Resistance and resilience: ten years of monitoring shrub and prairie communities in Orange County, CA, USA

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Abstract. Mediterranean-climate natural systems have high ecological value, yet the extent of their cover has diminished greatly due to changes in land use. Other stressors, ranging from intense short-term disturbances such as wildfire to more gradual events such as extended drought and continuous pressures including competition with invasive species, test the resistance and resilience of community composition and structure. Data from long-term monitoring provided an opportunity to evaluate the responses of three Southern California plant communities (chaparral, coastal sage scrub, and grassland) to disturbances. We analyzed ten years of point intercept and quadrat data from Orange County to describe trends through time and assess community resistance and resilience. We found that grassland communities, which were more degraded from the start of our study, were generally resistant to change. Chaparral was also fairly resistant to disturbance, while coastal sage scrub exhibited more variation, with some transects exhibiting more resilience than others. Transects with fewer native shrubs experienced less of a decline in shrub cover during drought than those with dense shrubs. Grasslands had the lowest native diversity. There were increases in native diversity in years with more precipitation that were preceded by dry years. There was a decline in native perennial bunchgrasses during our monitoring. Our analyses demonstrated the resilience of native shrub cover to fire and the susceptibility (low resistance) of dense native shrubs and native grasses to drought and increases in non-native species. We encourage academic ecologists to embrace diverse data sources available for hypothesis testing, especially monitoring efforts associated with regulatory purposes, to advance the goal of understanding long-term dynamics.

Key words: California grassland; chaparral; coastal sage scrub; community response to global change; drought; invasive species; long-term monitoring; Mediterranean-climate system; natural resource management; vegetation; wildfire.

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INTRODUCTION

Capturing extended time-series of ecological phenomena is a priority of funding agencies and scientists (Lindenmayer et al. 2012). Long-term data are critical for detecting patterns of change (Lindenmayer and Likens 2010), and the National Science Foundation invests in multiple programs to provide data testing ecological theory, including Long-Term Ecological Research Sites, Long-Term Research in Environmental Biology, and the National Ecological Observatory Network. Despite its importance, academic ecologists struggle to implement and maintain long-term studies for testing existing ecological theory and for developing new hypotheses. In contrast, long-term studies are common in the context of adaptive management of natural resources (Walters and Hilborn 1978, Westgate et al. 2013). Monitoring by land managers is conducted to document baseline conditions, evaluate management effectiveness, clarify thresholds, and identify emergent problems (Westgate et al. 2013, Mason et al. 2017). Much of the monitoring literature focuses on study design, demonstrating the importance of clearly stating research questions, designing appropriate sampling schemes, and conducting power analyses (Reynolds et al. 2011), so managers can implement cost-effective and rigorous programs. How monitoring can produce long-term data that are flexible so as to address unexpected research questions or used to address fundamental ecological theory is a challenge for both communities. Here, we report on 10 yr of vegetation monitoring in Orange County, California, USA, to address originally intended research questions as part of the design (trends in habitat quality through time), unexpected perturbations (wildfire and drought), and more theoretical questions (the ability of communities to recover following disturbance).

Shrub and prairie communities coexist in a mosaic across semi-arid ecosystems (Archer et al. 1995). In Southern California, this mosaic forms three key vegetation communities of concern. Herbaceous-dominated communities are known as California grassland or prairie, the latter name based on the desire to emphasize historically diverse and abundant native forbs (Holstein 2011). Two shrub-dominated systems, coastal sage scrub and chaparral, are distinguished from one another by whether the dominant shrub species are drought-deciduous or evergreen. Drought-deciduous coastal sage scrub species at lower elevations are gradually replaced by evergreen chaparral shrubs at higher elevations (Rundel 2007). Along with other Mediterranean-climate systems, these plant communities have been identified as biodiversity hotspots worthy of conservation (Myers et al. 2000) that cover only ~10% of their historic distribution due to urbanization (Soule et al. 1992). Remaining undeveloped, open space has experienced and is predicted to continue to experience massive biodiversity loss at the local scale due to land use change, invasion of non-native species, increasing fire frequency, nitrogen deposition, and severe drought (Allen et al. 1998, Talluto and Suding 2008, Kimball et al. 2014, Riordan and Rundel 2014).

Southern California ecosystems have been heavily invaded by non-native species, and especially by Eurasian annual grass and forb species. This invasion is exacerbated when coupled with other stressors, such as increasing fire frequency (Conlisk et al. 2016), cattle grazing in more xeric locations (Kimball and Schiffman 2003), atmospheric nitrogen deposition (Fenn et al. 2003), and drought (Kimball et al. 2014). All of the above factors, especially when combined, have occasionally led to vegetation-type conversions from perennial, native-dominated communities to annual, non-native-dominated communities (Eliason and Allen 1997, Stylinski and Allen 1999, Wood et al. 2006). The non-native invasive species are primarily ruderals that are able to take advantage of openings in native vegetation caused by disturbances (Eliason and Allen 1997) and can alter disturbance regimes in a classic grass-fire invasion cycle (Dantonio and Vitousek 1992). These invasive species tend to germinate early and grow quickly, allowing them to outcompete native perennial seedlings for water, space, and other resources (Wainwright et al. 2012, Balshor et al. 2017). Following invasion, it may be difficult for the community to return to a diverse native-dominated community without intervention in the form of ecological restoration (Suding et al. 2004). Likewise, there may be some threshold of native cover that indicates resilience

to disturbance (Lindenmayer et al. 2005, Bagchi et al. 2017).

The Southern California region is characterized by high inter-annual variability in precipitation, related to El Niño Southern Oscillation and to the pineapple express, or regions of atmospheric moisture associated with tropical intra-seasonal oscillations (Higgins et al. 2000, Castello and Shelton 2004, Jiang et al. 2016). Variation in the timing and abundance of precipitation influences plant abundance and alters the outcome of competitive interactions (Goldstein and Suding 2014). Variation in the timing and magnitude of early-season rain events influences plant community composition by providing different triggers for annual species with diverse germination requirements and altering relative abundance during establishment (Kimball et al. 2010, Horn et al. 2015). Along with a rise in global temperatures, there has been an increase in the severity and frequency of drought events (Dai 2013, AghaKouchak et al. 2014). Southern California experienced an extreme drought from 2011 through 2016, characterized by low precipitation combined with record-breaking high temperatures (Griffin and Anchukaitis 2014, Fahrenkamp-Uppenbrink 2015). Remote sensing techniques indicated that this drought led to dieback of woody shrub species (Coates et al. 2015).

Fire has increased in frequency in California, especially in areas with increasing human population density (Syphard et al. 2007). In Southern California shrub communities and other Mediterranean-climate systems, increasing fire frequency in more inland areas is correlated with a decrease in woody native vegetation (Diaz-Delgado et al. 2002, Talluto and Suding 2008). This is despite the fact that many of the dominant native California shrub species are able to crown-sprout following fire, and many other native shrubs and forbs exhibit increased seed germination post-fire (Keeley and Keeley 1984). Observational studies of shrub communities following fire indicate an increase in forbs immediately following fire and a more gradual increase in shrub cover each year for three to four years as long as precipitation is adequate to allow for shrub growth (Keeley et al. 2005b, Kimball et al. 2014). In a large-scale precipitation manipulation experiment, wildfire followed by drought resulted in vegetation-type conversions from shrub to non-native grass-dominated communities (Kimball et al. 2014, 2016). Similarly, fire followed by drought resulted in mortality of crown-sprouting shrub species (Pratt et al. 2014). Fire intervals of less than three years corresponded with decreases in native crown-sprouting shrubs and increases in non-native annual grasses in Mediterranean-climate systems in Australia (Enright et al. 2011). Herbaceous-dominated communities seem to exhibit a different response to fire, with native forb cover often increasing and invasive annual grasses decreasing following fire, such that prescribed burns are sometimes used as restoration tools (Meyer and Schiffman 1999, Harrison et al. 2003, Berleman et al. 2016). Some regions of California now manage the system for a near-complete absence of fire due to the threat to habitat and potential impacts on species of concern (NCC 2016). The role of fire, and especially interactions between fire, drought, and other global change factors (such as biological invasions) on the long-term health and persistence of native plant communities in Southern California, needs clarification.

We initiated a long-term vegetation monitoring program in 2007 to evaluate the biological integrity of Orange County prairie and shrub communities over time in the context of management of an extensive open-space reserve (~50,000 acres). These data may also be useful in understanding system response to inter-annual changes in weather and global change impacts. Here, we report on ten years of monitoring data, coinciding with a massive wildfire in November 2007 and an extreme drought from 2011 through 2016, in contrasting coastal and inland areas of the reserve. Our objectives are to identify the role of spatial and temporal environmental fluctuation in determining variation in plant community composition, to identify biotic and abiotic stressors that result in changes in the cover of key native and non-native species. We addressed the following questions: (1) What are the regional trends in plant cover across the study area, through time, and with changes in precipitation? This goal of identifying temporal trends, and especially assessing habitat quality for multiple species (Diffendorfer et al. 2007), was the primary goal of the monitoring program. (2) How has the proportion of native to non-native species changed through time and space and do

investigations of individual, particularly problematic, non-native species follow the same trend as the combined cover of all invasive species and of invasive grasses? We chose to focus on Eurasian grasses due to concerns about vegetation-type conversions from native shrub-dominated communities to annual Eurasian grasslands (Minnich and Dezzani 1998, Talluto and Suding 2008). We also decided to focus on three specific non-native species, due to the history of funding that focuses managers' efforts on controlling individual problematic invasive species. Artichoke thistle, *Cynara cardunculus*, was the focus of a major removal effort in Orange County, in which thousands of acres per year were treated with herbicide annually since 1994 (Dickens and Suding 2014). *Brassica nigra* has also been a primary concern for land managers, and is especially challenging to remove, in part due to below-ground processes inhibiting native plant establishment (Turk and Tawaha 2003, Grman and Suding 2010, Lankau and Lankau 2014). The third invasive species, *Salsola tragus*, was selected due to observations that this species has recently increased in cover in the County. (3) How did vegetation respond to extreme abiotic stress? In particular, what was the response to the Santiago Fire that burned approximately 28,445 acres (115 km^2) in late October to November 2007 and to the severe drought from 2012 to 2016? Were native communities with higher initial native cover more resilient to drought? This last question was driven by a desire to use the monitoring data opportunistically to evaluate vegetation response to these two abiotic perturbations.

