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BIODIVERSITY RESEARCH

Regional and temporal patterns of natural recruitment in a California endemic oak and a possible 'research reserve effect'

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ABSTRACT

Aim The perceived absence of young cohorts in many long-lived trees, particularly *Quercus* species, has raised concerns about their long-term viability. While there is a robust body of literature on valley oak (*Quercus lobata*) planting experiments, conducted mainly on research reserves, an assessment of natural recruitment across a range of climate and land use types has been lacking. At a regional scale over time, we explored patterns of natural recruitment in this endemic California oak reported to be experiencing persistent recruitment failure.

Location California.

Methods We conducted a regional-scale study, including dendroecology and historical resurveys, field surveys and published planting experiments to elucidate the prevalence, timing, distribution and relation to environmental drivers of valley oak sapling recruitment.

Results We detected a substantial increase in the presence of recruitment over time at 10 sites originally surveyed between 20 and 40 years ago (sites with sapling recruitment increased from 10% to 70%), potentially related to a corresponding period of relatively wetter years. We found saplings recruiting from a range of years in a variety of land management regimes, and surprisingly, sites designated as research reserves had lower recruitment than other sites. Sapling recruitment did not appear to be synchronous or episodic.

Main conclusions Our results indicate that sapling recruitment failure is not a persistent condition across our sites, and long-term conservation prospects for the species may be better than previously reported. Research reserves had lower natural sapling recruitment and lower seedling survival in experimental controls than other sites, and our findings highlight the importance of field data from sites with a representative range of climate and land use regimes.

Keywords

Demography, population dynamics, *Quercus lobata*, recruitment failure, research reserve effect, research reserves.

INTRODUCTION

Forest declines are occurring world-wide (Allen *et al.*, 2010) and projected to increase (Williams *et al.*, 2012). Recruitment failure of seedling and saplings has been observed in multiple tree genera across North America: *Populus* (Ripple & Larsen, 2000), *Acer* (Belden & Pallardy, 2009), *Pinus* (Perrakis & Agee, 2006) and others (Lopez & Terborgh, 2007). *Quercus* species appear particularly prone to recruitment failure globally (Saxena *et al.*, 1984; Loftis & McGee, 1993; reviewed in Abrams, 2003). In California, our case study species, valley oak (*Quercus lobata*), is reported to be experiencing persistent recruitment failure (Tyler *et al.*, 2006; Zavaleta *et al.*, 2007). We examine regional-scale, long-term trends in valley oak sapling recruitment, as an indicator of the overall future viability of California valley oak woodlands.

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Endemic to the California floristic province, the estimated current distribution spans the California Coast Ranges, Central Valley and Sierra Nevada foothills (Griffin & Critchfield, 1972), all in a Mediterranean climate with rainy winters and summer droughts. Valley oak appears to be declining with potential impacts on other native species and ecosystem services (Pavlik *et al.*, 1991). Mortality rates in adults outpace observed recruitment of young individuals into the canopy (Brown & Davis, 1991; Whipple *et al.*, 2011) and > 85% of past survey studies reported the complete absence of saplings in natural populations (Zavaleta *et al.*, 2007). Most of the species distribution occurs on private rangelands (Zack, 2002), making the study and conservation of this species uniquely challenging.

Experimentally, several drivers have been shown to impact valley oak seedling performance, including wild herbivores, domestic grazers, herb competition and water availability (reviewed in Tyler *et al.*, 2006; Davis *et al.*, 2011). In natural populations, McLaughlin & Zavaleta (2013) showed that within-site microenvironmental factors including groundwater availability and small mammal distributions were associated with sapling recruitment at the local scale.

Changes in California oak woodlands since European settlement can help explain perceived valley oak recruitment failure. Invasive annual grasses now dominate an understorey thought to have consisted previously of native forbs and grasses (Gordon *et al.*, 1989). These exotic grasses compete more strongly for water with young oaks than natives (Gordon *et al.*, 1989; Danielsen & Halvorson, 1991), create layers of thatch inhibiting natives (Huenneke *et al.*, 1990) and are favoured over natives by increases in atmospheric N deposition (Allen *et al.*, 2002). Temperatures have increased approximately 1 °C regionally (Ladochy *et al.*, 2007), and ground water levels have decreased (Howard & Merrifield, 2010), potentially lowering moisture availability to oaks that tap the water-table directly (Miller *et al.*, 2010). Increased tropospheric ozone levels may impact seedling physiology and reduce water use efficiency (Grulke *et al.*, 2007). Additionally, changes to fire regime (Keeley & Fotheringham, 2001; Anderson, 2007) and a shift in dominance of wild to domestic grazers (Anderson, 2005) also may have impacted recruitment.

