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STAND STRUCTURE AND ACORN PRODUCTION OF THE ISLAND SCRUB OAK (*QUERCUS PACIFICA*)

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ABSTRACT.—Island scrub oak (*Quercus pacifica*), a keystone chaparral species on Santa Rosa, Santa Cruz, and Santa Catalina islands, provides habitat for a diverse assemblage of plant and animal species. The restoration of oak habitat is a management priority, but little is known about *Q. pacifica* stand structure and acorn production, 2 parameters that are important in the species' recovery. To investigate whether species interactions and abiotic conditions have an effect on stand structure and acorn production, we sampled within-stand densities, tree sizes, and acorns in the 3 island populations that have been exposed to different herbivores, seed predators, and climate conditions. Stand densities varied more within than between islands; but Santa Rosa, the coldest of the 3 islands, had smaller trees with smaller acorns than the other 2 islands. To quantify the temporal and spatial variation in acorn production on Santa Cruz Island, we conducted acorn counts at 2 spatial scales: (1) an island-wide survey of 200 trees along the east–west axis of the island (2008–2012) and (2) small-scale surveys within three 100-ha study plots (150 trees; 2009–2012). Acorn production varied strongly, both temporally and spatially, with little temporal synchrony and spatial autocorrelation. Trees at higher elevations produced more acorns, but the roles of temperature and precipitation were unclear in this relatively short study. To increase our understanding of the drivers of *Q. pacifica* acorn production, we propose that annual oak surveys be incorporated into a long-term monitoring program across the California Channel Islands.

RESUMEN.—El roble de la isla (*Quercus pacifica*), una de las especies clave en el chaparral de las islas de Santa Rosa, Santa Cruz y Santa Catalina, proporciona un hábitat adecuado para una gran variedad de especies de plantas y animales. La restauración del hábitat del roble es una prioridad, pero se conoce poco sobre su estructura y la producción de bellotas de *Q. pacifica*, 2 parámetros muy importantes para la recuperación de la especie. Con el fin de investigar si la interacción de las especies y las condiciones abióticas tienen algún efecto sobre la estructura forestal y la producción de bellotas examinamos la densidad de pies, el tamaño de los árboles y el tamaño y producción del bellotas en las poblaciones de las 3 islas, las cuales han estado expuestas a diferentes herbívoros, depredadores de semillas y condiciones climáticas. Las densidades variaron más dentro de la misma isla que entre islas, pero Santa Rosa, la más fría de las 3 islas, tenía árboles más pequeños con bellotas más pequeñas que las otras 2 islas. Para cuantificar la variación temporal y espacial en la producción de bellotas en la isla de Santa Cruz, estimamos la producción de bellotas en 2 escalas espaciales: (1) mediciones de 200 árboles en el eje este-oeste de la isla (2008–2012) y (2) en el interior de 3 parcelas de 100 ha (150 árboles; 2009–2012). La producción de bellotas varió considerablemente, tanto temporal como espacialmente, con poca sincronización temporal y autocorrelación espacial. Los árboles situados a mayor altura produjeron más bellotas, pero el papel de la temperatura y las precipitaciones no quedó claro en este estudio relativamente corto. Proponemos que se incorporen controles anuales de los robles en un programa de monitoreo de larga duración a lo largo de las Islas del Canal de California (o Archipiélago del Norte) con el fin de aumentar nuestro conocimiento sobre la producción de bellotas de *Q. pacifica*.

Oak (*Quercus* spp.) woodlands and chaparral form the majority of woody vegetation on the California Channel Islands and represent an ecosystem of conservation concern (Schoenherr et al. 1999, Knapp 2010a). Restoring native oak habitat is a management priority because these keystone organisms facilitate establishment of other native plants and herbs, as well as harbor an array of vertebrates and invertebrates (Borchert et al. 1991, Knapp 2010a).

Endemic island scrub oaks (*Quercus pacifica* Nixon & C.H. Muller) are the dominant species of chaparral on Santa Cruz, Santa Rosa, and Santa Catalina islands (Junak et al. 1995), yet little is known about their reproductive strategies and interactions with other species (Knapp 2010a, Stratton 2010). We surveyed the 3 island populations for systematic differences in stand structure potentially caused by interactions with herbivores and seed dispersers.

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We also present the first 5 years of data from longitudinal surveys we established to monitor the spatial and temporal variation in acorn production of *Q. pacifica* on Santa Cruz Island.