Our expectation was that native shrubs would exhibit less fluctuation in response to inter-annual variation in precipitation than annuals due to their longer life cycle. We hypothesized that native shrub communities would show some resilience to fire, as this is a system that only converts to invasive grasses with increases in fire frequency or when fire coincides with other disturbances (Keeley 2002, Dickens and Suding 2014). We also hypothesized that native shrubs would be negatively influenced by the multi-year drought exhibiting low resistance, while non-native invasive grasses and forbs would be more resistant and perhaps show an increase in cover in previously shrub-dominated areas due to an increase in bare ground with

drought-induced shrub mortality (Kimball et al. 2014). Since long-lived species may increase community resilience (Eriksson 2000), we hypothesized that areas with higher initial native cover would be more resilient when faced with drought. We were not certain whether any shifts from native shrub-dominated systems to invasive annual-dominated systems would be more likely in regions near the coast or inland. In a study across the state of California, near-coast regions were more heavily invaded (Seabloom et al. 2006). However, the factors that lead to conversion of native shrubs to non-native annuals, such as N-deposition and high fire frequency, increase with distance from the coast, suggesting that inland areas may be more heavily invaded (Talluto and Suding 2008, Fenn et al. 2010).

Methods

Data collection

Field data were collected between 2007 and 2016, in grassland, coastal sage scrub, and chaparral plant communities across a ~50,000 acre reserve, the Nature Reserve of Orange County, a set of coordinated open-space reserves in southern California (Fig. 1). Plots were selected using a stratified semi-random design, with points buffered to be located between 30 and 300 m of an accessible road, and under a 35% slope (Deutschman and Strahm 2009). In 2007, eight sites were sampled, followed by 20 in 2008, 27 in 2009, and 22 in 2010 (Table 1). Power analysis was used to determine the optimal sample size for detecting meaningful changes in conservation values of vegetation while minimizing cost and resulted in a recommended sample size of eight plots in chaparral, 22 plots in coastal sage scrub, and 12 plots in grasslands (Deutschman and Strahm 2011). Sampling from 2011 through 2016 followed this recommended sample size guidance. Sites within each plant community were found to exhibit similar change over time, so a rotating panel design in which not all sites are visited each year was recommended (Deutschman and Strahm 2011). The rotating panel design allowed for greater spatial coverage while avoiding excessive observer impacts that might occur with annual visits to the same transects.

Each sampling location consisted of a 50-m linear transect, permanently marked at the

A. Data from all transects
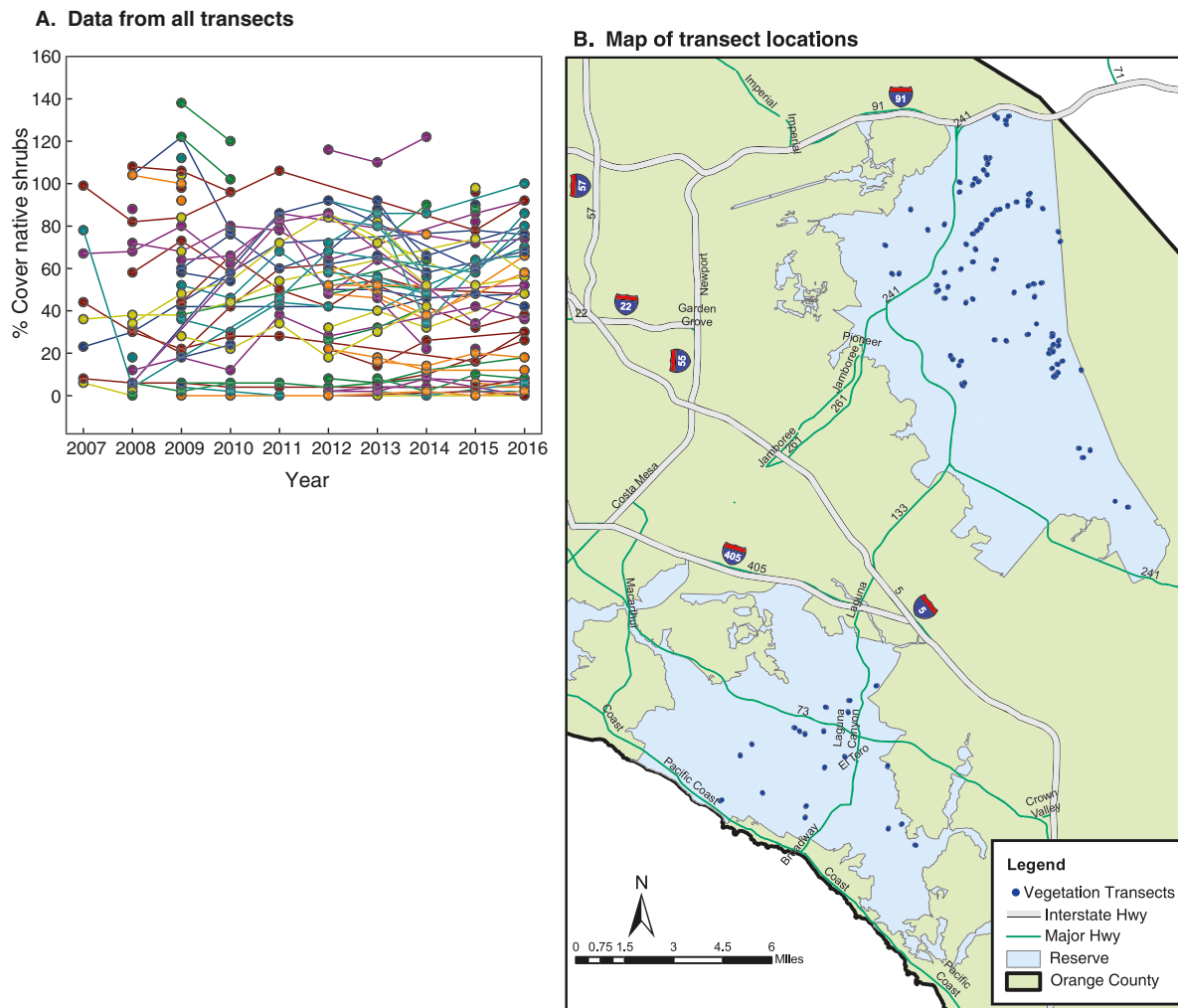

B. Map of transect locations

Fig. 1. The vegetation transects associated with a 10-yr monitoring effort for an expansive ecological reserve. (A) The percent cover of native shrubs at each transect location, sampled through time. Different transect locations are identified with different colors. Lines connect transects sampled across years (breaks indicate years where the transect was not sampled). In a rotating panel design, not all locations are sampled in all years. (B) Map showing the location of all transects in Orange County, California, USA, associated with the Nature Reserve of Orange County (shaded blue). Note that some transects were inland, while others were near the coast.

beginning and end. Data collection included 50 point intercepts, in which a wooden dowel was dropped perpendicular to the transect line at 1-m intervals (from 0 to 49 m), and all plant species touching the 0.5 inch diameter dowel were recorded. Plants were recorded by species and may have overlapped in layers, resulting in greater than 100% absolute cover. Ground cover (bare ground, rock, cryptobiotic crust, etc.) was also recorded at all points. We calculated percent cover by counting the number of intersections made by each species and ground cover class and multiplying by two. In addition to the point intercept data, 1-m^2 quadrat frames were placed every 5 m along the transect, starting at 0 on the left as one faces the transect, and switching to the opposite side every 5 m. All species inside each quadrat were recorded. Ground cover was recorded as a continuous two-dimensional surface adding up to only 100%, visually estimated to the nearest 1%. We used point intercept data for

Table 1. Number of transects in each plant community sampled from near-coast and inland regions of Orange County by year.

Region	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Inland + near-coast										
Chaparral	3	5	10	6	5	9	8	8	8	8
Coastal sage scrub	3	14	21	14	13	21	20	21	20	20
Grassland	2	8	11	8	5	10	12	13	16	17
Total	8	27	42	28	23	40	40	42	44	45
Inland										
Chaparral	3	5	6	5	5	9	8	8	8	8
Coastal sage Scrub	3	9	12	11	13	21	20	21	20	20
Grassland	2	6	9	6	5	10	12	13	16	17
Near-coast										
Chaparral	0	0	4	1	0	0	0	0	0	0
Coastal sage scrub	0	5	10	4	0	0	0	0	0	0
Grassland	0	2	4	2	0	0	0	0	0	0

all analyses of plant percent cover and quadrat data for all analyses of species richness and ground cover.

Data analysis

Regional trends in space and time.—In order to understand how the different plant communities changed through time in different ways, we used repeated-measures, mixed-model ANOVAs with community (chaparral, coastal sage scrub, or grassland), year of measurement, and the interaction between the two as fixed factors. Transect was included as a random, repeated factor. We ran separate analyses on several variables of interest, including total plant cover, native shrub cover, native forb cover, proportion of native plants, and non-native grass cover as calculated by point intercept. More species were recorded in the quadrats along each transect because they covered greater area. Thus, we used the same model to analyze total species richness and native species richness, calculated from the quadrat data. We also used quadrat data to analyze ground cover variables, including cover of thatch, woody debris, and bare ground. Only inland transects (N = 91) were included in these analyses, since coastal transects were not sampled 2011 through 2016. Average values of all inland variables of interest were used in regression analyses to detect linear trends through time.

To compare the proportion of native plants (% cover of natives/% cover of all plants) in the transects near the coast to that in the inland transects, we used repeated-measures, mixed-model ANOVA with region (near-coast or inland) and community (chaparral, coastal sage scrub, or grassland) as fixed factors, year as a random factor, and transect as a repeated factor. Only data collected between 2008 and 2010 from transects not burned in the 2007 wildfire were included in the analysis (near-coast N = 20; inland N = 24). We repeated this analysis using native cover, non-native grass cover, native species richness, and total species richness as the dependent variables.

Species composition data were analyzed by ordination, implemented with PC-ORD, to understand how composition of all transects (N = 111 transects) differed from one another (McCune and Mefford 1999). We used nonmetric multi-dimensional scaling (NMMDS) on Bray-Curtis distance measures to plot transects in species space according to their degree of dissimilarity in species composition (Faith et al. 1987). For each transect location, we calculated the average percent cover of each species across all years for that transect and used the average cover values of each transect to calculate z scores. The transects were colored by plant community labels to observe whether plant community labels separated out in ordination space. The ordination plot can be used to determine whether the plant community, as subjectively assigned by researchers during transect establishment, related to the actual data on the average cover of species recorded at each transect

over many years. Other variables, including the total cover of various functional groups and of ground cover types, were correlated with ordination space after NMMDS was completed to clarify their relationships with species composition.

