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Impacts of climate, disturbance and topography on distribution of herbaceous cover in Southern California chaparral: Insights from a remote-sensing method

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Abstract

Aim: While chaparral communities have historically been considered resistant to invasion and type conversion into grasslands, interacting global changes such as increased drought and anthropogenic disturbance may have reduced this resistance. Existing monitoring methods are not well-suited to evaluate the distribution of invasive herbs and grasses within chaparral at regional scales. In this study, we determine the extent of invasions by forbs and grasses into formerly chaparral vegetation and evaluate contributions of moisture, disturbance and anthropogenic activity and topography to the distribution of herbaceous cover throughout chaparral-dominated communities.

Location: The Angeles National Forest (ANF), California, USA.

Methods: We developed a remote-sensing method to estimate the distribution of herbaceous cover within chaparral by leveraging intra-annual phenological differences in normalized difference vegetation index (NDVI) between herbaceous forbs and grasses and evergreen shrublands using Landsat remote-sensing imagery. The distribution of herbaceous cover was then related to multiple spatially explicit variables describing individual and interactive effects of local moisture availability and anthropogenic disturbance.

Results: Herbaceous cover represents approximately 31% of the ANF within the elevation range typically dominated by chaparral. Disturbance-related and anthropogenic factors explained 17% of observed variation, while differences in moisture availability explained 47% of observed variation in herbaceous cover and were associated with increased invasive cover.

Main conclusions: Landscapes historically dominated by chaparral may exhibit high degrees of herbaceous cover. While fire frequency and other anthropogenic disturbances are likely the primary catalyst for invasion of chaparral by herbaceous species, this study shows that moisture availability is a more important factor in determining which locations are successfully invaded. These results indicate that chaparral vulnerability to invasion in southern California may increase in the next century due to reduced precipitation associated with projected climate change.

KEYWORDS

Angeles National Forest, chaparral, invasion, normalized difference vegetation index, phenology, remote sensing

1 | INTRODUCTION

Chaparral shrublands represent a critical and iconic part of the California landscape that serves not only as a critical habitat for many native flora and fauna but also as a major carbon sink in semi-arid environments (Quideau, Graham, Chadwick, & Wood, 1998; Ulery, Graham, Chadwick, & Wood, 1995). Unlike many other California ecosystems, chaparral has historically been considered resistant to invasion and type conversion to exotic grasslands (Allen et al., 2005; Lambrinos, 2006; Minnich & Bahr, 1995). Nevertheless, the native perennial grasslands that historically bordered chaparral have been almost completely replaced by exotic invasive grasses, which now make up the majority of herbaceous cover (D'Antonio, 2017; Hamilton, 1997; Minnich, 2008). This close proximity of exotic-dominated landscapes, in combination with increasing drought intensity and anthropogenic disturbance such as altered fire regimes, encroaching urbanization and increased dissection of chaparral landscapes, may push many of these systems to tipping points of shrub mortality and possible type conversion (Hamilton, 1997; Keeley & Brennan, 2012; Meng, Dennison, D'Antonio, & Moritz, 2014; Syphard, Regan, Franklin, Swab, & Bonebrake, 2013). However, current monitoring methods are not well-suited to detecting invasion and type conversion of chaparral into invasive-dominant grasslands or other herbaceous cover due to the vast extent of chaparral vegetation and the steep, often impassable terrain in which chaparral occurs. Here, we present a remote-sensing method for rapidly evaluating the distribution of herbaceous cover within perennial shrublands, which primarily consists of invasive-dominated grasslands (Franklin, 2002) throughout historically chaparral landscapes. Further, we identify the factors influencing the distribution of herbaceous cover throughout areas previously dominated by chaparral shrubs.

Some disturbances, such as fire, are necessary for chaparral to maintain community composition (Keeley, 2006). However, the natural fire interval for chaparral can be long, in some cases exceeding 100 years (Keeley, 1992). Rapid fire cycles can reduce both the population of chaparral shrub species and their ability to replace herbaceous vegetation during post-fire succession (Haidinger & Keeley, 1993; Lippit, Stow, O'Leary, & Franklin, 2013; Meng et al., 2014). Additionally, evidence is mixed concerning the frequency and extent of chaparral type conversion even under extremely rapid fire regimes. Some studies have found that lowered success of chaparral shrubs may lead to increased cover by invasive forbs and grasses (Haidinger & Keeley, 1993; Zedler, Gautier, & McMaster, 1983) and type conversion to more open, invasive-dominant grasslands (Jacobsen & Davis, 2004). However, other evidence indicates that type conversion may be rare even amidst extremely rapid burn cycles and may be primarily influenced by site-specific environmental and compositional factors (Meng et al., 2014).

Anthropogenic activity may also play a role in the conversion of chaparral into invaded grasslands or other herbaceous cover. Roads and other man-made features that dissect the landscape may deleteriously impact chaparral not only by direct displacement of native vegetation but also by increasing the vulnerability of surrounding plant communities to invasion. Roads have been found to act as invasive corridors through chaparral and to represent areas of increased susceptibility to invasion (Davies, Nafus, & Madsen, 2013; Lambrinos, 2006). Even in the absence of fire, roads and pipeline corridors into intact native chaparral have been found resistant to recolonization by native species and to act as a vector for further invasions into surrounding native communities (Zink, Allen, Heinde-Tenhunen, & Allen, 1995).

In addition to fires and other anthropogenic disturbances, differences in local moisture availability are also critical in determining the susceptibility of chaparral to invasion. Chaparral shrubs typically require significantly more water than the invasive grasses that often replace them under type conversion (Corbett & Crouse, 1968; Williamson, Graham, & Shouse, 2004). Reduced moisture availability can increase the persistence of grasses in invaded coastal sage scrub communities (Kimball, Goulden, Suding, & Parker, 2014) and reduce the survival and recruitment of chaparral shrub seedlings during post-fire vegetation recovery (Frazer & Davis, 1988; Keeley, Fotheringham, & Baer-Keeley, 2005b). Similarly, local slope and topography have also been shown to significantly influence type conversion of coastal sage scrub (CSS) communities (Cox, Preston, Johnson, Minnich, & Allen, 2014). These various factors may interact to directly or indirectly influence the distribution of herbaceous cover throughout areas that were historically chaparral shrublands at organismal to regional scales.

Attempts to map intrusions of invasive-dominated grasslands or other herbaceous cover into chaparral shrublands have historically been restricted by the intensive work required to conduct plot-based forest inventories (Franklin, 1998; Gordon & White, 1994; Warbington, Levien, & Rosenberg, 2000). There is a need for landscape-scale vegetation maps that can be updated at frequent enough intervals to accurately monitor the process of invasion over space and time without reliance on field intensive methods exclusively. High-resolution imagery captured from fixed cameras on ridgelines has been used at scales better suited to the highly heterogeneous nature of many chaparral sites but is still often restricted to limited spatial coverage by the time required to acquire such imagery (Moody & Meentemeyer, 2001), and the difficulty of locating and traversing to appropriate vantage points from which to capture such imagery in the steep, often densely vegetated terrain. Some existing vegetation surveys, such as the forest inventory and analysis, can provide high spatial resolution and extensive coverage (Franklin, Woodcock, & Warbington, 2000; Pfeffer, Pebesma, & Borough, 2003; Warbington, Scwind, Brohman, Brewer, & Clerke, 2002). However, due to their focus on tree species, these models often undersample shrub or grassland communities (Franklin, Simons, Beardsley, Rogan, & Gordon, 2001; Franklin et al., 2000). While high-resolution imagery products such as those produced by the Worldview, IKONOS or QuickBird platforms may offer a solution, these products are cost-prohibitive and often cannot be acquired for the entirety of a broad study area each year. High-resolution imagery developed through the National Agricultural Imagery Program (NAIP) circumvents these difficulties but dates back only to 2003 and is produced only every 5 years, limiting its utility in evaluating long-term changes in chaparral cover.

