–2048. https://doi.org/10.1016/j.foreco.2011.02.030

Syphard, A. D., Keeley, J. E., Massada, A. B., Brennan, T. J., & Radeloff, V. C. (2012). Housing arrangement and location determine the likelihood of housing loss due to wildfire. *PLoS ONE*, *7*(3).

Syphard, A. D., Radeloff, V. C., Hawbaker, T. J., & Stewart, S. I. (2009). Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems. *Conservation Biology*, *23*(3), 758–769. https://doi.org/10.1111/j.1523-1739.2009.01223.x

Talluto, M., & Suding, K. (2008). Historical change in coastal sage scrub in southern California, USA in relation to fire frequency and air pollution. *Landscape Ecology*, *23*(7), 803–815. https://doi.org/10.1007/s10980-008-9238-3

Tonnesen, G., Wang, Z., Omary, M., & Chien, C. (2007). *Assessment of nitrogen deposition: Modeling and habitat assessment*. Sacramento, CA: California Energy Commission, PIER Energy-Related.

Wells, P. V. (1962). Vegetation in relation to geological substratum and fire in the San Luis Obispo quadrangle, California. *Ecological Monographs*, *32*, 79–103. https://doi.org/10.2307/1942361

Westman, W. E., & O'Leary, J. F. (1986). Measures of resilience: The response of coastal scrub to fire. *Vegetatio*, *65*, 179–189. https://doi.org/10.1007/BF00044818

Zedler, P. H. (1995). Fire frequency in southern California shrublands: Biological effects and management options. In J. E. Keeley, & T. Scott (Eds.), *Brushfires in California wildlands: Ecology and resource management* (pp. 101–112). Fairfield, Washington: International Association of Wildland Fire.

Zedler, P. H., Gautier, C. R., & McMaster, G. S. (1983). Vegetation change in response to extreme events – The effect of a short interval between fires in California chaparral and coastal scrub. *Ecology*, *64*(4), 809–818. https://doi.org/10.2307/1937204

BIOSKETCH

Alexandra D. Syphard's research focuses on issues related to vegetation dynamics and wildfire in Mediterranean ecosystems; fire science and ecology; feedbacks and interactions among multiple ecological threats; biogeography and species distribution modelling; land use/land cover change; and the influence of humans and climate on fire regimes.

Author contributions: ADS, TEJ, and JEK designed research; ADS and TEJ performed research; ADS, TEJ, and JEK analyzed data; ADS, TEJ, and JEK wrote paper.

How to cite this article: Syphard AD, Brennan TJ, Keeley JE. Drivers of chaparral type conversion into herbaceous vegetation in coastal Southern California. *Divers Distrib*. 2018;00:1–12. https://doi.org/10.1111/ddi.12827