We performed a second ordination using Bray-Curtis distance measures calculated from the raw % cover values from all transects in all years (N = 111 transects). The purpose of this second ordination was to visually assess the amount of variation in community composition in each community. We calculated the average value of each community-year combination in ordination space to investigate the resilience of each plant community in terms of how species composition varied from year to year. For transect locations that were sampled for five or more of the ten total years (N = 94 transects), we also used ANOVA with Levene's test for homogeneity of variance and Welch's test comparing means on values of transects ordinated in species space to evaluate the variance in species composition in space and over multiple years. Each community was analyzed separately, and standard deviation values were compared by ANOVA with community as a fixed factor.

We used linear regression to determine whether vegetation in each year was related to growing season precipitation. We ln-transformed total precipitation from October through March (months of maximum precipitation for the primary growing season and influencing water balance and vegetation response prior to sampling) and asked whether average annual native species richness in quadrats, average annual total plant cover measured with point intercept, or the average annual cover of various functional groups from point intercept varied depending on growing season precipitation. Separate regressions were performed on each plant community. Since conditions in the previous growing season may have influenced the current growing season, we also included the previous growing season's precipitation in the models. We used all inland transects for this analysis (91 total transects: chaparral N = 18; coastal sage scrub N = 40; grassland N = 33). We repeated this analysis using only unburned, inland transects (79 total transects: chaparral N = 17; coastal sage scrub N = 36; grassland N = 26).

Non-native, invasive species.—We tested how the abundance of all non-native annual grasses, non-native forbs, and the proportion of native species changed depending on year and community. These analyses, as part of our investigation of vegetation trends in space and time, are described in the previous section. In addition, we used logistic regression to determine whether the presence of three priority non-native species (*Brassica nigra*, *Cynara cardunculus*, and *Salsola tragus*) changed through time in the quadrats. Of these three species, only *B. nigra* was abundant in all communities and all years. For this species, we also used repeated-measures ANOVA to determine whether the percent cover, as calculated with point intercept, varied depending on year and community.

Fire and drought.—We ran repeated-measures, mixed-model ANOVAs to determine whether vegetation varied depending on whether or not the transect was burned in the 2007 wildfire, year of measurement, or the interaction between the two factors. Transect was included as a random repeated factor. For this analysis, only years that included sampling of both burned and unburned inland transects were included (burned N = 7; unburned N = 15).

Did the ability of shrub communities to withstand drought vary depending on the initial cover of shrubs? We tested the resilience of vegetation to prolonged drought by comparing data from transects measured in 2011 (prior to drought) and in 2016 (after several years of drought, Fig. 2, N = 18). This was done by linear regression to determine whether the change in shrub cover (2016–2011) was related to the initial shrub cover in 2011. We also calculated response ratios to drought as ln(shrub cover in 2016/shrub cover in 2011) and tested whether this varied depending on the initial proportion of native species (native species/native + non-native species).

Results

Regional trends in space and time

The total cover of all plants changed significantly through time, with greater variation in coastal sage scrub and grassland transects than in chaparral transects (Fig. 3, Table 2). Native shrubs showed high resilience in all communities as indicated by the significant fluctuations
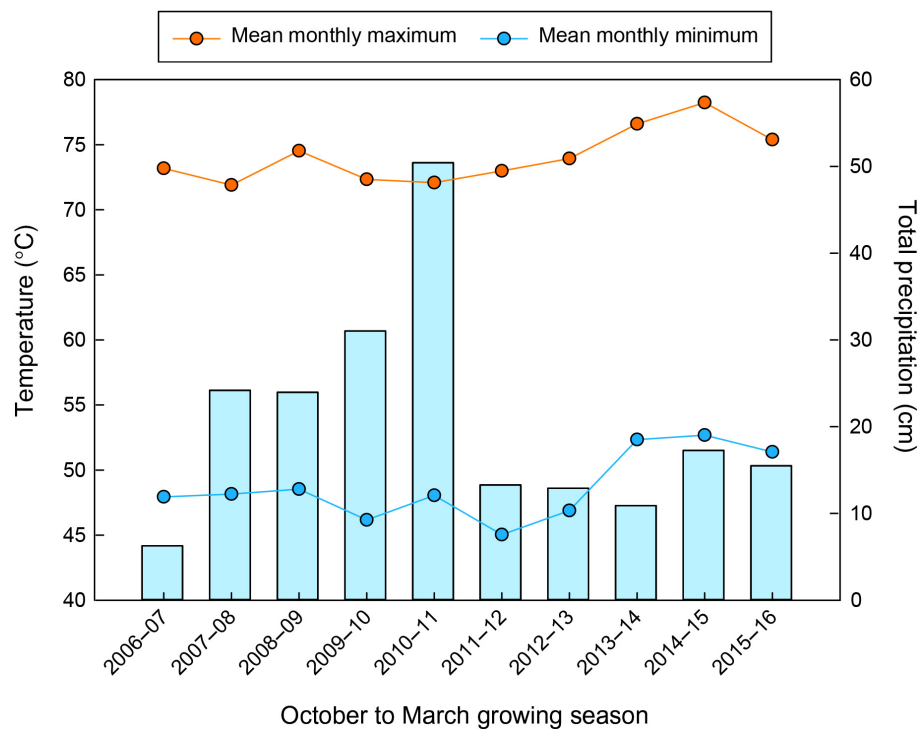
Fig. 2. Average temperature and cumulative precipitation for the growing season (October–March) in each year for which vegetation data were collected. Data are from the Irvine Ranch Weather Station.

through time (strong effect of year; Fig. 3, Table 2) without any significant trend up or down when year was treated as a quantitative variable (Table 3). Chaparral transects had the greatest % cover of native shrubs, followed by coastal sage scrub. Most other functional groups, including native forbs, also exhibited resilience despite extreme inter-annual fluctuations (Fig. 3, Tables 2 and 3). The proportion of native plants was highest in chaparral, intermediate in coastal sage scrub, and lowest in grassland transects. The driest year (2014) had the highest proportion of natives in coastal sage scrub and grassland, presumably due to lower non-native annual grass cover and lower thatch cover (Figs. 3, 4). Native grasses (all perennials) were less resilient and decreased through time in grassland transects, a pattern that was also reflected by a decline in the proportion of all native species over time (Table 3). However, this pattern was driven by high native grass cover in the initial year of 2007, which may or may not have been unusual. When that year was removed from the analysis, the trend became insignificant in

grassland transects ($R^2 = 0.24$, slope = -1.06, $P = 0.103$). Chaparral transects exhibited a significant decline in native grasses when 2007 was removed from the analyses ($R^2 = 0.42$, slope = -0.43, $P = 0.035$).

Between 2008 and 2010, coastal sage scrub transects located near the coast contained a significantly greater proportion of native species than inland transects (Fig. 5, Table 4). For grassland transects, there was no effect of region (near-coast vs. inland) on the proportion of native cover. Native shrub cover was highest in near-coast chaparral and coastal sage scrub transects, intermediate in inland chaparral and coastal sage scrub transects, and lowest in inland and near-coast grassland transects (Fig. 5). Non-native grass cover roughly followed the opposite pattern, with significantly greater cover in the grassland transects than in coastal sage scrub and chaparral, and greater cover inland than in near-coast transects. There was no difference in native species richness in near-coast compared to inland transects, but inland transects had significantly more species overall (native plus invasive)
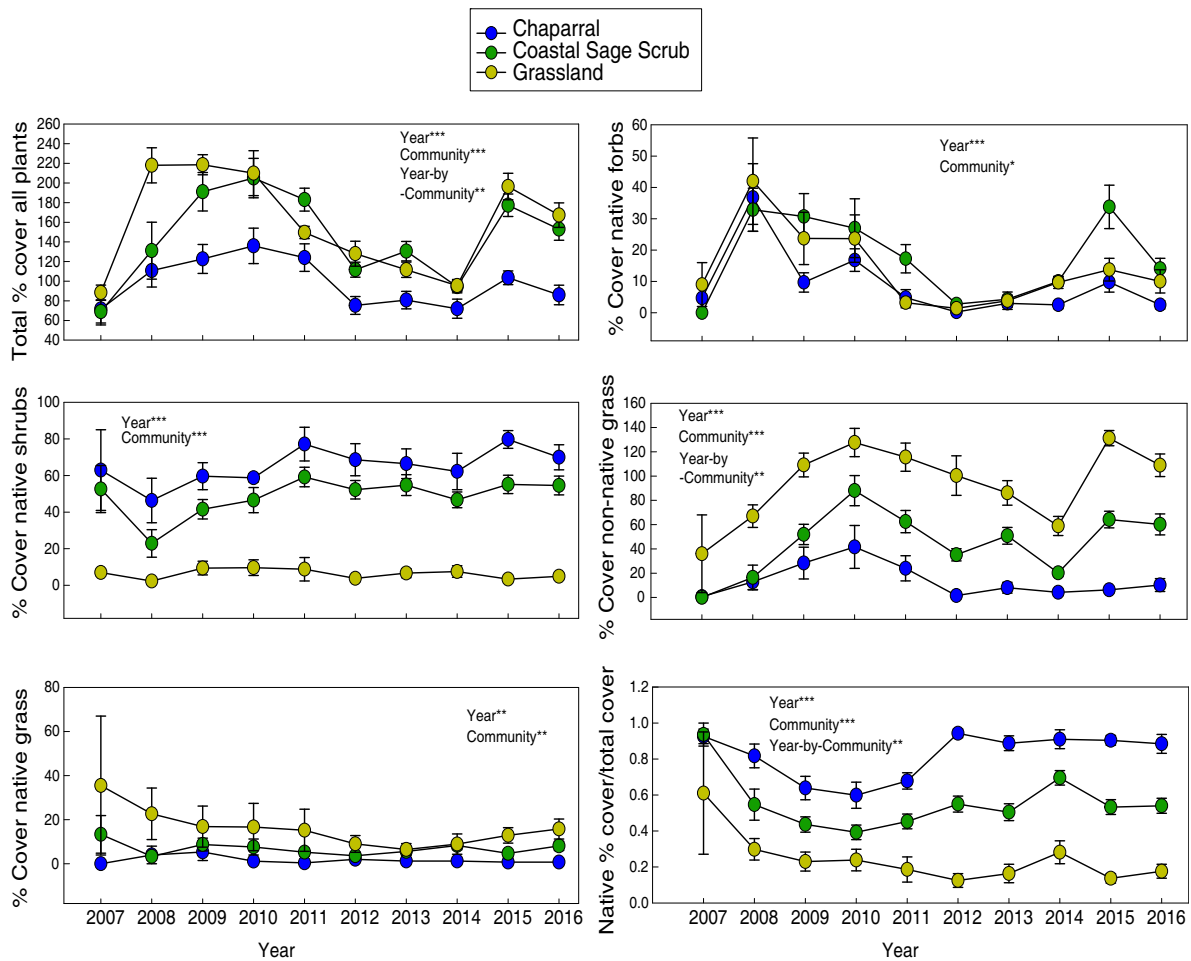
Fig. 3. Average percent cover in each year collected from inland transects and averaged by plant community (chaparral, coastal sage scrub, and grassland). Sample sizes are given in Table 1. Data were analyzed by repeated-measures, mixed-model ANOVAs with year, community, and the interaction as fixed factors, and transect as the random, repeated factor. Significant factors are included on the graph, where *** indicates $P < 0.0001$ and ** indicates $P < 0.01$.

due to a greater diversity of invasive species inland (Fig. 6, Table 4).