In this study, we develop a remote-sensing approach capable of addressing the difficulties in mapping grass and herbaceous cover across wide areas using freely available Landsat TM-based products. This method leverages phenological differences to map the distribution of herbaceous cover in historically evergreen shrub-dominated communities by capitalizing on the extensive record of satellite-based normalized difference vegetation index (NDVI) data. NDVI represents a widely used metric associated with leaf area index, per cent cover by photosynthesizing vegetation and plant biomass (Carlson & Ripley, 1997; Huete, Liu, Batchily, & Leeuwen, 1997) that is well correlated with leaf dynamics throughout both deserts and grasslands (Choler, Sea, Briggs, Raupach, & Leuning, 2010; Griffith, Alpert, & Loik, 2010). Native chaparral shrubs, which are typically evergreen, maintain a relatively constant NDVI throughout the year, while invasive grasses and forbs are highly drought deciduous or senesce in summer, and exhibit larger seasonal variations in NDVI (Gamon et al., 1995). In this study, we build on previous techniques that used phenological differences in NDVI to characterize local ground cover (Buma, 2012; Shmidt, Luscas, Bunting, Verbesselt, & Armston, 2014) and develop a technique to determine whether seasonal changes in NDVI can be used to measure the deciduousness of local vegetation (Costa, Viana, & Ribeiro, 2014; Cuba et al., 2013) and thereby separate grasslands and herbaceous cover from intact chaparral and conifer forest. As most grass and herbaceous communities throughout California chaparral are typically dominated by exotic species (Keeley, 2001), and native grasses typically exist within a matrix of exotics (D'Antonio, Malmstrom, Reynolds, & Gerlach, 2007), no attempt will be made to separate native and exotic grasses or forbs in this study.

We then use this method to quantify the extent and distribution of herbaceous cover throughout historically chaparral areas of the Angeles National Forest, a region traditionally considered to be resistant to invasion. We evaluate the relationship of local disturbance, climate and moisture availability (as measured by precipitation and climatic moisture deficit), and topographic conditions to the distribution of herbaceous cover and grasslands. Specifically, this study will address the following questions: (1) What is the extent of herbaceous cover in chaparral-dominated landscapes throughout the Angeles National Forest, located in southern California? (2) What is the relative importance of moisture availability, disturbance and local topography in determining the distribution of herbaceous cover, which consists primarily of invaded grasslands, (Franklin, 2002)?

2 | METHODS

Our study site is the Angeles National Forest (ANF), a, high-traffic forest located immediately adjacent to the Los Angeles megacity which receives over 3.5 million visitors per year (English et al., 2002) and exhibits a highly diverse topography as well as accelerated fire intervals (Safford, Van Water, & Clark, 2013), and high atmospheric nitrogen deposition due to pollution from the Los Angeles megacity (Bytnerowicz & Fenn, 1995; Fenn et al., 2010). The national forest covers 2,653 km^2 and is characterized primarily by chaparral shrublands composed of a wide array of species including various species of *Adenostoma*, *Arctostaphylus* and *Ceanothus*, as well as oak woodlands and coniferous forests (Parker, Pratt, & Keeley, 2016). However, the ANF is increasingly threatened by a wide array of invasive herbs and grasses including *Bromus tectorum*, *Bromus madritensis* and *Spartium junceum* (Merriam, Keeley, & Beyers, 2006; Myers, Stoughton, Walker, & Zylstra, 2009).

The distribution of herbaceous cover throughout the ANF was derived from NDVI estimates produced as part of the Landsat TM 4–5 surface reflectance data (Masek et al., 2006) collected from 1 January through 31 December 2008. These data combine a 30-metre spatial resolution with a frequent rate of image capture (15 usable images in 2008, with images typically 3–4 weeks apart) to characterize the minimum and maximum local NDVIs throughout the entire year. As cloud cover, dust and other atmospheric distortions could reduce observed NDVI in specific images and pixels, estimates of minimum and maximum NDVIs for each pixel were derived using the maximum NDVI across each set of three successive Landsat images to eliminate bad pixels using a moving window method. The year 2008 was chosen for this study as it coincided with an aerial imagery campaign that provided high-resolution (0.3 m) orthoimagery across the entire ANF and represented a year in which mean annual precipitation was similar to long-term normals (7.2 mm below 1981–2010 normals) as estimated from PRISM climate data. To limit this analysis only to areas that were until recently dominated by chaparral shrublands, only Landsat pixels that were classified as shrublands based on 2006 National Land Cover Database (NLCD) data were utilized in this study. From the selected pixels, all locations that occurred below 500 m or above 1600 m, and were therefore outside of the elevational range of chaparral (Keeley, Bond, Bradstock, Pausas, & Rundel, 2012), were also excluded. Pixels characterized by annual precipitation under 305 mm were also eliminated, as such areas often represented desert rather than semi-arid landscapes (Pase, 1982), and were likely to be dominated by ephemeral herbaceous species.

As this study evaluated herbaceous cover only in a single year, we eliminated sites that were likely still in the process of immediate post-fire recovery, and thus in which the cover could not be assumed to be stable even over a short span of years. Although previous research has determined that chaparral shrubs reassert themselves as the dominant cover as rapidly as 4–5 years post-fire (Keeley, 1986), NDVI-based LAI studies have determined that LAI typically takes 15 years to recover to pre-fire levels, with approximately 85% recovery of LAI within the first 10 years (McMichael, Hope, Roberts, & Anaya, 2004). Therefore, all pixels that had burned from the years 1998 through 2008 (representing 14.4 km^2 across the study area) were excluded from this study. The remaining dataset consisted of 1.93 million individual 30-metre pixels, covering an area of approximately 858 km^2, which represents 32% of the total area enclosed by the Angeles National Forest. While this dataset includes all recent fires of >4 ha, small fires were not always recorded and may be overlooked in this analysis (Safford et al., 2013).

Digital elevation data used in this study consisted of 3.05 m digital elevation model (DEM) data acquired as part of the Los Angeles Regional Imagery Acquisition Consortium in 2006. Slope and mean annual insolation were calculated for each pixel using the slope and area solar radiation (irradiation) functions in ArcGIS. Mean irradiation was used in preference to aspect, as it incorporates information as to both the direction of slope facings as well as shade from surrounding features and solar geometry, thereby representing a better metric of exposure to water limitation (Boyko, 1945; Sears, 1947). Precipitation data were derived from 800 m PRISM climate data (PRISM 2010), while climatic moisture deficit data were estimated using the ClimateNA v5.10 software package (Wang, Hamann, Spittlehouse, & Carrol, 2016). All climate data were based on 1980–2010 climate normals. Fire return interval data were computed from data produced by the United States Forest Service using records of past fires from 1908 to 2008 (Safford et al., 2013) and included all fires of >4 hectares in area. Water, roads, and urban or residential features were identified using 2006 NLCD land cover classification data (Fry et al., 2011). Forest boundaries were derived from USFS forest perimeter data. Euclidean distance of each pixel from roads or urban features was then calculated using ArcGIS.

2.1 | Manual cover assessment using high-resolution imagery

Throughout the study area, 275 pilot sites, each of which corresponded to an individual Landsat pixel, were identified (Figure 1b). These calibration pixels were dispersed across the ANF and were chosen from locations that included both intact chaparral, highly invaded grasslands and mixed chaparral and herbaceous cover. Herbaceous cover within each pixel was assessed relative to manual cover assignment of 50 randomly placed points within each pixel (Figure 1a) through visual assessment of 0.3 metre (1 foot) resolution, three-band true-colour orthoimagery collected in January 2008.

Each point was assigned a cover classification of either woody, herbaceous or bare soil. Dirt roads and firebreaks were present in some calibration pixels, although no pixels containing paved roads or structures were included.

2.2 | Determining and validating estimates of herbaceous cover

For each 30-metre pixel, the annual minimum and maximum NDVI ($NDVI_{min}$ and $NDVI_{max}$ respectively) were calculated using the NDVI estimates previously developed. The magnitude of annual fluctuation in NDVI (ΔNDVI) was calculated as $NDVI_{max} - NDVI_{min}$. Similarly, the ratio of $\Delta NDVI/NDVI_{min,}$ which was empirically found to be useful in separating herbaceous and woody cover, was also calculated.

Optimal parameters for estimating % cover by herbaceous species from min, max and ΔNDVI were calculated using stepwise regression analysis. Parameters were added to the model using a minimum threshold of $p \leq .05$ and removed if $p > .10$ upon addition of subsequent parameters.