Rare large-scale episodic recruitment events have been proposed as an explanation for observed long gaps in regional recruitment in California oaks (Mensing, 1988; McClaren & Bartolome, 1989). With such a reproduction strategy, absence of young cohorts would be a 'normal' condition in most populations most of the time. Valley oak acorn masting is regionally synchronous (Koenig & Knops, 1998), potentially facilitating regional-scale mass recruitment events after heavy mast years. However, the episodic recruitment theory has not been tested across sites in natural populations of valley oak.

Recruitment in valley oaks appears to have been limited for decades, but research gaps have prevented a comprehensive assessment of the species' conservation status (Tyler *et al.*, 2006). Early observational work documented demographic patterns but did not relate environmental factors to recruitment. Experimental work has focused on identifying mechanisms for recruitment failure; however, most studies were conducted at a handful of research reserves, a limited representation of the species distribution (Tyler *et al.*, 2006).

In this study, we explored regional patterns of valley oak sapling recruitment over time with a set of historical surveys, current field surveys, dendroecology and Geographic Information Systems (GIS) analysis. We addressed gaps in the research by assessing the current recruitment status of valley oaks in natural populations over a range of land use and climate. We addressed the questions of (1) how sapling recruitment in valley oak woodlands has changed over the past 40 years; (2) whether recruitment patterns are explained by changes in fire, land management or climate; and (3) whether sapling establishment patterns are consistent with the theory of episodic recruitment: synchronous within or across sites, confined to particular years or related to specific regional-scale events.

METHODS

We focused our field study on sapling rather than seedling recruitment to target the reproduction bottleneck in valley oak (Tyler *et al.*, 2006). Saplings were defined as between 1 and 9 cm at base diameter and > 0.5 m (with no maximum) height (Zavaleta *et al.*, 2007). Saplings have a greater chance than seedlings of surviving herbivory (Bartolome *et al.*, 2002), drought (Mahall *et al.*, 2009) and fire (Swiecki & Bernhardt, 2002), making sapling recruitment a better indicator of future population viability.

Field sites

All survey sites were 'natural populations' of valley oak (not planted or manipulated), had dominant valley oak cover and an understory dominated by exotic annual grasses (primarily *Bromus* spp. and *Avena* spp.). We conducted resurveys of 10 historically surveyed valley oak woodlands (Fig. 1) identified by Zavaleta *et al.* (2007), conducted between 1975 and 1989. Surveys were selected based on willingness of land owners to allow access and availability of sufficient original data. We compared the presence/absence of saplings, as data on densities were insufficient in the original surveys. Sites were approximately 1 km^2. We identified sites as 'recruiting' when there was more than 1 sapling within 1 km^2. Recruiting resurvey sites ranged in sapling densities between 2 and 179 saplings per km^2. We also included another set of field sites selected based on the presence of sapling recruitment (Fig. 1), which were not resurveys but instead were identified by a phone/email survey of land managers and site visits. We contacted 215 land managers based on the GIS layer of land use across the species distribution – including parks and reserves staff, ranchers and ranchers' organizations, NGOs and Native Plants Society chapters – and found 19 targeted sites with recruitment. We excluded areas that were within 5 m of human disturbance such as roads because of association of these areas with increased recruitment (Kuhn, 2010) and to ensure that our study areas could support a viable adult oak woodland. We also excluded areas with mixed *Quercus lobata* and *Quercus garryana* adults, which overlap in the northern part of the *Q. lobata* distribution, and have morphologically similar saplings, making field identification unreliable. Thus, the distribution of our sites does not represent the entirety of the species distribution, and our conclusions are most applicable to the western/central and southern portions of the distribution. Surveys were conducted between late May and August of 2009.

Field surveys

In resurvey sites, we established 10 randomly located 50-m-diameter plots, centred on an adult valley oak. In each 50-m plot, we established a randomly located 6-m-diameter plot. We mapped each 6-m plot and counted valley oak seedlings, gopher mounds and ground squirrel holes. To quantify herbaceous vegetation, three 1-m-diameter subplots were placed at random throughout each 6-m plot, in which we measured vegetation height at three random points. In all sites with valley oak sapling recruitment, a field crew conducted a sweep of the entire site and took geographic coordinates for all valley oak saplings. To explore factors associated with successful recruitment, 6-m-diameter plots (sampled as described above) were randomly established throughout the recruiting areas, with approximately one plot per 1500 m^2.