There were more native species in coastal sage scrub and chaparral quadrats than in grassland quadrats, which were dominated by non-native species (Fig. 5). Native species richness tended to rise and fall along with changes in precipitation, but was overall resilient and did not trend up or down through time (Fig. 4, Table 3). 2010 and 2015 were characterized by high native species richness and also had the high non-native grass cover. Total species richness (including non-native species) varied depending on the year and

the community. There was a significant year-by-community interaction such that in most years, diversity (number of species) was highest in coastal sage scrub, intermediate in chaparral, and lowest in grassland, but grassland quadrats had the highest species richness in 2008 and averaged more species than chaparral in 2012 and 2014.

The ordination of transects in species space indicated that the three plant communities were characterized by distinct community composition. Transects, when arranged in space by their degree of dissimilarity in species composition

Table 2. Results from repeated-measures, mixed-model ANOVAs on the effect of community, year, and the year-by-community interaction on vegetation and ground cover.

Variable	Effect	df	F	P
Total plant cover	Community	2, 189	13.14	<0.0001
	Year	9, 189	20.33	<0.0001
	Year × Community	18, 189	2.73	0.0004
Native shrub cover	Community	2, 189	79.18	<0.0001
	Year	9, 189	4.88	<0.0001
	Year × Community	18, 189	1.57	0.0717
Native forb cover	Community	2, 189	3.31	0.0387
	Year	9, 189	14.4	<0.0001
	Year × Community	18, 189	1.3	0.1936
Native grass cover	Community	2, 189	5.4	0.0052
	Year	9, 189	3.1	0.0017
	Year × Community	18, 189	1.33	0.1741
Non-native grass cover	Community	2, 189	63.79	<0.0001
	Year	9, 189	16.77	<0.0001
	Year × Community	18, 189	2.34	0.0024
Proportion of native plants	Community	2, 189	86.82	<0.0001
	Year	9, 189	17.26	<0.0001
	Year × Community	18, 189	2.64	0.0006
Brassica nigra cover	Community	2, 189	2.65	0.0733
	Year	9, 189	4.28	<0.0001
	Year × Community	18, 189	1.51	0.0912
Species richness	Community	2, 189	9.52	0.0001
	Year	9, 189	24.24	<0.0001
	Year × Community	18, 189	2.27	0.0033
Native species richness	Community	2, 189	15.94	<0.0001
	Year	9, 189	24.8	<0.0001
	Year × Community	18, 189	1.53	0.0843

(averaged over multiple years), were grouped according to the plant community originally assigned in the design selection process (chaparral, coastal sage scrub, or grassland; Fig. 6). Axis 1 of the ordination on mean values was positively correlated with native shrub cover and negatively correlated with non-native grass cover (Table 5). This axis separated the grassland transects with high cover of non-native grasses from the chaparral transects with low non-native grass cover and high cover of native shrubs. Coastal sage scrub transects were intermediate on this axis. Axis 2 separated transects with high plant cover near to the coast from transects located inland, especially chaparral transects that had higher cover of rocks and bare ground.

The second ordination of all transect-year combinations in species space demonstrated that the communities differed in species composition in all years (Fig. 6B, C). The grassland transects exhibited higher resistance, as evidenced by less

variation from year to year, and were grouped in the lower left corner of the plot. Coastal sage scrub transects exhibited the most variation in species composition over time, as is evident from the greater space between the triangles in Fig. 6C. The first year, in particular, was characterized by lower cover of invasive grasses and higher cover of native shrubs than subsequent years. The chaparral transects were more similar to the coastal sage scrub transects in 2009, 2010, and 2011 due to a greater cover of non-native grasses in those years. 2008 was a year in which chaparral transects had species composition that was different from other years, perhaps due to the high cover of native annual forbs (Table 5). Chaparral transects were similar to each other in terms of species composition, while the 13 coastal sage scrub transects sampled in five or more years exhibited greater variation from place to place and from year to year (Table 6). The four grassland transects sampled in five or more years

Table 3. Results from linear regressions on the mean values from inland transects through time.

Variable	Community	Slope	R^2	P
Prop. natives	Chaparral	0.01646	0.0407	0.2736
	Coastal sage scrub	−0.01168	0	0.529
	Grassland	**−0.03071**	**0.3637**	**0.0382**
Total plant cover	Chaparral	−2.36273	0	0.4058
	Coastal sage scrub	1.82551	0	0.7346
	Grassland	−2.26662	0	0.7107
Native shrub cover	Chaparral	1.96323	0.3055	0.0566
	Coastal sage scrub	1.73855	0.1618	0.1366
	Grassland	−0.21023	0	0.4992
Native forb cover	Chaparral	−1.76158	0.1445	0.151
	Coastal sage scrub	−0.32077	−0.1188	0.8381
	Grassland	−1.94036	0.1228	0.1712
Native grass cover	Chaparral	−0.2101	0.0349	0.2828
	Coastal sage scrub	−0.28699	0	0.418
	Grassland	**−1.95473**	**0.4418**	**0.0215**
Non-native grass cover	Chaparral	−1.23189	0	0.4347
	Coastal sage scrub	3.50653	0.0536	0.254
	Grassland	4.33589	0.0718	0.229
Native S	Chaparral	0.335	0	0.6584
	Coastal sage scrub	1.18608	0.1335	0.161
	Grassland	0.23575	0	0.7049
Total S	Chaparral	0.36372	0	0.4215
	Coastal sage scrub	0.64274	0.1073	0.187
	Grassland	−0.01568	0	0.968
Non-native cover	Chaparral	−2.51768	0.0321	0.2875
	Coastal sage scrub	0.80325	0	0.8559
	Grassland	1.84038	0	0.7275

Bold indicates significant relationships ($P < 0.05$).

were more similar to each other than coastal sage scrub transects. They had with similar mean and variance values for Axis 1 and different mean values (but similar variances) for Axis 2 of ordination space (Table 6). The ANOVA on standard deviation values of transects in ordination space indicated that chaparral and coastal sage scrub transects varied more through time than grasslands (lower resistance), since they exhibited significantly greater variation than grassland transects along Axis 1 of the ordination ($F_{2,21} = 4.85$, $P = 0.020$). There was no difference among standard deviation values of transects from different communities for Axis 2 ($F_{2,21} = 1.5$, $P = 0.249$).

Species richness was positively related to growing season precipitation in all plant communities (Fig. 7). However, there was an interesting effect of the previous season's precipitation on native diversity, possibly driven by competition with non-native species. For quadrats in grassland, native species richness was significantly higher in wet years that were preceded by dry years, as demonstrated by the significant positive relationship between number of species and the current year's precipitation, along with the significant negative relationship between species richness and the previous growing season's precipitation (Fig. 7, Table 7). Plant cover was significantly related to the current growing season's precipitation in all plant communities, but not significantly related to precipitation in the previous year (Table 7). Shrubs, in contrast, did not exhibit a strong response to precipitation. We repeated these analyses with only unburned transects and found similar results (Appendix S1: Table S1).

Non-native, invasive species

Non-native annual grasses reached much higher cover than native perennial grasses and showed greater inter-annual fluctuation as would be expected due to their differences in lifespan (Fig. 3, Table 2). Non-native grasses had highest
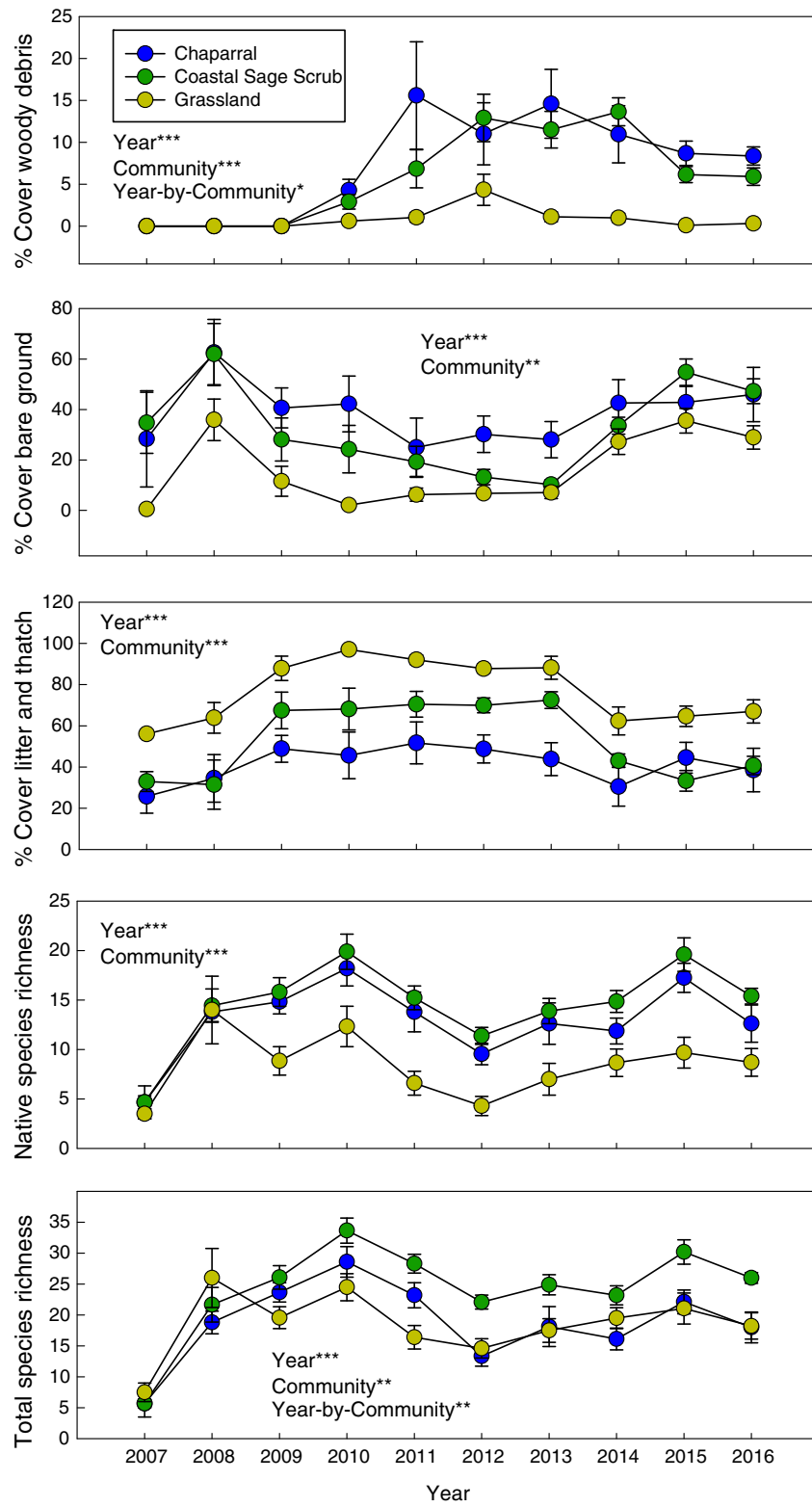
Fig. 4. Average annual values for the percent cover of woody debris, bare ground, and litter and thatch, as