Using the model parameters selected through stepwise regression, the accuracy of the index was validated using 10-fold cross validation (Hastie, Tibshirani, & Friedman, 2009). Pilot sites (Landsat pixels) were randomly divided into ten equally sized subsamples. In iterative fashion, nine of these subsamples (representing 90% of Landsat Pixels) were used to calibrate an estimate of the per cent cover by grasses and

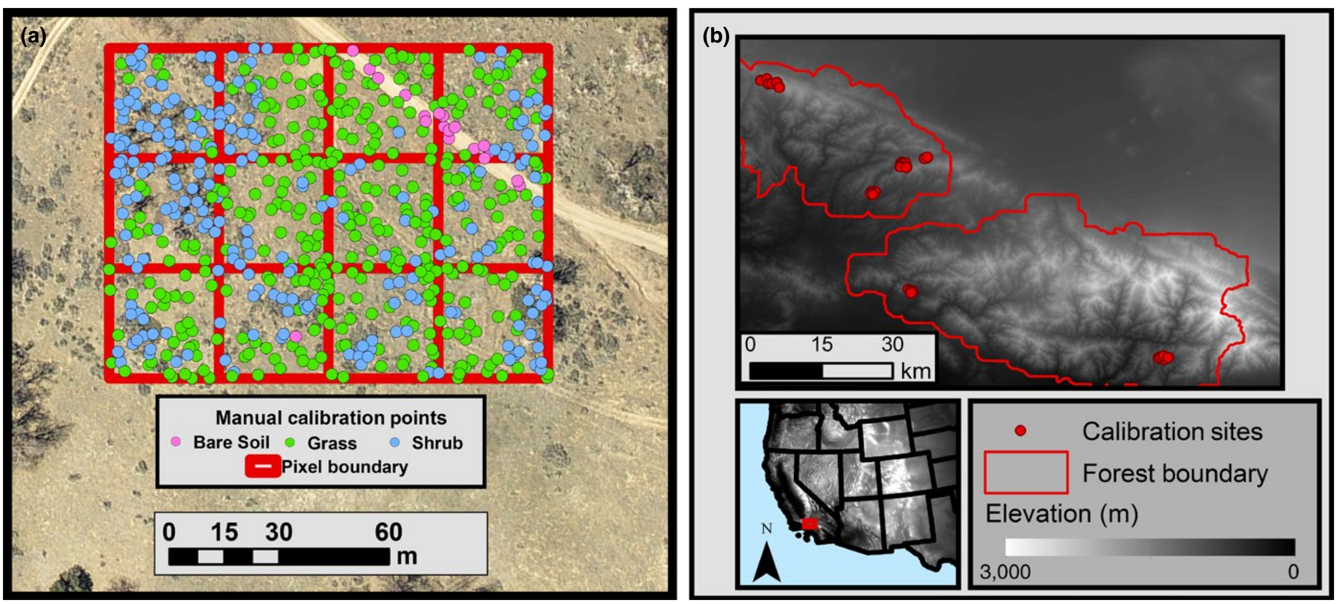

FIGURE 1 (a) Example subset of calibration sites and site locations. Circles indicate points of manual cover calibration, while squares indicate the extent of individual Landsat pixels. In all cases, 50 land cover classification points were randomly placed within each of the Landsat pixels used in calibrating estimates of herbaceous cover. (b) Inset map indicates forest extent and site placement. Line indicates forest boundary. Red dots indicate placement of the 275 Landsat Pixels used in manual cover classification. Calibration pixels were sited to be dispersed across the Angeles National Forest (ANF) and to ensure that a variety of intact chaparral, highly invaded grasslands, and mixed chaparral and herbaceous cover were included in model development. [Colour figure can be viewed at wileyonlinelibrary.com]

herbaceous species. The predicted values produced by that model for the remaining subsample, which represented the 10% of data not used in model calibration was tested against the observed cover values for those locations using bivariate correlation analysis. This process was conducted iteratively for all ten combinations of data subsamples. The regression parameters and correlation values between predicted and observed herbaceous cover at all validation sites were then averaged across all iterations to estimate the accuracy of the model and to produce the final model parameters. The parameters derived and validated using 10-fold cross validation were then used to estimate the proportion of herbaceous cover throughout the entire study area based on Landsat NDVI data. To test whether these estimates exhibited any systematic bias, we also conducted linear regression analysis on the residuals and the observed herbaceous cover.

2.3 | Relating local conditions to herbaceous cover

Each predictor variable was placed into one of three categories to evaluate the role of local moisture availability, anthropogenic disturbance and topography on the distribution of herbaceous cover throughout the ANF. Mean annual precipitation, mean annual climatic moisture deficit and mean annual insolation were used to represent moisture availability at each pixel. Precipitation was initially separated into October through April precipitation, which represented the wet season (Reever Morghan, Corbin, & Gerlach, 2007), and May through September precipitation, which represented the dry season. However, as wet- and dry season precipitations exhibited similar general relationships to herbaceous cover and were highly correlated to each other (R^2 = .80, Figure S1), mean annual precipitation was utilized in this analysis. Distance from roads or urban features and from the perimeter or the ANF, which often represented a transition to more heavily managed, grazed or otherwise disturbed groundcover, and year of most recent fire were considered to reflect various forms of disturbance. Local slope and elevation were used to characterize local topography. To control spatial autocorrelation and reduce the dataset to a manageable size, a subset of the data were selected by identifying a randomly placed seed pixel and selecting pixels spaced regularly at 1-km interval from it. The resulting dataset consisted of 1327 individual Landsat pixels.

The relationship between estimated per cent herbaceous cover and each explanatory variable was evaluated using linear, logarithmic, quadratic and cubic regression (SPSS). The optimal curve type for each parameter was selected using the Akaike information criterion (AIC) (Cook & Weisber, 2009). While some correlation was present between different explanatory factors in this study, such relationships were typically limited; with absolute correlations below 0.38, with the exception of climatic moisture deficit and precipitation, which were correlated at −0.71 (Table S1).

We examined the cumulative effect of moisture-, disturbance- and topography-related parameters on the distribution of herbaceous cover throughout the ANF using regression models that incorporated (1) moisture-related predictors, (2) disturbance-related predictors, (3) topographic predictors and (4) all moisture-related, disturbance-related and topographic predictors.

3 | RESULTS

Estimates of herbaceous cover derived from remote-sensing data successfully predicted per cent herbaceous cover to within 5% of observed cover among 48% of sites not used in model development within each fold (based on manual cover assessments from high-resolution orthoimagery) and predicted herbaceous cover to within 25% accuracy among 90% of sites not used in model development, with an overall R^2 value of .86 (Figure 2, Table 1). Overall, this index indicates that herbaceous cover represents 31.3% of the ANF within the elevational range evaluated in this study (Figure 3). However, this method did exhibit a slight overprediction of herbaceous cover among sites with low herbaceous cover and a slight underprediction of herbaceous cover among herb and grass-dominated sites (B = −0.20, R^2 = .31, p = .01).

Local precipitation was the best single predictor of herbaceous cover, (R^2 = .30, Figure 4a, Table 2), which decreased strongly in association with increasing precipitation, particularly among sites in which precipitation was below 600 mm. Climatic moisture deficit was the second-best predictor of herbaceous cover, which again increased sharply among sites experiencing high moisture deficits (R^2 = .25, Figure 4b, Table 2). Higher mean annual insolation was also associated with increased herbaceous cover (R^2 = .100, Figure 4c, Table 2), implying a negative association between moisture availability and local herbaceous cover.

Herbaceous cover also decreased in association with increasing distance from national forest boundaries and from roads or urban

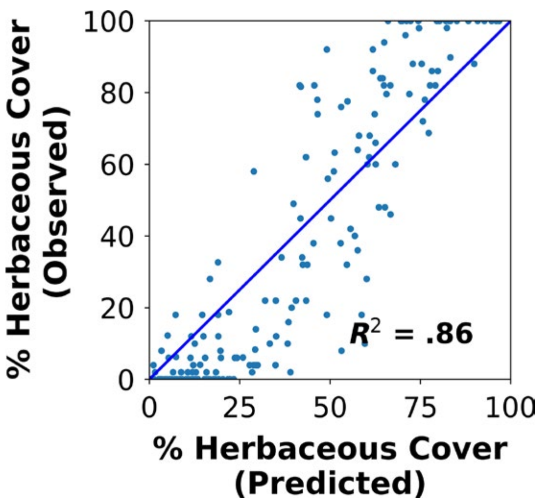

FIGURE 2 Relationship of observed versus predicted herbaceous cover in the chaparral-dominated areas of the Angeles National Forest (ANF), California based on 275 pilot sites. R^2 value represents the relationship between predicted and observed cover only for those points not included in model development using 10-fold calibration. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Alternate models (A, B, C) for estimating per cent herbaceous cover

Model	Independent variables	Parameters	R^2	AIC
A	Intercept	26.2	.01	615.2
	ΔNDVI	0.01		
B	Intercept	160.18	.79	440.4
	ΔNDVI	−0.01		
	NDVImin	−0.03		
C[a]	Intercept	116.37	.86	404.5
	ΔNDVI	−0.03		
	NDVImin	0.01		
	NDVImax	−0.02		
	ΔNDVI/NDVImin	132.17		

p-values were <.01 in all cases.
[a]Indicates selected model.