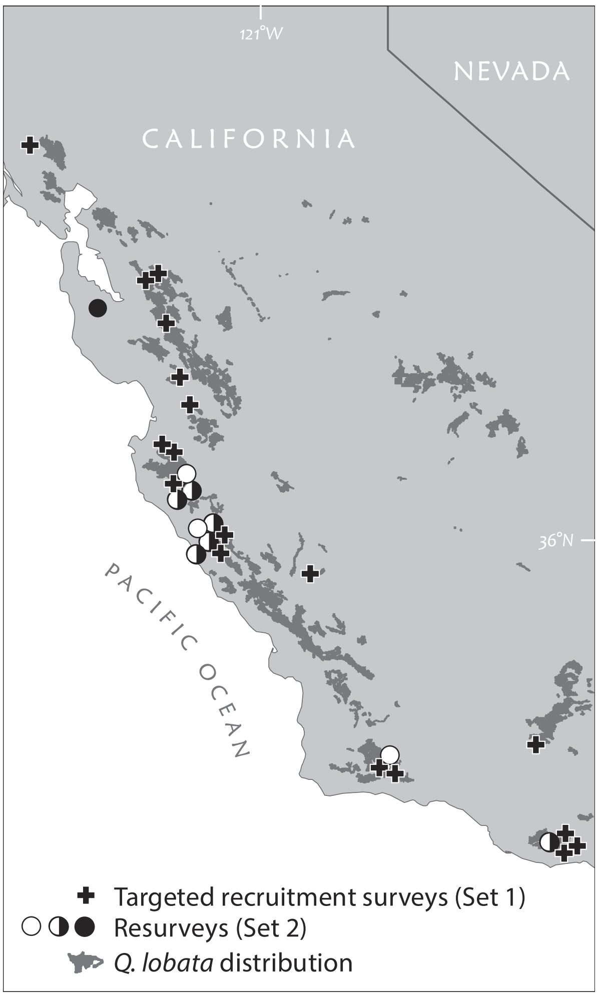

Figure 1 Map of study sites and valley oak central and southern distribution, California, USA. Crosses represent targeted recruitment survey sites identified by land stewards. Circles represent resurvey sites. Black indicates recruitment is present and white indicates recruitment is absent. The left half of the circle represents the site's recruitment status in the original survey and the right half represents recruitment status in our 2009 resurvey.

Dendroecology

We obtained sapling samples for dendroecological analysis whenever land managers would permit. We sampled saplings from one of our resurvey sites as well as from a subset of targeted recruitment field sites. When possible, saplings were randomly selected within patches of high-density recruitment; however, land manager preferences also directed selection. We selected 2–6 saplings at a total of 10 sites that spanned a range of climate and land use, and cut saplings at base ($N = 43$). We measured diameter at base and height of each sample. Diameter measurements did not include bark. We used the bottom surface for ring analysis. We sanded each sample and counted and measured each ring under a microscope. We recorded a date of establishment based on the earliest year present. Because oak seedlings may resprout after the stem has been browsed (Tyler *et al.*, 2006), our establishment dates do not necessarily represent the date of seedling emergence, but represent the year in which the seedling developed a persistent stem. The stem ages we present represent a minimum and estimated age for our sampled individuals. We compared establishment dates with the year-specific average precipitation (PRISM Climate Group, Oregon State University, created 2009), fire history (Calfire FRAP data, updated 2009, http://www.frap.fire.ca.gov) and valley oak masting data from 1994 to 2009 (W. Koenig, unpublished data).

GIS analysis

We used ARCGIS 10 (ESRI, 2010) for GIS analysis. We used the CA Gap analysis (UCSB biogeography laboratory 1998, updated 2002) to identify the extent of valley oak distribution, and we created our own GIS layer with our mapped study site centres, plots centres and all saplings. We used PRISM (PRISM Climate Group, Oregon State University, created 2009) 30-year means for average annual precipitation and maximum August temperatures and data from individual months/years when specified. For fire history data, we used Calfire FRAP data, updated 2009 (http://www.frap.fire.ca.gov).