(Fig. 4. *Continued*)

well as the number of native species and the number of all species, including native and non-natives, in quadrats of each community type. Data were analyzed by repeated-measures, mixed-model ANOVAs with year, community, and the interaction as fixed factors, and transect as the random, repeated factor. Significant factors are included on the graph, where *** indicates $P < 0.0001$, ** indicates $P < 0.01$, and * indicates $P < 0.05$.

cover in grassland transects, followed by coastal sage scrub, with the lowest cover in chaparral transects. Non-native annual grass cover was similar to or actually exceeded native shrub cover in some years in coastal sage scrub transects. The cover of non-native annual grasses increased significantly with precipitation in grassland and chaparral transects (Table 7). Precipitation in the previous growing season was not significantly related to non-native grass cover (Table 7).

Brassica nigra cover changed from year to year ($X^2 = 7.84$, $P = 0.0051$; Fig. 8) and was significantly greater in grassland than in coastal sage scrub or chaparral transects ($X^2 = 26.53$, $P < 0.0001$; also see *Results* of repeated-measures, mixed-model ANOVA in Table 2). *Brassica cover* tended to be highest when the previous growing season was dry (Table 7). The cover of *Cynara cardunculus* was close to 0 in all years and in all communities, with no significant difference in the probability of occurrence depending on year ($X^2 = 0.4881$, $P = 0.478$) or community ($X^2 = 0.502$, $P = 0.479$; Fig. 8). *Salsola tragus* increased significantly through time (Year $X^2 = 0.417$, $P = 0.0002$; Fig. 8) and was equally likely to be found in all communities ($X^2 = 3.227$, $P = 0.199$).
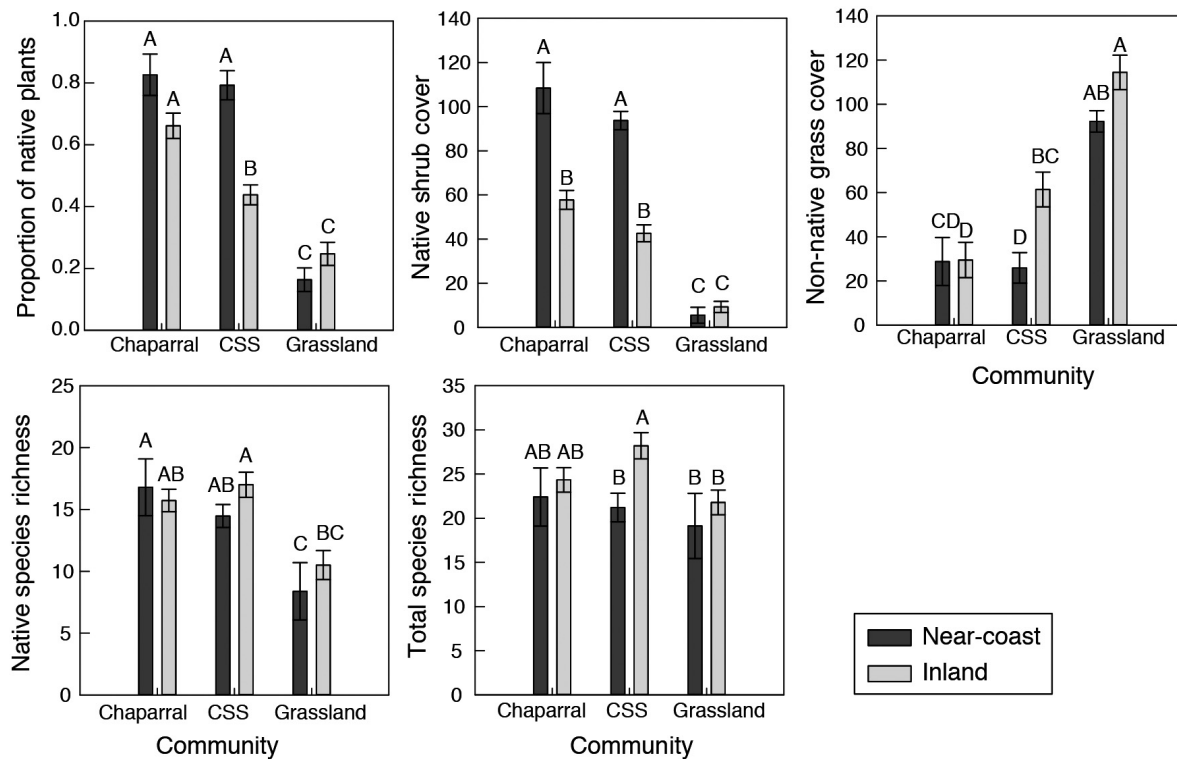

Fig. 5. Mean and SE for the proportion of native plants, percent cover of native shrubs and of non-native grasses, number of native species, and total number of species in near-coast and inland transects from 2008 to 2010. Areas that burned in the 2007 wildfire were excluded. On the *x*-axis, CSS is used as an abbreviation for coastal sage scrub. Letters refer to the result from Tukey post-hoc tests, where shared letters indicate no significant difference ($P > 0.05$).
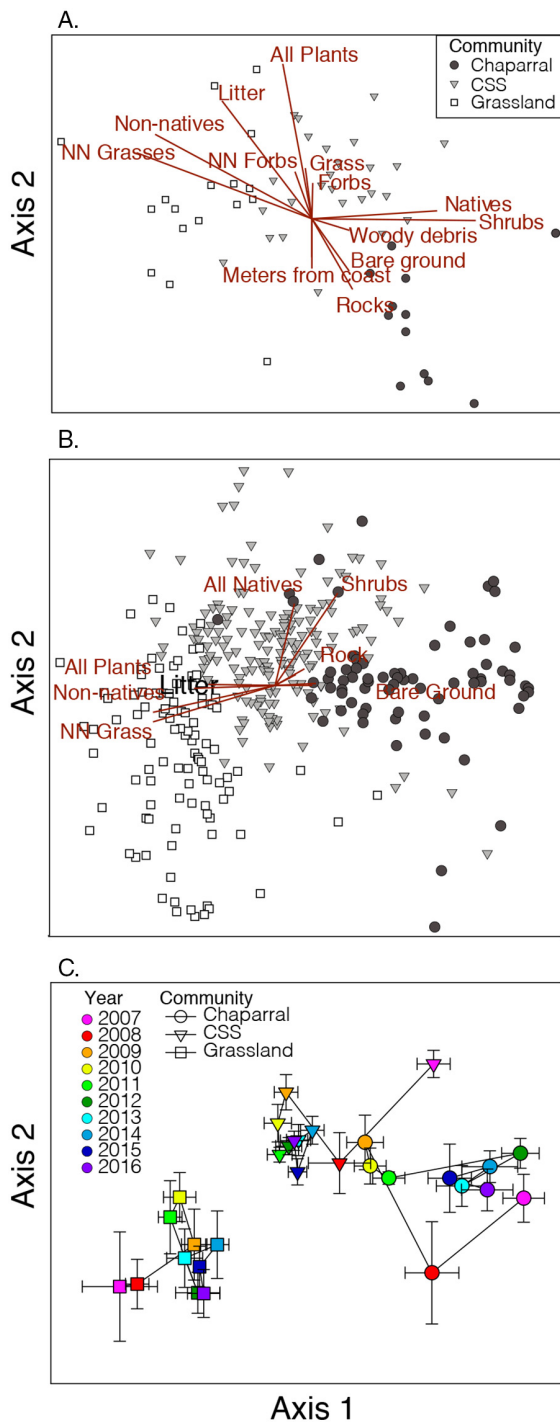
Fig. 6. Ordination of transects in species space. (A) Each symbol represents one transect location that was measured in three or more years. Average percent cover values of all species were used as the raw values from which distance measures were calculated.

Table 4. Results from repeated-measures, mixed-model ANOVAs on the effect of region (coast vs. inland), community (chaparral, coastal sage scrub, or grassland), and the region-by-community interaction.