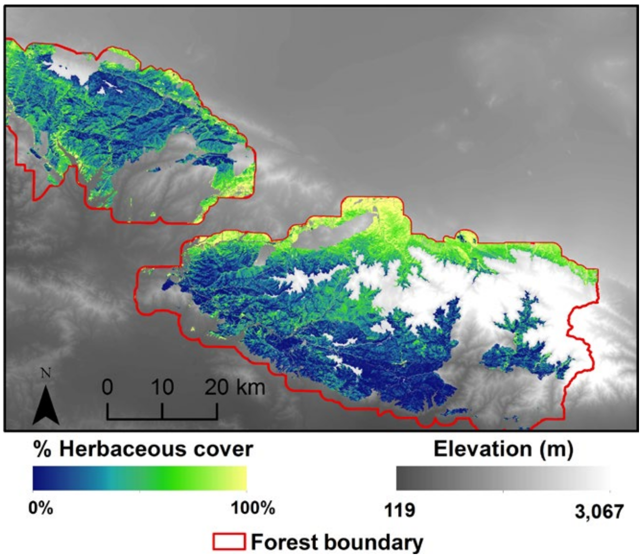

FIGURE 3 Estimated herbaceous cover across study footprint within Angeles National Forest. Blue, Green and Yellow areas represent the area evaluated in this study. Red lines indicate the forest boundary. [Colour figure can be viewed at wileyonlinelibrary.com]

features. Distances from the national forest boundary explained 17% of observed variation in herbaceous cover (Figure 4d, Table 2) and the distance from the nearest road explained 16% of observed variation in cover (Figure 4e, Table 2). In both cases, close proximity to forest boundaries and roads or urban features was associated with increased herbaceous cover. Longer fire return intervals were associated with a slight increase in herbaceous cover, but explained only 7% of observed variation in herbaceous cover (Figure 5, Table 2).

Herbaceous cover was also found to decrease in response to increasing slope (R^2 = .13, Figure 4f, Table 2). Elevation was only minimally related to differences in herbaceous cover and explained only 3% of observed variation (Figure 4g, Table 2).

All variables included in this study collectively explained 51% of observed variation in herbaceous cover throughout the ANF (Figure 6a, Table 2). Herbaceous cover was strongly associated with moisture-restricted sites, with factors related to local moisture availability cumulatively explaining 47% of variation (Figure 6b, Table 2). In comparison, disturbance-related parameters explained 25% of observed variation in herbaceous cover (Figure 6c, Table 2), while topographic parameters explained only 13% of observed variation (Figure 6d, Table 2). While this analysis was conducted on only a subset of the available data to minimize spatial autocorrelation, the results were consistent with observations analysing all 1.92 million pixels (Figures S2–S6).

4 | DISCUSSION

These results indicate that, contrary to historic expectations of chaparral resistance to invasion, herbaceous cover is prevalent throughout the study footprint in the ANF. The dominant factor in determining the distribution of grasses and other herbaceous cover is site-specific moisture limitation. Just as this study identifies spatial differences in moisture availability as the dominant factor in determining the distribution of herbaceous cover (Figure 7), reduced precipitation and severe drought events have been previously associated with increased post-fire success and diversity of invasive species in chaparral (Keeley, Fotheringham, & Baer-Keeley, 2005a) and CSS communities (Kimball et al., 2014). High aridity has been found to control the rate and extent of post-fire recovery by chaparral shrubs (Keeley et al., 2005b), while low-precipitation years may thin young shrubs significantly (Keeley, Baer-Keeley, & Fotheringham, 2005). Thus, although differences in microclimate (Davis, Borchert, & Odion, 1989; Johnson-Maynard, Shouse, Graham, Castiglione, & Quideau, 2004), herbivory (Lambrinos, 2006) and extreme climate events that are not captured in this study may also impact invasion into chaparral, it is clear that differences in long-term moisture availability are essential to understanding and predicting the distribution of herbaceous cover and invasive grasses throughout chaparral at both highly local and broader scales.

4.1 | Mapping invasion into chaparral

This work demonstrates that intra-annual variation in NDVI can be used successfully to map per cent cover by herbaceous species compared with evergreen woody shrubs and trees in Southern California chaparral. While this method does not discriminate among types of herbaceous vegetation (i.e., native and invasive grasses) or among types of shrub or tree assemblages, it does provide a high-resolution approach for assessing the distribution and relative cover by herbs or grasses into chaparral across wider areas than has previously been available. As a result of how this model combines all woody and all herbaceous cover into separate cover types, the model may overlook some differences in the extent of seasonal changes in NDVI among different species within each cover type. As even evergreen shrubs exhibit some variation in seasonal NDVI, and some herbaceous species may not completely brown in the dry season, the lack of interspecific

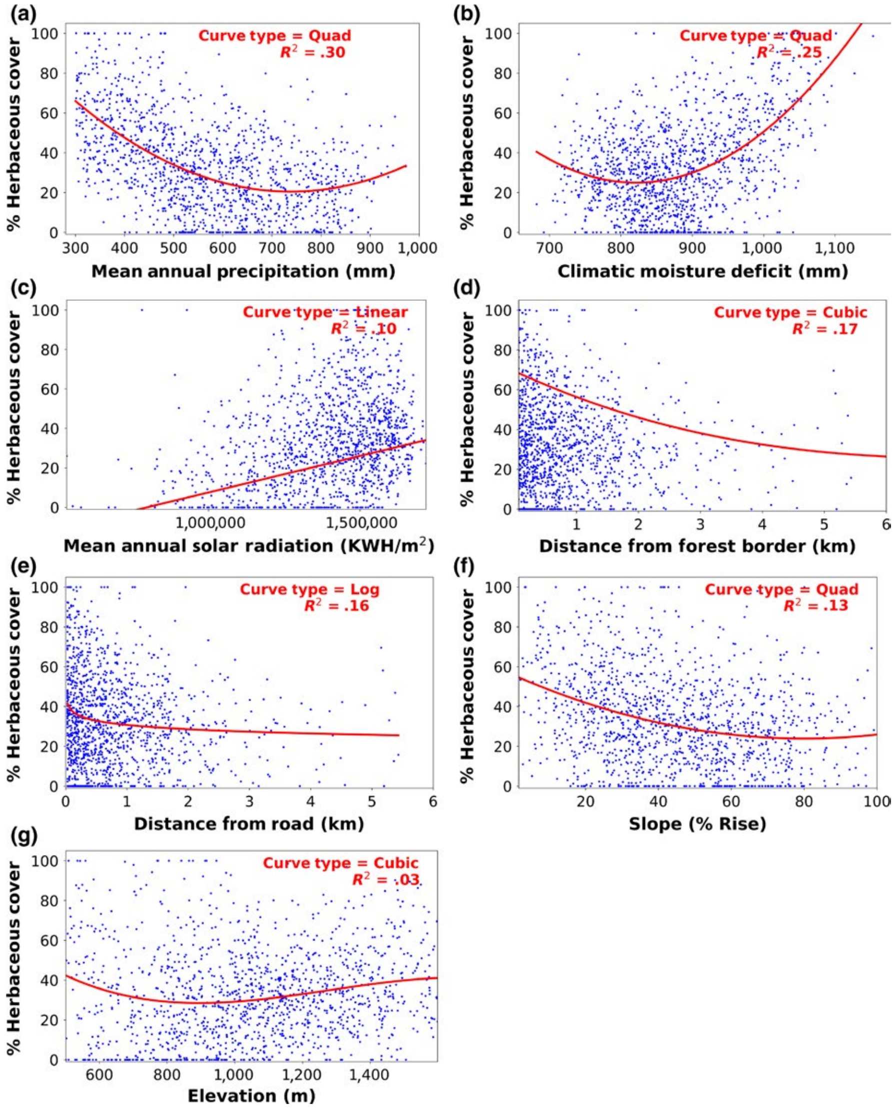

FIGURE 4 Single-factor models of herbaceous cover as predicted by local precipitation normals (a), climatic moisture deficit (b), mean annual solar radiation (c), distance from forest border (d), distance from roads (e), slope (f) and elevation (g). Red lines indicate significant relationships between observed and predicted herbaceous cover. Curve types for each factor were selected from linear, inverse, logarithmic, quadratic and cubic curves using AIC-derived maximum likelihood methods. [Colour figure can be viewed at wileyonlinelibrary.com]