Literature survey

To explore what percentage of studies were taking place at the three research reserves identified by our study to have low recruitment (Hastings Reserve in the Carmel Valley, Sedgwick

Reserve in Los Olivos and Jasper Ridge Biological Preserve in Palo Alto), we conducted a Web of Science and Google Scholar search for the terms 'valley oak' and '*Quercus lobata*'. We included in our analysis, all available published studies from these searches in which valley oak was the species of focus of original research. We excluded greenhouse and container studies. We found a total of 60 studies conducted between 1973 and 2012. We calculated the percentage of these studies conducted at the three research reserves. We estimated the percentage of the valley oak distribution represented by these three reserves based on the reported reserve size and the extent of valley oak woodlands and compared these to estimates of the current valley oak distribution (Davis *et al.*, 1998).

To explore whether there was evidence of a 'research reserve effect' in experimental data consistent with the differences we saw in our resurveys, we also analysed a subset of planting studies reporting % survival after 1 year in the control treatments for *Q. lobata* and closely related *Q. douglasii,* in the areas of the species distribution covered by our study. We used both species to increase the power of the data set and because qualitatively the species showed similar results individually. We averaged studies at the same site conducted in the same year, but treated separate studies from different years at the same site as independent (research reserves = 7 studies, 2 sites; non-research reserve = 14 studies, 7 sites).

Statistical analysis

We used a Fisher's exact test to compare counts of recruiting and non-recruiting sites during the first set of surveys and the 2009 resurveys. To explore overall changes in regional climate, land use and fire history potentially driving the overall increase in sites with sapling recruitment, we compared the 15-year periods before each original survey to the 15-year period between 1990 and 2005, based on the age of our youngest sapling sample (subsequently we refer to this time period as the '15 year period before the second surveys'). We compared fire history (the presence/absence of a major fire), mean average annual precipitation and grazing status (the presence/absence of grazing, as we did not have sufficient information to evaluate grazing intensity or timing). The duration of the 15-year time period was established by the difference in recruitment age of the oldest and youngest sampled saplings (Fig. 2). We used a paired, two-tailed *t*-test to compare the mean climate values before the 1st and 2nd sets of surveys and a Pearson's Chi-Square test to explore differences in the presence/absence of a major fire and the presence/absence of grazing.

To examine differences between the resurvey sites that had recruitment and did not have recruitment in the 2009 surveys, we used a stepwise logistic multiple regression model to explore relationships between the presence/absence of recruitment and the main effects and interactions of the following variables: small mammal activity, herbaceous vegetation height, average annual precipitation, fire, grazing, time since original survey and precipitation crossed with grazing and

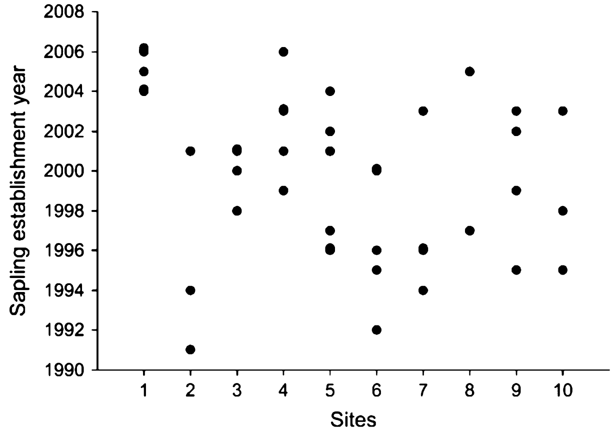

Figure 2 Stem age of valley oak saplings collected at field sites. The *x*-axis represents individual sites where saplings were sampled, and the *y*-axis shows the estimated stem age (ring count) for each sapling. Sapling recruitment took place in at least one of the sample sites in every year between 1991 and 2006 and in multiple years within individual sites.

small mammal activity. To compare whether the same variables predicted densities of saplings or seedlings, we used a stepwise general linear model with the same terms listed above. In all models terms were included up to a significance of 0.15. To explore specific differences in recruitment between research reserves and other sites, we tested whether seedling and sapling densities at sites designated as research reserves were different than non-research reserves using a two sample 2-tailed separate variance *t*-test (Welch's method).