Variable	Effect	df	F	P
Proportion of natives	Region	1, 80	11.88	0.0009
	Community	2, 80	58.44	<0.0001
	Region × Community	2, 80	12.82	<0.0001
Native shrub cover	Region	1, 80	58.95	<0.0001
	Community	2, 80	111.54	<0.0001
	Region × Community	2, 80	19.32	<0.0001
Non-native grass cover	Region	1, 80	5.11	0.0265
	Community	2, 80	33.7	<0.0001
	Region × Community	2, 80	1.4	0.2524
Native species richness	Region	1, 79	0.67	0.4157
	Community	2, 79	17.14	<0.0001
	Region × Community	2, 79	0.59	0.5544
Total species richness	Region	1, 79	4.25	0.0427
	Community	2, 79	3.75	0.0278
	Region × Community	2, 79	1.17	0.3144

Fire and drought

The analyses comparing transects that burned in November 2007 to those that did not burn revealed significant effects of the 2007 wildfire, year, and a significant year-by-fire interaction (Fig. 9, Table 8). As expected, Tukey post hoc tests revealed that, in 2008, shrub cover was significantly lower in burned plots than in unburned plots. Data were not collected in burned areas in 2009 or 2010 due to a request that burned areas be left unvisited to aid natural recovery. By 2011, when burned transects

(Fig. 6. *Continued*)

Correlations between total cover of key functional groups and environmental variables with ordination space are plotted as red vectors. Complete lists of correlations of species with ordination space and of environmental variables are provided in Table 2. Transects are shaded by the subjectively assigned plant community value. Final stress = 13.4, instability = 0.0001. (B) Ordination of all transects and years in species space. Each symbol represents one transect location in one year. The different communities are distinguished by shapes (circle = chaparral, triangle = coastal sage scrub, and square = grassland). (C) The average value of each community-year combination in species space. Shapes are coded by community and colored by year.

Table 5. Correlations of secondary variables with ordination space.

Variable	Ordination on means		Ordination all years	
	Axis 1 R	Axis 2 R	Axis 1 R	Axis 2 R
Bare ground	0.39	−0.46	0.40	−0.01
Rock	0.40	−0.53	0.42	−0.10
Twigs	0.39	−0.21	0.29	−0.21
Branches	0.15	−0.31	0.15	−0.07
Litter	−0.60	0.69	−0.59	0.11
Moss	0.13	0.14	0.04	−0.17
Cryptobiotic crust	−0.05	−0.23	0.03	−0.07
Native plants	0.71	0.18	0.29	−0.59
Forbs	0.04	0.38	−0.12	−0.07
Shrubs	0.81	−0.08	0.52	−0.63
Grasses	−0.18	0.45	−0.33	−0.03
Non-native grasses	−0.84	0.52	−0.72	0.39
Non-native forbs	−0.26	0.43	−0.35	0.06
Non-native plants	−0.80	0.59	−0.72	0.34
All plants	−0.34	0.79	−0.53	−0.05
Latitude	−0.04	−0.39	—	—
Longitude	0.11	−0.50	—	—
Meters from coast	−0.01	−0.45	—	—

Note: Values are Pearson's R.

were re-visited, there was no longer a significant difference between burned and unburned areas for any of the variables analyzed (proportion of native plants, cover of native shrubs, grasses, or forbs, cover of non-native grasses or forbs). However, investigation of species composition indicated that, while native shrub cover recovered, this cover changed after the fire and continued through 2016 to contain higher cover

of the fire-following shrub, *Acmispon glaber*, and lower cover of *Artemisia californica*.

Across all vegetation communities and in contrast to our hypothesis, transects with a greater initial cover of native shrubs (in 2011) tended to be more negatively impacted by drought than those with a lower initial % cover of native shrubs ($R^2 = 0.39$, $P = 0.0034$; Fig. 10). Sites with greater than 50% native shrub cover in 2011 demonstrated a substantial reduction in native shrub cover, up to ~30% for plots with the highest cover classifications by 2016. The opposite was true for low initial % cover localities, where increases in native shrub cover occurred through the protracted drought. Likewise, transects with a greater initial proportion of native species had negative response ratios (ln(shrub cover in 2016/ shrub cover in 2011)), while those with a lower initial proportion of native species had positive response ratios ($R^2 = 0.30$, $P = 0.012$).

DISCUSSION

Long-term data are critical for ecologists working in all biomes to understand species and community responses to disturbances and to changing weather patterns (Lindenmayer and Likens 2010). Even longer time frames are necessary for understanding the resistance and resilience of ecological systems in environments characterized by high inter-annual variation in precipitation, such as the grass-shrub mosaic characteristic of Mediterranean climates. Our

Table 6. Results of tests comparing the mean and variance of ordination axes for transects sampled in more than three years.

| Community	df	Ordination axis 1		Ordination axis 2	
		F	P	F	P
Chaparral					
Transect	4, 29	0.46	0.763	2.31	0.082
Levene's test for homogeneity of variances	4, 29	0.41	0.802	1.45	0.243
Welch's ANOVA	4, 14.26	0.36	0.834	1.28	0.332
Coastal sage scrub					
Transect	12, 75	11.36	<0.0001	2.58	0.007
Levene's test for homogeneity of variances	12, 75	25.25	<0.0001	1.13	0.351
Welch's ANOVA	12, 27.66	0.36	0.834	2.88	0.010
Grassland					
Transect	3, 21	0.85	0.484	27.58	<0.0001
Levene's test for homogeneity of variances	3, 21	0.09	0.965	0.84	0.487
Welch's ANOVA	3, 11.56	0.74	0.547	18.5	0.000
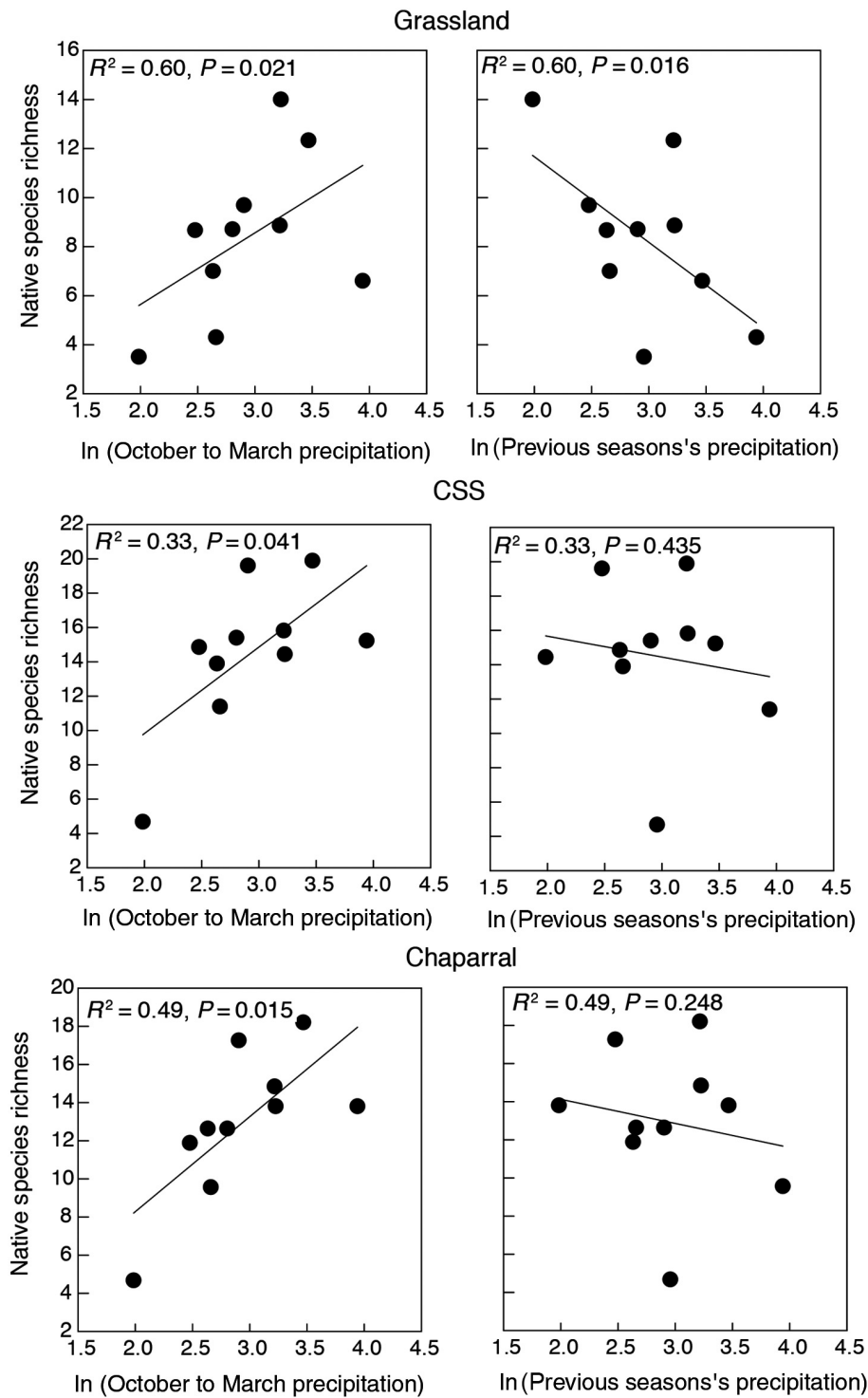
Fig. 7. Relationships between native species richness, current growing season precipitation, and previous growing season precipitation in each plant community. R^2 and P-values are from multiple regressions that included both the current and previous season's precipitation in the model.

Table 7. Standardized regression coefficients from multiple regressions to determine the relationships between precipitation and vegetation.