discrimination may explain this method's tendency to underpredict the per cent herbaceous cover in highly invaded areas and overpredict herbaceous cover in areas with extremely low herbaceous cover. These limitations may represent some inherent limitation in using phenologically based mapping with existing publicly available data (i.e., Landsat). Despite this issue, this method is sensitive to even small amounts of herbaceous cover that occur interstitially within shrub or tree cover, which would be overlooked in previous cover maps that focused exclusively on identifying the dominant cover type within each Landsat pixel or wider area (Franklin et al., 2000; Fry et al., 2011; Homer et al., 2015). This allows assessments of the degree of invasion within even relatively intact chaparral stands, rather than simple binary classification as either shrub-dominant or herb-dominant vegetation. Further, this method utilizes only freely available pre-processed Landsat NDVI Data, to develop these cover estimates and can be mapped directly onto existing NLCD cover data to eliminated water, roads and other undesirable features. Thus, the method provides new opportunities for evaluating and managing invasion and type conversion of chaparral into herbaceous grasslands. Because of the rapid, easily automated nature of cover assessments, there is potential for global application to all chaparral-dominated ecosystems and extensions to other arid environments that incorporate similar combinations of evergreen and drought-deciduous cover types (e.g., coniferous forests). Further, annually updated cover assessments have potential for the evaluation of invasion and post-fire recovery in real-time throughout the lifetime of the Landsat programme.

4.2 | Drivers of invasion by herbaceous cover

Surprisingly, variables associated with disturbance and human activity played a secondary role in predicting the distribution of herbaceous cover throughout the forest. As fire return intervals observed in this study fell within historic norms, differences in the local fire return interval appeared to be relatively unimportant to predicting the distribution of herbaceous cover than were proximity to roads or the national forest border. Although proximity to roads, urban features and the forest border do explain a substantial portion of the distribution of herbaceous cover, the influence of roads appeared to be

TABLE 2 Relationship of individual parameters to estimated % herbaceous cover across study area in Angeles National Forest (ANF)

Explanatory factors	Curve type	R^2 (Model)	*df*
Moisture			
Precipitation	Quadratic	.30	1324
Climatic Moisture Deficit	Quadratic	.25	1324
Insolation	Quadratic	.10	1324
Combined	—	.37	1322
Disturbance & Anthropogenic Effects			
Fire Return Interval	Linear	.07	1325
Distance to NF Border	Cubic	.17	1323
Distance to Roads	Logarithmic	.16	1325
Combined	-	.25	1321
Topographic			
Slope	Quadratic	.13	1324
Elevation	Cubic	.03	1323
Combined	-	.13	1321
All Parameters	-	.52	1311

p < .001 in all cases.

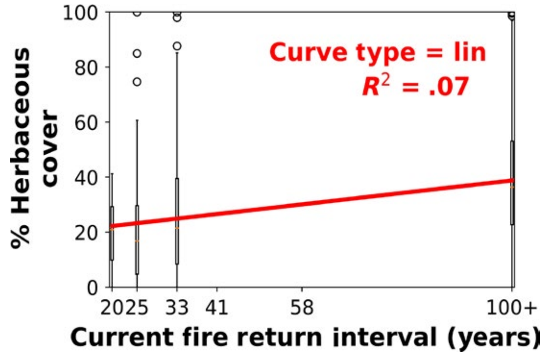

FIGURE 5 Single-factor models of herbaceous cover as predicted by current fire return interval (FRI). Rectangles span the 25th through 75th percentile of pixels for each fire return interval. Blue hashes indicate outliers, and red hashes indicate mean per cent cover among all pixels for each fire return interval. The red line indicates a significant linear relationship between observed and predicted herbaceous cover. Curve type was selected from linear, inverse, logarithmic, quadratic and cubic curves using AIC-derived maximum likelihood methods. [Colour figure can be viewed at wileyonlinelibrary.com]

most important within 1 km of roadside features, while distances to the border of the ANF appeared to persist across a wider distance band (Figure 4c,d). This result supports prior findings that while roadside areas are susceptible to invasion, roadside invasions typically progress only limited distances into the interior of intact chaparral stands (Davies et al., 2013). However, further dissection of existing chaparral by additional roadworks could increase the area of chaparral at risk of invasion. While this study only considers the effects of paved roads that were visible in NLCD cover maps due to unavailability of high-resolution map data for unpaved roads, power lines, firebreaks and off-road vehicle use areas throughout the ANF, it is likely these features also contribute to the distribution of herbaceous cover. As paucity of spatial records regarding these forms of anthropogenic impacts on the landscape represent the primary obstacle to evaluating the role of human activity on chaparral invasion, this highlights the need for high-quality spatial recording of human activity and land use within national forests.

This work extends previous research which also predicted that, except in cases of rapid (<20 years) fire intervals, climate and moisture were the primary factors driving range contractions of chaparral (Syphard et al., 2013). Although increased disturbance may act as the catalyst for the invasion of chaparral and conversion into herbaceous-dominant grasslands (Keeley, 2006; Keeley, Baer-Keeley, et al., 2005), local precipitation and moisture regimes appear to be the primary determinants of which locations are successfully invaded and type-converted during post-disturbance succession. Low moisture availability in the years immediately following fire has been observed to limit recruitment and increase seedling mortality (Keeley et al., 2005b; Kummerow, Ellis, & Mills, 1985) among chaparral shrubs, while increasing water availability. Thus, low moisture availability likely limits chaparral by restricting colonization and increasing mortality at the seedling phase, when shrubs are typically most vulnerable to drought stress (Williams, 1997). However, extreme or prolonged droughts have been observed to result in major diebacks and high mortality even among mature stands of shallow-rooted and non-sprouting chaparral shrubs (Davis et al., 2002; Paddock et al., 2013), indicating that severe drought may facilitate type conversion of intact chaparral by reducing biotic resistance to invasion (D'Antonio, Levine, & Thomsen, 2001). It should be noted our study specifically excluded all areas that had burned since 1998, as such locations were likely to still be in the process of immediate post-fire succession. Locations with extremely rapid (<20 years) fire intervals are inherently likely to have burned within that timeframe and therefore likely removed. Thus, this study does not fully reflect the impacts of extremely rapid fire intervals, in which fire likely does play the dominant role in determining invasion success (Haidinger & Keeley, 1993; Syphard et al., 2013). However, it does indicate differences in local fire frequency that remains within historical norms are unlikely to result in major conversion from chaparral into grasslands. It should also be noted that this study only examines the relationship of local cover to long-term climate norms. Interannual changes in moisture or precipitation may have effects that operate differently, or at different scales than were observed in this study.

4.3 | Management implications

Our results indicate not only that invasion by herbaceous cover is widespread in southern California chaparral ecosystems, but also that reductions in moisture that are predicted under future climate change (National Assessment Synthesis Team, 2000) may alter the degree of invasion by exotic herbs and grasses into intact chaparral. While mean