Oaks have long-lasting effects as ecosystem engineers by changing the biotic and abiotic environment (Jones et al. 1994, Johnson et al. 2009). Carbon and nitrogen deposition enhance available nutrients in the soil (Dahlgren et al. 1997, Fralish 2004). Deep roots and the ability to tolerate water stress allow oaks to establish in seasonally dry areas intolerable to other chaparral species (Davis and Mooney 1986). Acorns provide an important food resource for many animals, including endemic subspecies of the deer mouse (*Peromyscus maniculatus*) and the Island Scrub-Jay (*Aphelocoma insularis*), which occurs only on Santa Cruz Island (Schoenherr et al. 1999). Oak habitat throughout the California Channel Islands is recovering from livestock overgrazing and woodcutting during the 19th and 20th centuries (Schoenherr et al. 1999). Once-common oak woodland and chaparral on Santa Rosa Island were reduced to remnant populations (Lombardo and Faulkner 2000). On Santa Catalina Island, continued herbivory by nonnative ungulates coupled with adult dieback of stem tips have reduced the scrub oak distribution by 31% since 1943 (Knapp 2010b), and a variety of restoration strategies have produced mixed results (Stratton 2010). On the other hand, management actions on Santa Cruz and Santa Rosa islands show promising results. Native vegetation on Santa Cruz Island has experienced a strong recovery following the removal of feral sheep (*Ovis aries*) by the late 1990s and pigs (*Sus scrofa*) by 2007 (Schuyler 1993, Faulkner and Kessler 2011, Morrison 2011). Similarly, since the removal of introduced mule deer (*Odocoileus hemionus*) and Roosevelt elk (*Cervus canadensis*) from Santa Rosa Island in 2011, seedlings of woody species are slowly reappearing in areas where they were long absent (K. McEachern, USGS, personal communication). Nonnative mule deer are still common on Santa Catalina (Schoenherr et al. 1999, Manuwal and Sweitzer 2010).

Acorn production and seed dispersal will likely play an important role in habitat recovery (Stratton 2010), but we have no data on the spatial and temporal patterns of acorn production in *Q. pacifica* and other oak species on the islands. The annual size of

acorn crops varies tremendously in most oaks and is often synchronized over relatively large geographical areas—a reproductive pattern called masting (Koenig and Knops 2000, Kelly and Sork 2002). Masting occurs in response to environmental cues and may be driven by limitations in plants' abilities to pollinate (Kelly and Sork 2002). The temporal variation in seed crops may be an evolved strategy with endogenous cyclical patterns, rather than only a response to environmental cues, but precipitation and temperature also appear to affect pollination and fertilization (Sork et al. 1993, Koenig and Knops 2013). Acorn crop sizes in drought-stressed areas of Florida, for example, appear to be strongly dependent on precipitation (Abrahamson and Layne 2003).

Temperature and seed disperser selectivity have both been suggested as determinants of acorn size (Aizen and Woodcock 1996, Koenig et al. 2009). Plants that depend on few or even a single animal species for dispersal often experience selective pressures created by the disperser's behavior and selectivity (Gómez 2004). Jays are perhaps the most important avian dispersers of acorns, and their local preferences can result in selection pressure on acorn size (Gómez 2004). Acorn germination and survival data suggest that larger acorns are more likely to survive drought and have a greater chance of reaching the seedling stage (Aizen and Woodcock 1996, Bonfil 1998). Acorn sizes decrease with increasing latitude within (Aizen and Woodcock 1992, Koenig et al. 2009) and between species (Aizen and Patterson 1990), mirroring a global pattern across a majority of seed-producing plants (Moles et al. 2007). The latitudinal gradient in acorn sizes across North America could have arisen from differential dispersal of small seeds northward as hardwood populations expanded after glacial maxima (Aizen and Patterson 1990, Aizen and Woodcock 1992). More recent work, however, failed to support this hypothesis, and abiotic parameters such as temperature and precipitation appear to explain the pattern, at least in some oaks (Koenig et al. 2009).