Comm	Chap		Coastal sage scrub		Grass	
	October–March precip.	Prev. season precip.	October–March precip.	Prev. season precip.	October–March precip.	Prev. season precip.
Native S	0.766	−0.303	0.701	−0.231	0.64	−0.679
Total S	0.858	−0.128	0.724	−0.006	0.687	−0.527
Prop. native cover	−0.835*	−0.078	−0.706*	−0.095	−0.505	−0.1
All plant cover	0.834*	−0.077	0.877**	−0.107	0.752*	−0.292
Native cover	0.694*	−0.203	0.683*	−0.336	0.239	−0.493
Shrub cover	0.196	0.504	0.395	0.377	0.344	−0.027
Native grass cover	0.279	0.059	−0.455	−0.183	−0.259	−0.076
Non-native grass cover	0.892**	−0.169	0.656	0.035	0.667*	0.173
Native forb cover	0.470	−0.674*	0.698*	−0.520	0.407	−0.613
Non-native forb cover	0.792**	0.086	0.797	−0.172	0.466	−0.545
Brassica nigra cover	−0.351	−0.340	−0.261	−0.097	0.227	−0.672*

Note: N = 10.
*$P < 0.05$; **$P < 0.01$.

analyses of 10 yr of vegetation monitoring data revealed sometimes unexpected patterns to assist our understanding of the integrity of critical habitat in Southern California over time. Some of the patterns that we found were expected based on existing literature and supported our hypotheses. For example, native shrub communities were resilient and recovered relatively quickly from wildfire (Fig. 9), something that is typical of Mediterranean shrub communities in the absence of other global change stressors and without an acceleration of the fire cycle (Keeley and Keeley 1984, Malanson and Westman 1985, Pausas et al. 2008). Our analyses also revealed some surprising patterns, such as the negative relationship between previous year's precipitation and current native species richness (Fig. 7). Native forbs, more than
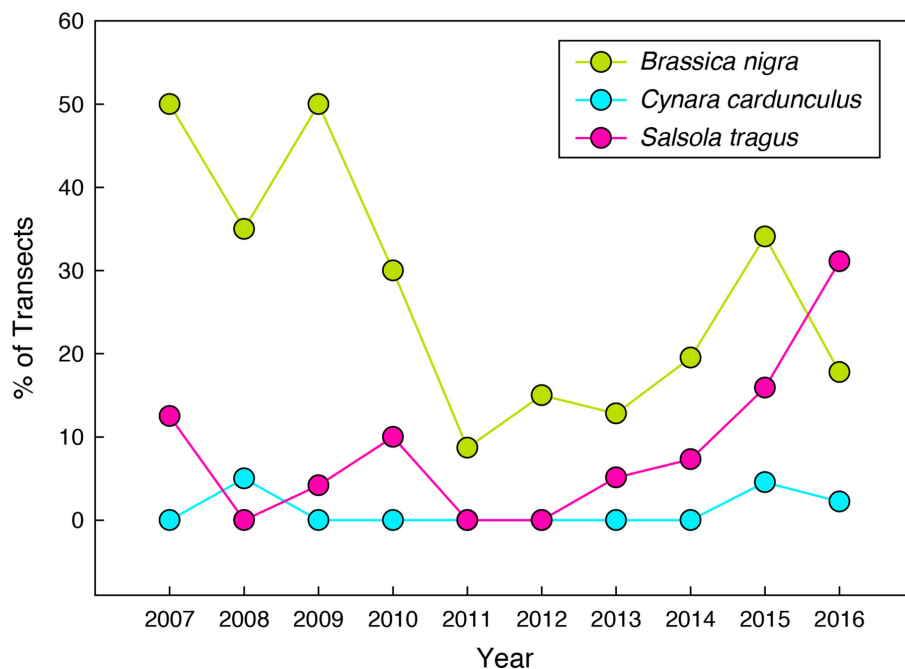

Fig. 8. The percentage of transects in which three non-native species were found in each year of measurement.
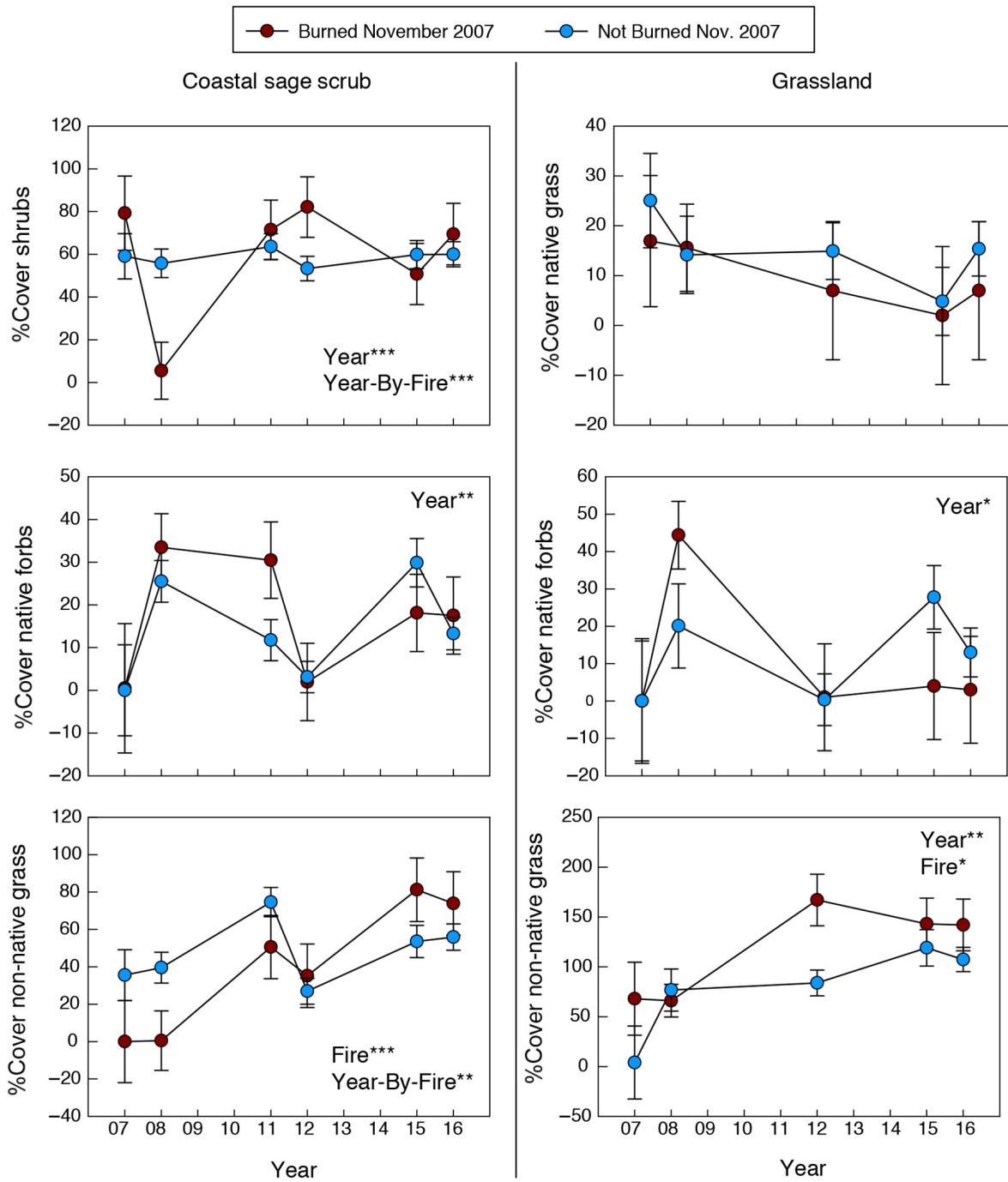
Fig. 9. Percent cover values for major functional groups in transects that burned in the 2007 wildfire compared to values from transects that did not burn in 2007. Coastal sage scrub transects are on the left, and grassland transects are on the right. Only years with both burned and unburned transects were included. Values are LS means ± 1 SE. Significant factors from the ANOVA are included in the insert, where *denotes $P < 0.05$, **$P < 0.01$, and ***$P < 0.0001$. F statistics and df are provided in Table 8.

Table 8. Results from repeated-measures, mixed-model ANOVAs on the effect of fire (burned in 2007 vs. not burned in 2007), year, and the interaction between fire and year.

Community and variable	Effect	df	F	P
Coastal sage scrub				
Proportion of native plants	Fire	1, 42	1.23	0.2739
	Year	5, 42	13.19	<0.0001
	Fire × Year	5, 42	3.25	0.0143
Native shrubs	Fire	1, 42	0.01	0.9325
	Year	5, 42	16.8	<0.0001
	Fire × Year	5, 42	14.75	<0.0001
Native forbs	Fire	1, 42	0.28	0.5968
	Year	5, 42	5.63	0.0005
	Fire × Year	5, 42	1.08	0.3859
Non-native grasses	Fire	1, 42	0.27	0.6089
	Year	5, 42	16.36	<0.0001
	Fire × Year	5, 42	5.7	0.0004
Grassland				
Proportion of native plants	Fire	1, 8	7.54	0.0252
	Year	4, 8	4.77	0.0291
	Fire × Year	4, 8	3.72	0.054
Native grass	Fire	1, 8	0.25	0.6287
	Year	4, 8	1.11	0.4172
	Fire × Year	4, 8	0.2	0.933
Native forbs	Fire	1, 8	0.18	0.6866
	Year	4, 8	6.14	0.0147
	Fire × Year	4, 8	2	0.1869
Non-native grasses	Fire	1, 27	6.3	0.0184
	Year	4, 27	5.01	0.0038
	Fire × Year	4, 27	1.53	0.2211

Note: Coastal sage scrub and grassland transects were analyzed separately.

other functional groups, showed low resistance and high resilience, increasing after fire (Keeley et al. 1981) and decreasing in dry years and in years following significant precipitation. Such time lags in the effects of precipitation on forbs are often overlooked, yet have recently been identified in other systems (Jones et al. 2016, Dudney et al. 2017). Non-native annual grasses fluctuated from year to year, responding positively to high rainfall, likely contributing to the negative correlation between native diversity and previous growing season precipitation. Native grasses (consisting primarily of the perennial bunchgrass, *Stipa pulchra*) showed low resilience and declined over the last ten years in grassland areas. Native perennial grasses have been out-competed by invasive annual grasses in many Mediterranean systems, but their decline is often driven by disturbances such as

cattle grazing, something that did not occur in our area in the last ten years (Seabloom et al. 2003, Clary 2012). Such information regarding population dynamics of major functional groups assists stakeholders with decision-making regarding management actions (when to monitor native forbs, which invasive species to target, etc.) under different weather conditions.

Our first research question asked how plant community composition changed across the study area, through time, and within the context of variation in precipitation associated with the time-series. Our subjective assignments of vegetation communities and establishment of transects consistently ordinated in species space, supporting a resilience of community structure. While other studies investigating Mediterranean shrub communities have documented vegetation-type conversions from native-dominated to non-native-dominated communities inland (Talluto and Suding 2008), we did not find any long-term trend toward decreasing native shrub cover. While the coastal sage scrub transects exhibited greater variance than grassland transects, they did not trend toward grassland transects in terms of their species composition and did not show evidence of transitioning to a new stable state (Beisner et al. 2003, Suding et al. 2004, Bagchi et al. 2017), even though non-native annual grass cover was equal to or greater than native shrub cover in three out of the ten years. Despite demonstrating no changes in vegetation state, the multivariate trajectories, mean distances, and patterns of variation among transects associated with the ordination suggest an interesting hypothesis—chaparral communities likely demonstrate substantial resilience in composition, while coastal sage scrub appears to demonstrate greater variation in the amount of resistance and resilience. The degree of resistance and resilience depends on the timescale and metric, such that native shrub cover is resilient over the long term, suggesting that both chaparral scrub and coastal sage scrub are resistant to change, but with coastal sage scrub shrub cover resisting change even in the face of widely fluctuating non-native grass cover and drought. Grasslands showed high resistance because they are already highly degraded.