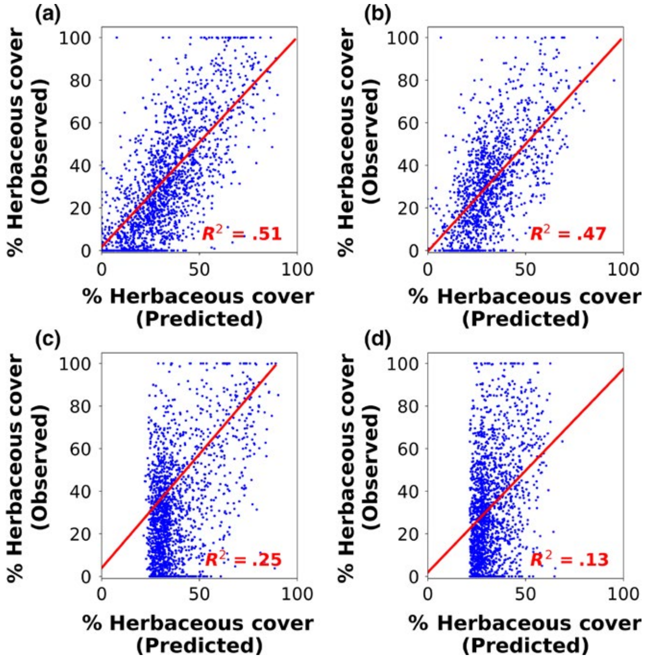

FIGURE 6 Comparisons of observed herbaceous cover (as derived from 0.3 metre (1 foot) resolution orthoimagery) and modelled herbaceous cover as predicted by all moisture, disturbance or anthropogenic and topographic factors (a), by moisture-related factors only (b), by disturbance or human-related factors only (c) and by topographic factors only (d). Red lines indicate linear relationships between observed and predicted herbaceous cover. R^2 values indicate correlation between observed and predicted herbaceous cover for each model. [Colour figure can be viewed at wileyonlinelibrary.com]

annual precipitation throughout the area examined in this study is expected to increase very slightly (0.25 mm), CMD is expected to increase by only 0.25 mm over 1980–2010 normals by 2085, the mean climatic moisture deficit is predicted to increase by 14.5% by 2085 based on mean predicted values of the 15 General Circulation Models selected for inclusion in the IPCC under RCP 4.5 and 8.5 emission scenarios (IPCC Wang et al., 2016), driven by to increasing ambient temperatures and associated evaporative demand. Thus, the vulnerability of chaparral to invasion by grasses and herbaceous species is likely to increase. Old-growth chaparral has also been identified as a major carbon sink that outperforms both tallgrass prairies and grazed grasslands (Luo et al., 2007), and the conversion of native shrublands into invaded grasslands can greatly reduce ecosystem carbon sequestration (Bradley, Houghton, Mustard, & Hamburg, 2006). Thus, widespread conversion of chaparral to invaded grasslands would likely cause major shifts in composition across other trophic levels, reduce the ability of those ecosystems to function as carbon sinks, and significantly alter the hydrology of the landscape by reducing near-surface water availability while decreasing total water uptake (Davis, 1984; Davis & Mooney, 1985; Eliason & Allen, 1997; Hibbert, 1971; Orme & Bailey, 1970; Williamson, Graham, et al., 2004; Williamson, Newman, et al., 2004). Post-conversion, historically chaparral areas have been found to exhibit significantly increased groundwater recharge, throughflow and soil moisture below the rooting depth of invasive grasses (Davis, 1984; Debano et al., 1984; Hibbert, 1971; #520; Williamson, Newman, et al., 2004), but increasing the aridity of near-surface soil (Eliason & Allen, 1997; Davis & Mooney, 1985). Similarly, studies of type-converted chaparral conducted within the ANF found that type conversion reduced rainfall interception throughout the year, converted many streams from ephemeral to perennial flow, and increased soil slippage and erosion risk during major precipitation events (Corbett & Crouse, 1968; Dunn et al., 1988; Orme & Bailey, 1971). Invasion and type conversion of California chaparral have also been documented to reduce arthropod diversity and also produce substantial shifts in the composition of small mammal communities, benefitting some species and extirpating others (Lambrinos, 2000).

As this method is capable of rapidly producing annual estimates of the distribution and per cent cover by herbs and grasses, it also represents a mechanism for rapidly areas of recent invasion or in which chaparral is actively being displaced. By providing accurate, extensive and annually repeating measures of the intactness of chaparral cover, this method provides an important resource for prioritizing management activities from a landscape perspective.

5 | CONCLUSIONS

Our study demonstrates a method for assessing invasion of chaparral by herbaceous species at broadscales that can readily identify highly invaded, moderately invaded or largely intact shrublands. Our results show that invasion of herbaceous cover into chaparral is already

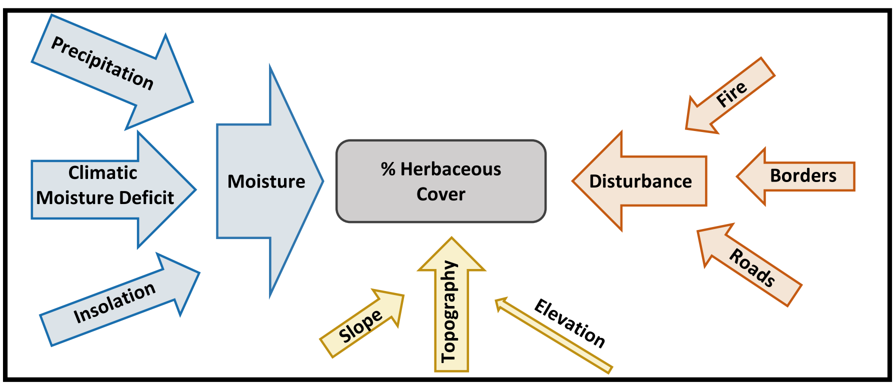

FIGURE 7 Contributions of all factors to distribution of herbaceous cover. Arrow weights correspond to relative importance of each factor in predicting the per cent of herbaceous cover. [Colour figure can be viewed at wileyonlinelibrary.com]

widespread and suggest that local moisture availability should be the primary concern when assessing the risk of post-disturbance type conversion. Additionally, while dissection of the forest vegetation by roadways plays a role in the distribution of herbaceous cover throughout chaparral-dominated vegetation, greater human traffic and disturbance experienced near the border of the ANF plays a significant role in determining the distribution of herbaceous cover that is independent of roadways and development.

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REFERENCES

Allen, E. B., Sirulnik, A. G., Egerton-Warburton, L., Kee, S. N., Bytnerowicz, A., Padgett, P. E., … Meixner, T. (2005). Air Pollution and Vegetation Change in Southern California Coastal Sage Scrub: A Comparison with Chaparral and Coniferous Forest. In B. E. Kus & J. L. Beyers (Eds.), *Planning for biodiversity: Bringing research and management together. Gen. Trch. Rep. PSW-GTR-195* (pp. 79–95). Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture.

Boyko, H. (1945). On forest types of the semi-arid areas at lower altitudes. *Palestine Journal of Botany, Rehovot Series*, *5*, 1–21.

Bradley, B. A., Houghton, R. A., Mustard, J. F., & Hamburg, S. P. (2006). Invasive grass reduces aboveground carbon stocks in shrublands of the western US. *Global Change Biology*, *12*, 1815–1822. https://doi.org/10.1111/j.1365-2486.2006.01232.x

Buma, B. (2012). Evaluating the utility and seasonality of NDVI values for assessing post-disturbance recovery in a subalpine forest. *Environmental Monitoring and Assessment*, *184*, 3849–3860. https://doi.org/10.1007/s10661-011-2228-y

Bytnerowicz, A., & Fenn, M. E. (1995). Nitrogen deposition in California forests: A review. *Environmental Pollution*, *902*, 127–146.

Carlson, T. N., & Ripley, D. A. (1997). On the relation between NDVI, fractional vegetation cover, and leaf area index. *Remote Sensing of the Environment*, *62*, 241–252. https://doi.org/10.1016/S0034-4257(97)00104-1

Choler, P., Sea, W., Briggs, P., Raupach, M., & Leuning, R. (2010). A simple ecohydrological model captures essentials of seasonal leaf dynamics in semi-arid tropical grasslands. *Biogeosciences*, *7*, 907–920. https://doi.org/10.5194/bg-7-907-2010

Cook, D. R., & Weisber, S. (2009). *Applied regression including computing and graphics*. Hoboken, NJ: John Wiley & Sons.

Corbett, E. S., & Crouse, R. P. (1968). Rainfall interception by annual grass and chaparral; losses compared. U.S.F.S.R.P. Psw-48 (pp. 1–12). Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station.

Costa, T. C.e. C.d., Viana, J. H. M., & Ribeiro, J. L. (2014). Semideciduous seasonal forest production of leaves and deciduousness of the water balance, LAI, and NDVI. *International Journal of Ecology*, *2014*, 15. https://doi.org/10.1155/2014/923027

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. *Global Ecology and Conservation*, *2*, 190–203. https://doi.org/10.1016/j.gecco.2014.09.008

Cuba, N., Rogan, J., Christman, Z., Williams, C. A., Schneider, L. C., Lawrence, D., & Milllones, M. (2013). Modelling dry season deciduousness in Mexican Yucatán forest using MODIS EVI data (2000-2011). *GIScience & Remote Sensing*, *50*, 26.