To determine whether sapling establishment (stem age) was associated with wetter-than-average precipitation years, we compared the ratio of site-specific precipitation from the establishment year, determined by our dendroecological samples, to the site-specific average precipitation for all years in which we recorded that sapling establishment took place (1991–2005) to 1 in a 1-tailed, one sample *t*-test. We also used a general linear model to examine whether fire history (year of a major fire), valley oak annual masting and site- and year-specific precipitation predicted establishment dates, including 1-year time lags for each factor.

To explore differences between seedling survival rates in planting study control plots on and off research reserves, we conducted a separate variance two-sample, two-tailed *t*-test (Welch's method). In all data, we checked for violations of normality and transformed when necessary. All statistical analyses were performed using SYSTAT 12 (Systat Software Inc., 2007, San Jose, CA, USA).

RESULTS

Resurveys

There was a significant increase in sites with sapling recruitment between the original surveys and our 2009 resurveys, with 10% of sites recruiting in the first set of surveys and

70% of sites recruiting in the second set of surveys ($P = 0.02$; Table 1). Across the resurvey sites, the 15-year time period before the second (2009) survey was wetter than the 15-year time period before the first survey ($P < 0.0001$, $t = 9.4$, $N = 10$, DF = 9). We did not find significant differences in grazing or fire during the periods preceding each set of surveys ($P > 0.05$).

In comparing the sites that did and did not support sapling recruitment in the 2009 resurveys, our multiple logistic regression model did not detect significant differences in precipitation, small mammal activity, vegetation height, fire history, the presence/absence of grazing or the interaction terms. Our general linear models (using the same terms listed above) did not predict seedling or sapling densities across resurveys sites.

Research reserves had lower sapling densities ($N = 3$, mean 0.66 saplings per km^2, SE = 0.66), than sites that were not research reserves ($N = 7$, mean 76 saplings per km^2, SE = 25.1; $P = 0.02$; Fig. 3) Two of the research reserves supported no sapling recruitment and the other supported densities of two saplings per km^2. Of the non-research reserve sites, six of seven supported sapling recruitment at densities of 21 saplings per km^2 or above. In the set of targeted sites with recruitment (separate from the resurvey sites), the mean number of saplings was 189 per km^2 ($N = 19$, SE = 57.6). We did not detect differences in seedling densities between research reserves and other sites.

Dendroecology

Sapling establishment was not restricted to particular years, took place in at least one of the sampled sites in every year between 1991 and 2006 and occurred in multiple years within each individual site (Fig. 2). There was a weak association of establishment with years of higher than average rainfall ($P = 0.06$, $t = 1.5$, $N = 43$, DF = 42). Precipitation, fire history and masting (with 1 year time lags) did not predict years of establishment in a general linear model.

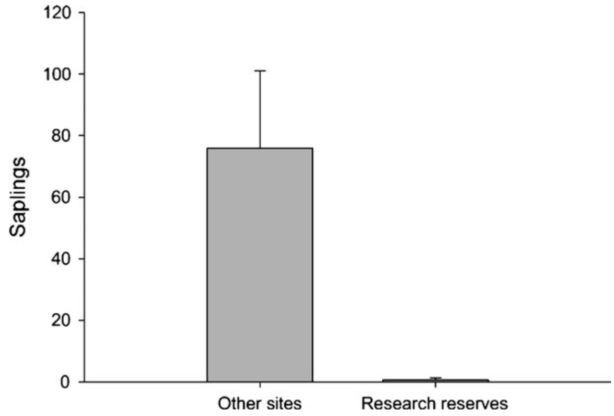

Figure 3 Valley oak saplings per km^2 on resurvey sites, showing research reserves and other mixed land use sites. Error bars show 1 standard error.

Studies on research reserves

Of the field studies identified through our literature search, 43% took place on one of the three research reserves in our resurvey study. Over the past decade (2002–2012), this percentage increased to 59%. These three research reserves represent approximately 3% of the spatial extent of the species distribution. Of planting studies conducted on and off research reserves on blue and valley oaks, seedling survival in control plots after 1 year was lower on research reserves that on other sites ($P = 0.004$; Fig. 4).

Table 1 Survey sites with environmental factors before the original surveys 'Surveys 1' and our 2009 resurveys 'Surveys 2'.