Regional studies have documented a greater degree of invasion in coastal areas, corresponding
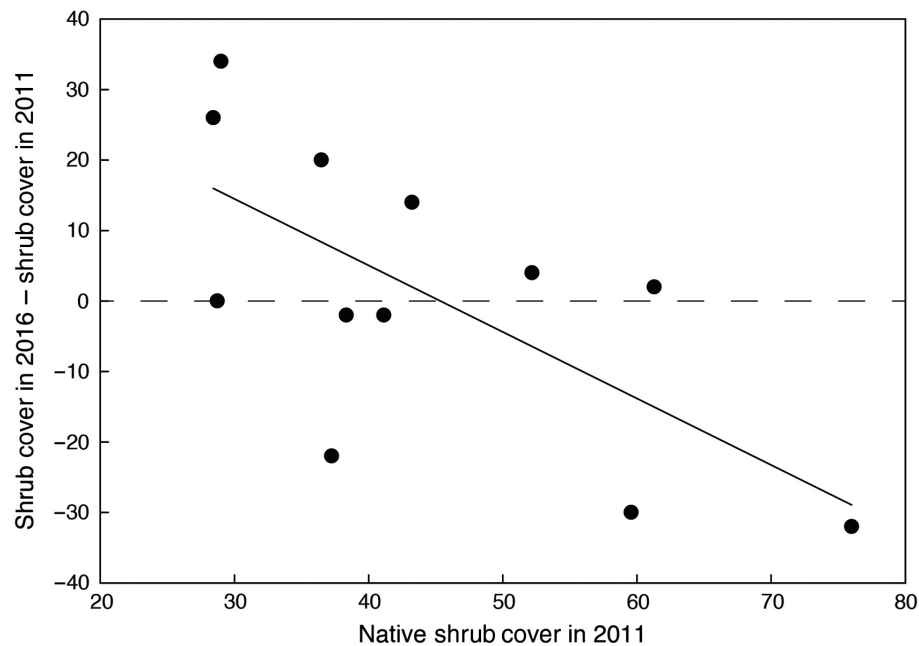
Fig. 10. The change in shrub cover in response to drought (comparing transects sampled in both 2011 and 2016). The dashed line indicates no change in shrub cover.

with greater human disturbance in those areas (Schwartz et al. 2006, Seabloom et al. 2006). Most studies specific to coastal sage scrub in this region of Southern California have occurred in more inland coastal sage scrub communities that seem to be threatened by conversion to Eurasian annual grassland (Minnich and Dezzani 1998). This may be due to interactions among the multiple threats, such as an interplay between greater atmospheric nitrogen deposition that occurs inland (Allen et al. 1998) and a higher frequency of summer fires inland (Faivre et al. 2016). Coastal sage scrub communities located near the coast, such as those in this study, may be more resistant to vegetation-type conversion due to less nitrogen deposition, longer fire intervals, or greater water availability (Keeley et al. 2005b, Fenn et al. 2010). Within our sampling area, the near-coast locations had higher native shrub cover and a greater proportion of native species than the inland areas sampled, lending further support to the idea that proximity to the coast may reduce vegetation-type conversion from shrub to grassland, despite coastal sage scrub transects showing the most variability in our data set. Within the inland region, transects located in chaparral were characterized by a greater

proportion of native species than coastal sage scrub transects, which fits with other studies indicating low invasibility and long-term persistence of chaparral vegetation (Keeley 1992, Callaway and Davis 1993).

There was a slight decline in the cover of native perennial bunchgrasses over the last 10 yr, suggesting that persistence of native grasslands is a management concern. California native grassland (aka prairie) habitat has been heavily invaded by non-native species in the past, such that native *S. pulchra* has been replaced by Eurasian species of *Bromus, Avena, Erodium,* and other genera (Bartolome et al. 2007). Restoration practitioners have found that native grasslands are more challenging to restore than shrub-dominated habitats (Holl et al. 2014, Kimball et al. 2015). This may be because native shrubs, once established, more effectively exclude invasive species than native grasses and forbs (Goldstein and Suding 2014). Thus, the ability to assemble grassland communities using species combinations that introduce native resistance and resilience in the face of non-natives is a challenge for restoration.

Native grasslands consist of a huge diversity of native annual forbs, such that any restoration

efforts must focus on these species as well. Native forbs reached highest cover in wet years that were preceded by dry years, as indicated by multiple regression with current and previous growing season precipitation as continuous variables. It may be that the non-native invasive grasses, which responded positively to rain, outcompeted native forbs when the seed bank was saturated with non-native grass seeds. The invasive grasses germinate before most native forbs, giving them a competitive advantage in years when they have abundant seeds in the soil (Wainwright et al. 2012, Balshor et al. 2017). However, the non-native forb *Brassica nigra* also had highest cover in wet years preceded by dry years according to our multiple regression, indicating the ability of non-native forbs to increase when released from competition by non-native grasses (Cox and Allen 2011).

Our second research question asked how the cover of particularly problematic non-native species and the proportion of native to non-native species changed through time and space. The cover of particularly problematic non-native species and the proportion of native to non-native species is a key indicator of habitat quality used by practitioners assessing conservation management impacts (Diffendorfer et al. 2007, NCC 2016). The consistency observed in the proportion of native species in chaparral and coastal sage scrub transects over ten years supports the resistance of these communities, yet the significant fluctuations in species composition, especially the high variation in degree of fluctuation for coastal sage scrub transects, demonstrates reversible changes (resiliency) in species composition (Bagchi et al. 2017). The significant decline in the proportion of native plants for the grassland transects points to a concern regarding native grass persistence, yet investigating the variance of transects through time in species space demonstrated that grassland transects have not experienced significant variance and appear to be stable as a highly invaded community type that may be difficult to restore to a native-dominated community (Suding et al. 2004). One benefit of annual monitoring is the power to detect new invasions and monitor existing problematic invasive species (Dewey and Andersen 2004). The recent increase in *Salsola tragus* is a management concern, pointing toward

the need for research on its impact on natives. Continued monitoring will determine whether the increase of *S. tragus* is a long-term trend. This species is a problematic invader throughout the Western United States, and researchers have identified a biocontrol method that may be a management option in the future (Berner et al. 2014). *Cynara cardunculus*, which was problematic in the decades prior to this monitoring, had very low cover in all monitored areas.

Our third question asked how vegetation responded to fire and drought. We answered this by comparing transects that burned with those that did not and comparing vegetation from transects sampled before and after the drought. The Santiago fire burned some transects that were sampled in 2007, enabling us to compare vegetation in burned and unburned transects, although not with high replication and focusing primarily on coastal sage scrub and grassland communities. The burned transects had significantly lower native shrub cover than unburned transects in March 2008 (the fire occurred in late October to early November 2007), but the difference disappeared by March 2011, although species composition shifted following fire to favor *Acmispon glaber* rather than *Artemisia californica*. These temporal patterns are consistent with the timescale recorded in other regional studies documenting shrub recovery following wildfire (Westman 1981, Keeley and Keeley 1984, Keeley et al. 2005b) and an experimental approach manipulating rainfall to high and low levels following the Santiago fire (Kimball et al. 2014). It is possible that burned transects recovered earlier than 2011, but we cannot say for sure, because a decision was made to not sample them (for fear of disturbing recovery efforts) in 2009 or 2010. When transects from both communities were combined for analysis, there was a significant fire-by-year interaction ($F_{6, 116} = 2.58$, $P = 0.022$) driven by a post-fire increase in forbs. This high forb density following fire is due to increased seed germination and is an important part of the recovery process (Keeley 1991, Hanan et al. 2016). In general, despite a sampling design not optimized for understanding the impact of fire, our data support the experimental work on recovery from fire in the literature to date.

Burned transects had significantly more non-native annual grasses than unburned transects in

the grassland community in all years, suggesting that the non-natives were able to take advantage of open spaces and persist in greater numbers through time. Fire has been used as a restoration tool in California grasslands, with early spring burning most effective at reducing non-native annual grasses (Meyer and Schiffman 1999, Berleman et al. 2016). The Santiago fire was in late fall (end of October through November), so the timing of the burn was not optimal for reducing non-native grass seeds. In coastal sage scrub, the non-native grasses had lower cover in burned transects compared to unburned transects in the years right after the fire, but the pattern flipped after 2012, and burned transects had higher cover of non-native grasses. It was surprising that non-native grasses were not higher in burned transects right after the fire, because invasive grass cover has been found to be higher in coastal sage scrub sites with more frequent burning (Keeley et al. 2005a, Talluto and Suding 2008). However, our results may be explained in the context of non-native grass abundance fluctuating with precipitation. The year of the fire was very dry, and rainfall increased gradually along with shrub recovery, likely influencing the relative performance of native and non-native species.

While we might expect that areas with higher native cover would be more resilient to drought, instead we found that these transects were more negatively impacted by the recent reductions in precipitation. This was a surprise, because sites with the highest native shrub cover are generally considered to have greater biological integrity and to be more resilient (Miller et al. 2006, Diffendorfer et al. 2007). We found that the more transitional grass-shrub transects exhibited an increase in shrub cover. This may be due to lower soil moisture in areas with high shrub density, where established shrubs draw down most available soil water (Parolari et al. 2015). Our results fit with another study in the region, in which the proportion of dead shrubs during the recent drought was significantly greater in areas with high cover of living shrubs than in areas with lower shrub cover (Lulow 2017). These findings suggest that shrub communities with a lower % cover of native shrubs may have greater resilience under future climatic conditions that involve more frequent drought. We also observed a decrease in the cover of grasses in

response to the drought, something that was observed in another study in Orange County (Kimball et al. 2017).

Conclusions

Annual monitoring data revealed resilient native shrub communities faced with fire and non-native species and degrading native perennial bunchgrasses responding to invasion by non-native species and drought. Native shrubs were generally able to recover from wildfire within several years and maintained high cover in years of extreme drought, although areas with highest shrub cover demonstrated lower resilience and were more likely to experience drought-based mortality. Non-native grasses were a persistent problem, especially after fire in grasslands, and native diversity increased in years with high rainfall without heavy invasive grass seed banks. Based on our results, we expect continued annual monitoring to reveal additional patterns of long-term population dynamics in response to novel weather combinations and other disturbances.

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