D'Antonio, C. M., Levine, J. M., & Thomsen, M. (2001). Ecosystem resistance to invasion and the role of propagule supply: A California perspective. *Journal of Mediterranean Ecology*, *2*, 233–245.

D'Antonio, C. M., Malmstrom, C., Reynolds, S. A., & Gerlach, J. (2007). Ecology of invasive species in California grassland. In M. R. Stromberg, J. D. Corbin & C. M. D'antonio (Eds.), *California grasslands: Ecology and management* (pp. 67–86). Berkeley, CA: University of California Press.

Davies, K. W., Nafus, A. M., & Madsen, M. D. (2013). Medusahead Invasion along unimproved roads, animal trails, and random transects. *Western North American Naturalist*, *73*, 54–59. https://doi.org/10.3398/064.073.0105

Davis, E. A. (1984). Conversion of Arizona chaparral to grass increases water yield and nitrate loss. *Water Resources Research*, *20*, 1643–1649. https://doi.org/10.1029/WR020i011p01643

Davis, S. D., & Mooney, H. A. (1985). Comparative water relations of adjacent California shrub and grassland communities. *Oecologia*, *66*, 522–529.

Davis, F. W., Borchert, M. I., & Odion, D. C. (1989). Establishment of microscale vegetation pattern in maritime chaparral after fire. *Vegetatio*, *84*, 53–67. https://doi.org/10.1007/BF00054665

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*, 820–828. https://doi.org/10.3732/ajb.89.5.820

Debano, L. F., Brejda, J. J., & Brock, J. H. (1984). Enhancement of riparian vegetation following shrub control in Arizona chaparral. *Journal of Soil and Water Conservation*, *39*, 317–320.

Dunn, P. H., Barro, S. C., Wells, W. G., Poth, M. A., Wohlgemuth, P. M., & Colver, C. G. (1988). *The San Dimas experimental forest: 50 years of research*. In, p. 49. Pacific Southwest Forest and Range Experiment Station: United States Department of Agriculture. https://doi.org/10.2737/PSW-GTR-104

English, D. B. K., Kocis, S. M., Zarnoch, S. J., & Ross, A. J. (2002). *Forest Service National Visitor Use Monitoring Process: Research Method Documentation*. Gen. Tech. Rep. SRS-57 (14p). Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station.

Eliason, S. A., & Allen, E. B. (1997). Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology*, *5*, 245–255. https://doi.org/10.1046/j.1526-100X.1997.09729.x

Fenn, M. E., Allen, E. B., Weiss, S. B., Jovan, S., Geiser, L. H., Tonnesen, G. S., … Bytnerowicz, A. (2010). Nitrogen critical loads and management alternatives for N-impacted ecosystems in California. *Journal of Environmental Management*, *91*, 2404–2423. https://doi.org/10.1016/j.jenvman.2010.07.034

Franklin, J. (1998). Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *Journal of Vegetation Science*, *9*, 733–748. https://doi.org/10.2307/3237291

Franklin, J. (2002). Enhancing a regional vegetation map with predictive models of dominant plant species in chaparral. *Applied Vegetation Science*, *5*, 135–146. https://doi.org/10.1111/j.1654-109X.2002.tb00543.x

Franklin, J., Simons, D. K., Beardsley, D., Rogan, J. M., & Gordon, H. (2001). Evaluating errors in a digital vegetation map with forest inventory Data and accuracy assessment using fuzzy sets. *Transactions in GIS*, *5*, 285–304. https://doi.org/10.1111/1467-9671.00084

Franklin, J., Woodcock, C. E., & Warbington, R. (2000). Multi-attribute vegetation maps of forest service lands in California supporting resource management decisions. *Photogrammetric Engineering & Remote Sensing*, *66*, 1209–1217.

Frazer, J. M., & Davis, S. D. (1988). Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia*, *76*, 215–221. https://doi.org/10.1007/BF00379955

Fry, J., Jin, G., Dewitz, J., Homer, C., Yang, L., Barnes, C., … Wickham, J. (2011). Completion of the 2006 national land cover database for the coterminous United States. *Photogrammetric Engineering and Remote Sensing*, *77*, 858–864.

Gamon, J. A., Field, C. B., Goulden, M. L., Griffin, K. L., Hartley, A. E., Joel, G., … Valentini, R. (1995). Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. *Ecological Applications*, *5*, 28–41. https://doi.org/10.2307/1942049

Gordon, H., & White, T. C. (1994). Ecological guide to southern California chaparral plant series. Usda Forest Service & Pacific Southwest Region, (pp. 1–162). San Diego, CA.

Griffith, A. B., Alpert, H., & Loik, M. E. (2010). Predicting shrub ecophysiology in the Great Basin Desert using spectral indices. *Journal of Arid Environments*, *74*, 315–326. https://doi.org/10.1016/j.jaridenv.2009.09.002

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

Hamilton, J. G. (1997). Changing perceptions of pre-European grasslands in California. *Madroño*, *44*, 311–333.

Hastie, T., Tibshirani, R., & Friedman, J. (2009). *The elements of statistical learning: Data mining, inference, and prediction*. New York, NY: Springer. https://doi.org/10.1007/978-0-387-84858-7

Hibbert, A. R. (1971). Increases in streamflow after converting chaparral to grass. *Water Resources Research*, *7*, 71–80. https://doi.org/10.1029/WR007i001p00071

Homer, C. G., Dewitz, J.A., Yang, L., Jin, S., Danielson, P., Xian, G., … Megown, K. (2015). Completion of the 2011 national land cover database for the conterminous United States - Representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing*, *81*, 345–354.

Huete, A. R., Liu, H. Q., Batchily, K., & Leeuwen, W.V. (1997). A comparison of vegetation indices over a global set of TM images for EOS-MODIS. *Remote Sensing of the Environment*, *59*, 440–451. https://doi.org/10.1016/S0034-4257(96)00112-5

Jacobsen, A. L., & Davis, S. D. (2004). *Fire frequency impacts non-sprouting chaparral shrubs in the Santa Monica mountains of southern California*. 10th MEDECOS Conference (ed by Arianoutsou and Papanastasis). Rhodes, Greece.

Johnson-Maynard, J. L., Shouse, P. J., Graham, R. C., Castiglione, P., & Quideau, S. A. (2004). Microclimate and Pedogenic Implications in a 50-Year-Old Chaparral and Pine Biosequence. *Soil Science Society of America Journal*, *68*, 876–884. https://doi.org/10.2136/sssaj2004.8760

Keeley, J. E. (1986). Resilience of Mediterranean shrub communities to fires. In B. Dell, A. J. M. Hopkins & B. B. Lamont (Eds.), *Resilience in Mediterranean-type ecosystems* (pp. 95–112). Boston, MA: Dr W. Junk Publishers.

Keeley, J. E. (1992). Demographic structure of California chaparral in the long-term absence of fire. *Journal of Vegetation Science*, *3*, 79–90. https://doi.org/10.2307/3236001

Keeley, J. E. (2001). Fire and invasive species in Mediterranean-climate ecosystems of California. In K. E. M. Galley & T. P. Wilson (Eds.), *Proceedings of the invasive species workshop: The role of fire in the control and spread of invasive species. Fire conference 2000: The First National Congress on fire ecology, prevention, and management* (pp. 81–94). Tallahassee, FL: Tall Timbers Research Station.

Keeley, J. E. (2006). Fire management impact on invasive plants in the western United States. *Conservation Biology*, *20*, 375–384. https://doi.org/10.1111/j.1523-1739.2006.00339.x

Keeley, J. E., Baer-Keeley, M., & Fotheringham, C. J. (2005). Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecological Applications*, *15*, 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*. New York, NY: Cambridge University Press.

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

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

Keeley, J. E., Fotheringham, C. J., & Baer-Keeley, M. (2005b). Factors affecting plant diversity during post-fire recovery and succession of Mediterranean-climate shrublands in California, USA. *Diversity & Distributions*, *11*, 525–537. https://doi.org/10.1111/j.1366-9516.2005.00200.x

Kimball, S., Goulden, M. L., Suding, K. N., & Parker, S. (2014). Altered water and nitrogen input shifts succession in a southern California coastal sage community. *Ecological Applications*, *24*, 1390–1404. https://doi.org/10.1890/13-1313.1

Kummerow, J., Ellis, B. A., & Mills, J. N. (1985). Post-fire seedling establishment of *Adenostema fasciculatum* and *Ceonothus greggii* in southern California chaparral. *Madroño*, *32*, 148–157.