	Surveys 1				Surveys 2					
Site	Saplings (per km^2)	Precip (mm)	Grazed	Fire	Saplings (per km^2)	Precip (mm)	Grazed	Fire	Seedlings (per km^2)	Small Mammals (per m^2)
Poison Oak Hill$_R$		589				683			0	10
Sedgwick$_R$		552				638			1898	1.6
SA2		547				660			89	6.6
Plasket Ridge		486			21	683			331	24.7
Bear Trap		780			54	917			76	5.4
Chews Ridge		905			148	983			12	14.7
Nacimiento		526			179	617			318	12.9
SA1		512			42	611			178	5.8
Cheseboro		479			88	514			2942	14.9
Jasper Ridge$_R$		615			2	694			140	7.2

In the 'Saplings' columns, dark grey represents the presence and white represents the absence of saplings; numbers represent saplings per km^2. The 'Precip' columns represent the site-specific average annual precipitation (mm) for the 15-year periods before each survey. In the 'Grazed' and 'Fire' columns, light grey represents the presence and white represents the absence of grazing/fire in the 15-year period before each survey. The 'Seedlings' column represents seedlings per km^2. The 'Small Mammals' column represents the mean number of gopher mounds and ground squirrel holes per m^2 In the 'Site' column, 'R' designates sites that are research reserves.

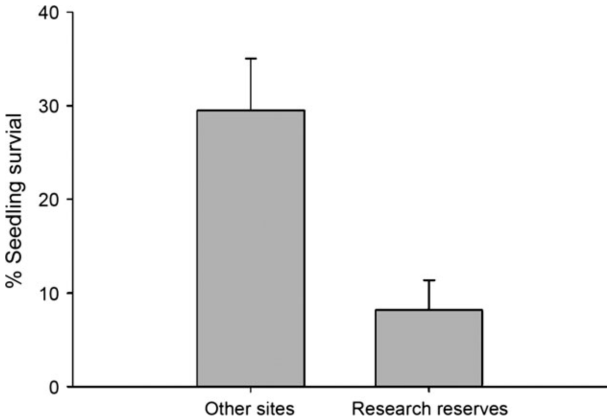

Figure 4 Percentage seedling survival after 1 year in controls of planting experiments of *Quercus lobata* and *Quercus douglasii* on research reserves and non-research reserve sites. Error bars show 1 standard error.

DISCUSSION

Valley oak saplings recruit today in a variety of land use types and climates and are more prevalent than previously reported (Table 1). Our results are consistent with an expected positive association between oak performance and higher moisture availability (Griffin, 1976; Tyler *et al.*, 2006; Davis *et al.*, 2011; McLaughlin & Zavaleta, 2012). Precipitation was higher in the 15-year time period preceding the 2009 resurveys than in that preceding the original surveys, indicating that the increase in recruitment during the second set of surveys may have been related to a period of relatively wetter years. We also note that our resurvey sites represent a disproportionately wet portion of the species distribution and thus may overestimate sapling recruitment in the species. However, sites that increased in recruitment were not significantly wetter than sites that did not increase in recruitment, indicating that interactions between precipitation and other factors that we have not identified in this study likely also are driving recruitment.

We did not detect significant associations of fire, grazing or other biotic factors with recruitment. This may have been due to our low N and low power to detect small effect sizes. Our results, at the regional scale, were contrary to studies of within-site patterns of recruitment, showing effects of small mammal herbivory, and interactions between precipitation and small mammal herbivory and competition from herbaceous vegetation (McLaughlin & Zavaleta, 2013). The differences in whole site versus within-site results suggest that different factors may control sapling recruitment at different scales. Recruitment at each site may be responding to different drivers, or these drivers may be interacting with each other, consistent with the 'multiple interacting hypothesis' recently proposed by McEwan *et al.* (2011) for recruitment in eastern North American oak forests. For example, in our system, grazing may impact recruitment differently at mesic versus xeric sites. We discuss below some trends within climatically grouped sites to prompt further research (Table 1).

The three wettest of the 10 resurvey sites, located in the Los Padres National Forest (Chews Ridge, Bear Trap and Plaskett Ridge), increased in sapling recruitment between the first and second surveys. Changes in climate and fire between surveys could explain this increase. Precipitation was higher in the time period before the second survey than the first, and fire was present in the time period before the second survey but absent in the time period before the first. Additionally, all three sites experienced one of the largest fires on record between survey periods. The original survey paper for these three sites reported dense growth of pines (*Pinus coulteri*) in the understorey and suggested that pines might eventually replace the oaks (Griffin, 1976). However, we did not detect dense pine growth in the understorey (unpublished data). A lack of fire in these sites prior to the first survey may have favoured pines that can inhibit oak recruitment (Van Lear & Watt, 1993; Barton, 1999). The fire in 1977, followed by a series of six consecutive wetter-than-average years, may have created conditions for a persistent oak seedling bed, reduced competition from pines and facilitated a subsequent increase in oak sapling recruitment. Grazing, present continuously before both surveys, does not appear to have driven the change in recruitment in these sites. Higher precipitation sites may be more resilient to grazing because saplings are less restricted to surface water than in dryer sites (McLaughlin & Zavaleta, 2013), reducing the impacts of cattle convergence around riparian areas.