Lambrinos, J. G. (2000). The impact of the invasive alien grass *Cortaderia jubata* (Lemoine) Stapf on an endangered mediterranean shrubland in California. *Diversity & Distributions*, *6*, 217–231. https://doi.org/10.1046/j.1472-4642.2000.00086.x

Lambrinos, J. G. (2006). Spatially variable propagule pressure and herbivory influence invasion of chaparral shrubland by an exotic grass. *Oecologia*, *147*, 327–334. https://doi.org/10.1007/s00442-005-0259-1

Lippit, C. L., Stow, D. A., O'Leary, J. F., & Franklin, J. (2013). Influence of short-interval fire occurrence on post-fire recovery of fire-prone shrublands in California, USA. *International Journal of Wildland Fire*, *22*, 184–193. https://doi.org/10.1071/WF10099

Luo, H., Oechel, W. C., Hastings, S. J., Zulueta, R., Qian, Y., & Kwon, H. (2007). Mature semiarid chaparral ecosystems can be a significant sink for atmospheric carbon dioxide. *Global Change Biology*, *13*, 386–396. https://doi.org/10.1111/j.1365-2486.2006.01299.x

Masek, J. G., Vermote, E. F., Saleous, N. E., Wolfe, R., Hall, F. G., Huemmrich, K. F., … Lim, T.-K. (2006). A landsat surface reflectance dataset for North America, 1990-2000. *IEEE Geoscience and Remote Sensing Letter*, *3*, 68–72. https://doi.org/10.1109/LGRS.2005.857030

McMichael, C. E., Hope, A. S., Roberts, D. A., & Anaya, M. R. (2004). Post-fire recovery of leaf area index in California chaparral: A remote sensing-chronosequence approach. *International Journal of Remote Sensing*, *25*, 4743–4760. https://doi.org/10.1080/01431160410001726067

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*, 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*, 515–527. https://doi.org/10.1890/1051-0761(2006)016[0515:FBANSA]2.0.CO;2

Minnich, R. A. (2008). *California's fading wildflowers: Lost legacy and biological invasions*. Berkeley, California: University of California Press.

Minnich, R. A., & Bahr, C. J. (1995). Wildland fire and chaparral succession along the California Baja-California boundary. *International Journal of Wildland Fire*, *5*, 13–24. https://doi.org/10.1071/WF9950013

Moody, A., & Meentemeyer, R. K. (2001). Environmental factors influencing spatial patterns of shrub diversity in chaparral, Santa Ynez Mountains, California. *Journal of Vegetation Science*, *12*, 41–52. https://doi.org/10.1111/j.1654-1103.2001.tb02615.x

Myers, K., Stoughton, T., Walker, K., & Zylstra, J. (2009). Burned Area Emergency Response Specialist Report: Noxious and invasive, non-native weeds specialist report and noxious weed detection survey plan. In P.S.R. Usda Forest Service (pp. 1–13).

National Assessment Synthesis Team (2000). *Climate change impacts on the United States: The potential consequences of climate variability and change*. Washington DC: US GCRP.

Orme, A. R., & Bailey, R. G. (1970). The effect of vegetation conversion and flood discharge on stream channel geometry: A case of southern California watersheds. *Proceedings of the American Association of Geographers*, *2*, 65–82.

Orme, A. R., & Bailey, R. G. (1971). Vegetation conversion and channel geometry in Monroe Canyon, southern California. *Yearbook of the Association of Pacific Coast Geographers*, *1971*, 65–82. https://doi.org/10.1353/pcg.1971.0004

Paddock, W. A. S., Davis, S. D., Pratt, R. B., Jacobsen, A. L., Tobin, M. F., López-Portillo, J., & Ewers, F. W. (2013). Factors determining mortality of adult chaparral shrubs in an extreme drought year in California. *Aliso: A Journal of Systematic and Evolutionary Botany*, *31*, 49–57. https://doi.org/10.5642/aliso

Parker, T. V., Pratt, R. B., & Keeley, J. E. (2016). Chaparral. In M. Harold, & Z. Erika (Eds.), *Ecosystems of California* (pp. 479–507). Oakland, CA: University of California Press.

Pase, C. P. (1982). Californian (coastal) chaparral. *Desert Plants*, *4*, 91–94.

Pfeffer, K., Pebesma, E. J., & Borough, P. A. (2003). Mapping alpine vegetation using vegetation observations and topographic attributes. *Landscape Ecology*, *18*, 759–776. https://doi.org/10.1023/B:LAND.0000014471.78787.d0

Quideau, S. A., Graham, R. C., Chadwick, O. A., & Wood, H. B. (1998). Organic carbon sequestration under chaparral and pine after four decades of soil development. *Geoderma*, *83*, 227–242. https://doi.org/10.1016/S0016-7061(97)00142-0

Reever Morghan, K. J., Corbin, J. D., & Gerlach, J. (2007). Water Relations. In M. R. Stromberg, J. D. Corbin & C. M. D'antonio (Eds.), *California grasslands* (pp. 87–93). Los Angeles, CA: University of California Press.

Safford, H. D., Van de Water, K., & Clark, C. (2013). California Fire Return Interval Departure (FRID) map, 2012 version. USDA Forest Service, Pacific Southwest Region and The Nature Conservancy-California. Sacramento and Vallejo, CA: http://www.fs.fed.us/r5/rsl/clearinghouse/r5gis/frid/

Sears, P. B. (1947). The insolation-exposure factor. *Ecology*, *28*, 316–317. https://doi.org/10.2307/1930518

Shmidt, M., Luscas, R., Bunting, P., Verbesselt, J., & Armston, J. (2014). Multi-resolution time series imagery for forest disturbance and regrowth monitoring in Queensland, Australia. *Remote Sensing of the Environment*, *158*, 156–168.

Syphard, A. D., Regan, H. M., Franklin, J., Swab, R. M., & Bonebrake, T. C. (2013). Does functional type vulnerability to multiple threats depend on spatial context in Mediterranean-climate ecosystems? *Diversity & Distributions*, *19*(10), 1263–1274. https://doi.org/10.1111/ddi.12076

Ulery, A. L., Graham, R. C., Chadwick, O. A., & Wood, H. B. (1995). Decade-scale changes of soil carbon, nitrogen and exchangeable cations under chaparral and pine. *Geoderma*, *65*, 121–134. https://doi.org/10.1016/0016-7061(94)00034-8

Wang, T., Hamann, A., Spittlehouse, D. L., & Carrol, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE*, *11*, e0156720. https://doi.org/10.1371/journal.pone.0156720

Warbington, R., Levien, L., & Rosenberg, M. (2000). Monitoring wildland vegetation in California on a 5-year coordinated schedule using remote-sensing, GIS, and ground-based sampling. *USDA Forest Service* (pp. 1–12). Sacramento, CA.

Warbington, R., Scwind, B., Brohman, R., Brewer, K., & Clerke, W. (2002). Requirements of remote sensing and geographic information systems to meet the new forest service existing vegetation classification and mapping standards. *USDA Forest Service* (pp. 1–12). San Diego, CA.

Williams, J. E. (1997). Xylem embolism in seedlings and resprouts of *Adenostema fasciculatum* after Fire. *Australian Journal of Botany*, *45*, 291–300. https://doi.org/10.1071/BT96030

Williamson, T. N., Graham, R. C., & Shouse, P. J. (2004). Effects of a chaparral-to-grass conversion on soil physical and hydrologic properties after four decades. *Geoderma*, *123*, 99–114. https://doi.org/10.1016/j.geoderma.2004.01.029

Williamson, T. N., Newman, B. D., Graham, R. C., & Shouse, P. J. (2004). Regolith water in zero-order chaparral and perennial grass watersheds four decades after vegetation conversion. *Vasose Zone Journal*, *3*, 1007–1016. https://doi.org/10.2136/vzj2004.1007

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 coaster scrub. *Ecology*, *64*, 809–818. https://doi.org/10.2307/1937204

Zink, T. A., Allen, M. F., Heinde-Tenhunen, B., & Allen, E. B. (1995). The effect of a disturbance corridor on an ecological reserve. *Restoration Ecology*, *3*, 304–310. https://doi.org/10.1111/j.1526-100X.1995.tb00098.x

BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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