The three drier resurvey sites that increased in sapling recruitment were Cheseboro Canyon, in the Santa Monica Mountains, and two sites in Fort Hunter Liggett Military Reservation, San Antonio 1 and Nacimiento. While none of these sites experienced a major fire between surveys, there were changes in all three sites in climate and grazing. Precipitation was higher in the time period before the second surveys than before the first. All three sites were grazed before the first surveys, and managers at these sites estimated that grazing was removed 15–20 years prior to the resurveys. Recruitment at each of these sites was highly constricted around surface water (McLaughlin & Zavaleta, 2013). Thus, cattle congregation around surface water may have had a higher impact on recruitment. This potential interaction between grazing and climate on recruitment has been suggested by experimental studies where winter/spring grazing was beneficial to oak seedling performance when cattle were removed during the driest part of the season (Tyler *et al.*, 2008). Additionally, land stewards at our sites reported that cattle browse oaks more intensively later in the season when other green forage is less available. Our results indicate that this interaction may occur with spatial variation in climate as well as seasonal variation in rainfall.

Episodic recruitment?

Episodic recruitment events in response to regional drivers have been proposed as a possible explanation for the observed absence of oak saplings (Mensing, 1988; McClaren

& Bartolome, 1989). However, our dendroecology results support an argument for the importance of site-specific conditions over an episodic regional-scale driver of recruitment. We saw high asynchrony both across and within sites in the timing of establishment (Fig. 2). Establishment occurred in at least one site in every year over the time period covered by our samples, and there were multiple establishment dates in each individual site. We found a weak correlation between establishment years and wetter-than-average years, but also saw some establishment in dryer-than-average years, indicating that precipitation may be an important but not synchronous driver of recruitment across sites. We saw no correlations between fire or grazing history and establishment dates.

As Davis *et al.* (2011) suggest, episodic recruitment could occur in response to complex suites of events such as synchronously timed wet years, masting and reduced herbivory. Such events may create seedling banks with extensive root structures that remain in the seedling size class for many years. The recruitment of persistent seedling banks after high rainfall and mast years could allow seedlings to establish and then take advantage of subsequently reduced herbivore pressure (MacDougall *et al.*, 2010; Davis *et al.*, 2011) or other favourable local conditions. We found that seedling densities did not differ between sites with and without sapling recruitment, consistent with the theory that the reproductive bottleneck in this species is at the sapling stage (Tyler *et al.*, 2006; Zavaleta *et al.*, 2007). Our findings support the theory that sapling recruitment is responding to factors distinct from those controlling seedling recruitment (Davis *et al.*, 2011), and the presence of seedlings may not ensure successful recruitment into the adult population.

A research reserve effect?

Surprisingly, research reserves supported lower levels of recruitment than other sites. Had we focused our study on the research reserves alone, we would have concluded that sapling recruitment in valley oaks was absent or rare. This potential 'research reserve effect' was observed across three data sets: (1) in resurveys, natural sapling recruitment was lower on the research reserves; (2) none of our naturally recruiting sites identified by land managers were located on research reserves; and (3) seedling survival in experimental controls was lower on research reserves than on other sites.

Our resurvey study showed a substantial difference in densities of sapling recruitment between research reserves and other sites (Fig. 3); however, we note that the Jasper Ridge site was in fact the only site to have supported at least low levels of sapling recruitment across both the historic and current surveys. Separate from our resurvey sites, we found 18 naturally recruiting sites, none of which were on research reserves. These naturally recruiting sites showed mean sapling densities more than double the levels at research reserves. However, the methods for finding these recruiting sites were not designed to evaluate the impacts of different land use types, and our research reserve sample was limited compared with other land use types, potentially biasing our results. Finally, lower seedling survival (evident in planting experiment controls) on research reserves may slow the accumulation of a seedling bank and ultimately be related to observed patterns of very low sapling recruitment. The absence of a comparable seedling recruitment difference between research reserves and other sites in our field surveys could be because we included seedlings of any age, whereas the experimental data only included those surviving > 1 year.

Two possible explanations could account for the 'research reserve effect' we observed: (1) the marginal lands hypothesis – that reserves tend to be more marginal habitats, at higher elevation and with lower productivity than private lands (Scott *et al.*, 2001) or (2) that a management regime particular to research reserves is contributing to lower recruitment. While the research reserves in question do not appear to be marginal habitats topographically or in terms of herbaceous productivity, there may be differences in other less visible factors, such as groundwater hydrology. In terms of management, a common characteristic that differentiates the research reserves from the other sites is a low-disturbance regime. Research reserves in our study were managed mainly as 'natural protected areas', excluded hunting, domestic grazing and heavy recreation (while Sedgwick Reserve allows grazing in selected areas, our survey sites had not been grazed for over a decade). The other sites had higher disturbance regimes, including grazing, active military use, hunting and heavy recreation.

Some previous evidence suggests that recruitment may be enhanced by disturbance. Within-site valley oak recruitment appears to be associated with disturbed areas (pers. obs.), and valley oak saplings have been reported to occur near human development even when absent in nearby woodlands (Kuhn, 2010). A positive impact of disturbance on recruitment could result from decreased competition from herbaceous plants due to grazing or human activity and/or a decrease in wild ungulate browsing due to hunting or deer avoidance of human activity.

Disturbance to herbaceous vegetation may reduce competition from annual grasses, known to be strong competitors with young oaks (Gordon *et al.*, 1989; Danielsen & Halvorson, 1991). Grazing impacts on recruitment are mixed (reviewed in Tyler *et al.*, 2006); however, grazing was beneficial to seedlings when cattle were removed during the driest season (Tyler *et al.*, 2008). The role of disturbance in promoting the success of natives has been demonstrated in other California grassland communities. Gopher disturbance to annual grasses allowed for the re-establishment of native forbs (Hobbs *et al.*, 2004), and cattle grazing reduced exotics and promoted native species (Weiss, 1999; Pasari, 2011). The lower disturbance regime on the research reserves may have led to more productive herbaceous vegetation (herbaceous vegetation height at the research reserves was double that at the other sites, unpublished data) potentially increasing competition with oak seedlings and reducing recruitment.

A management regime favouring wild ungulate herbivores also may impact recruitment (reviewed in Tyler *et al.*, 2006; Davis *et al.,* 2011). Valley oak has been reported as more palatable forage for deer than for cattle (Sampson & Jespersen, 1963), and wild ungulates are more prevalent in protected than in non-protected areas (Leopold *et al.*, 1963; Porter & Underwood, 1999). Human disturbance and development have been shown to reduce deer browse in valley oak woodlands (Kuhn, 2010). Hunting, (allowed by six of the seven other sites) may create a trophic cascade favourable to recruitment, comparable to that identified by Ripple & Beschta (2008), in which puma decreased deer browse and improved recruitment in black oak (*Q. kelloggii*).

Whatever the cause, the demographics on the research reserves are not representative of those across a broader sampling of the distribution, and a focus on data from research reserves with low or absent recruitment could distort perception of the conservation status of valley oak. A disproportionate amount of research is conducted at the three research reserves in our study, relative to the extent of the species distribution. This imbalance increased in the past decade, with close to two-thirds of all studies conducted on these research reserves, under 3% of the area of the species distribution. This trend flags an important consideration for the growing number of ecologists working on research reserves (Hobbie *et al.* 2003). Research reserves create critical infrastructure, invaluable for ecological studies. However, our findings illustrate the potential problems with over-extending conclusions derived from work concentrated in a few sites representing particular ecological conditions.

CONCLUSIONS

Drivers of valley oak recruitment are complex, and further research is needed to understand the mechanisms behind the patterns we identified. Much of the recruitment we documented occurred on grazed and recreational lands; thus, at a regional scale, mixed-use landscape matrices appear to offer viable conservation prospects. Excluding disturbance and managing for 'natural' conditions in systems that have experienced dramatic environmental change since their adult populations established may not optimize conditions for current recruitment. Our results emphasize the importance of complementing recent trends towards a mechanistic focus in ecology (Sagarin & Pauchard, 2010) with natural history and broad-scale observational study.

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