Herbivory, seed dispersal, and seed predation can also affect stand density of oaks. In Wisconsin, ungulate herbivory has been shown to reduce the number of red oak (*Q. rubra*) seedlings. This reduction resulted in lower adult densities and thus affected the structure of whole hardwood forest stands (Rooney and

Waller 2003). Similarly, herbivores negatively affect stand densities of Mediterranean oaks in Spain because many eat oak seedlings (Plieninger et al. 2003). The presence of seed predators can also affect within-stand densities by reducing the number of seeds dispersed by birds (Siepielski and Benkman 2008). Santa Cruz Island has no remaining introduced ungulates that are acorn or seedling predators (Bowen and VanVuren 1997, Schoenherr et al. 1999). Herbivory can cause resprouting in oaks, both in seedlings and in adults (Del Tredici 2001). Therefore, the 3 *Q. pacifica* populations on the Channel Islands may have been equally shaped by browsing, in addition to seed dispersal and seed predation.

We hypothesized that within-stand densities (the number of trees per area of oak habitat) would be greater on islands with prolific long-distance seed dispersers (Santa Cruz) than on the islands with only seed predators and herbivores (Santa Catalina, Santa Rosa). Island Scrub-Jays occur in high densities on Santa Cruz Island, and individual birds cache more than 3500 acorns a year, many of which remain in the ground (Sillett et al. 2012, Pesendorfer 2014). In contrast, other birds that handle acorns occur in low densities on all 3 islands. Northern Ravens (*Corvus corax*) tend to cache carrion, not seeds (Goodwin 1983); whereas Acorn Woodpeckers (*Melanerpes formicivorus*) store acorns in granaries (specialized storage areas in trees), a dead end in terms of seed dispersal (Koenig 1987). If herbivory, not seed dispersal, is the driving factor behind stand densities of *Q. pacifica*, we would expect to find little difference between the islands.

The distribution of *Q. pacifica* lends itself to addressing hypotheses about the drivers of seed size variation and stand structure on a small scale because the islands vary in abiotic parameters, such as temperature and precipitation, as well as in the presence or absence of seed predators, dispersers, and herbivores. In terms of temperature and precipitation, Santa Catalina and Santa Cruz islands experience similar temperatures, whereas Santa Rosa Island is colder, mainly due to localized oceanic currents and fog input (Spalding et al. 2007, Fischer et al. 2009). The annual average temperature from 2002 to 2012 was lower on Santa Rosa (13.02 ± 0.36 °C; mean \pm SD) than on Santa Cruz (15.38 ± 0.62 °C) and Santa

Catalina islands (15.90 ± 0.66 °C; WRCC 2013). Comparing the 3 populations of *Q. pacifica* thus allows us to gain an initial overview of differences between populations and to evaluate the potential role of biotic (dispersal and predation) and abiotic conditions (temperature) in shaping acorn production and stand structure. If temperature drives acorn size, we would expect smaller acorns on Santa Rosa Island, the colder island. In contrast, if seed dispersal affects acorn size of *Q. pacifica*, we would expect Santa Cruz Island acorns to differ systematically from the other 2 populations. We tested our predictions by comparing volumes and size categories of *Q. pacifica* acorns from all 3 islands.

To investigate whether *Q. pacifica* acorn production follows a masting pattern, we determined the spatial and temporal fruiting synchrony of individual trees. We also modeled the relationships between these data and tree characteristics, such as crown size and elevation. This effort establishes a baseline for future studies of *Q. pacifica* acorn production and can inform oak management on the Channel Islands. We also provide data on *Q. agrifolia* for comparison and discussion purposes.

METHODS

Island Comparison

We measured stem density and distribution of crown sizes on Santa Cruz, Santa Rosa, and Santa Catalina islands by using point-centered quarter transects (PCQT; see below) through intact *Quercus* stands (Mitchell and Evans 2006, Siepielski and Benkman 2008; Table 1, Fig. 1). On Santa Cruz Island, we selected 2 stands (one north facing, one south facing) on each of 3 study plots used for a long-term avian study (Caldwell et al. 2013; Fig. 1). These stands were near but not overlapping the areas selected for annual acorn surveys. On Santa Catalina and Santa Rosa islands, we selected stands accessible from roads. For PCQT, points were marked every 50 m (depending on stand size) along straight 300–500-m transects through continuous stands; and at each point, the distance to the nearest oak (taller than 30 cm) in each quadrant (NW, NE, SW, SE) was measured (Mitchell and Evans 2006, Siepielski and Benkman 2008). In September and October 2010 and 2011, we conducted 12 PCQT on Santa Cruz (446 trees)

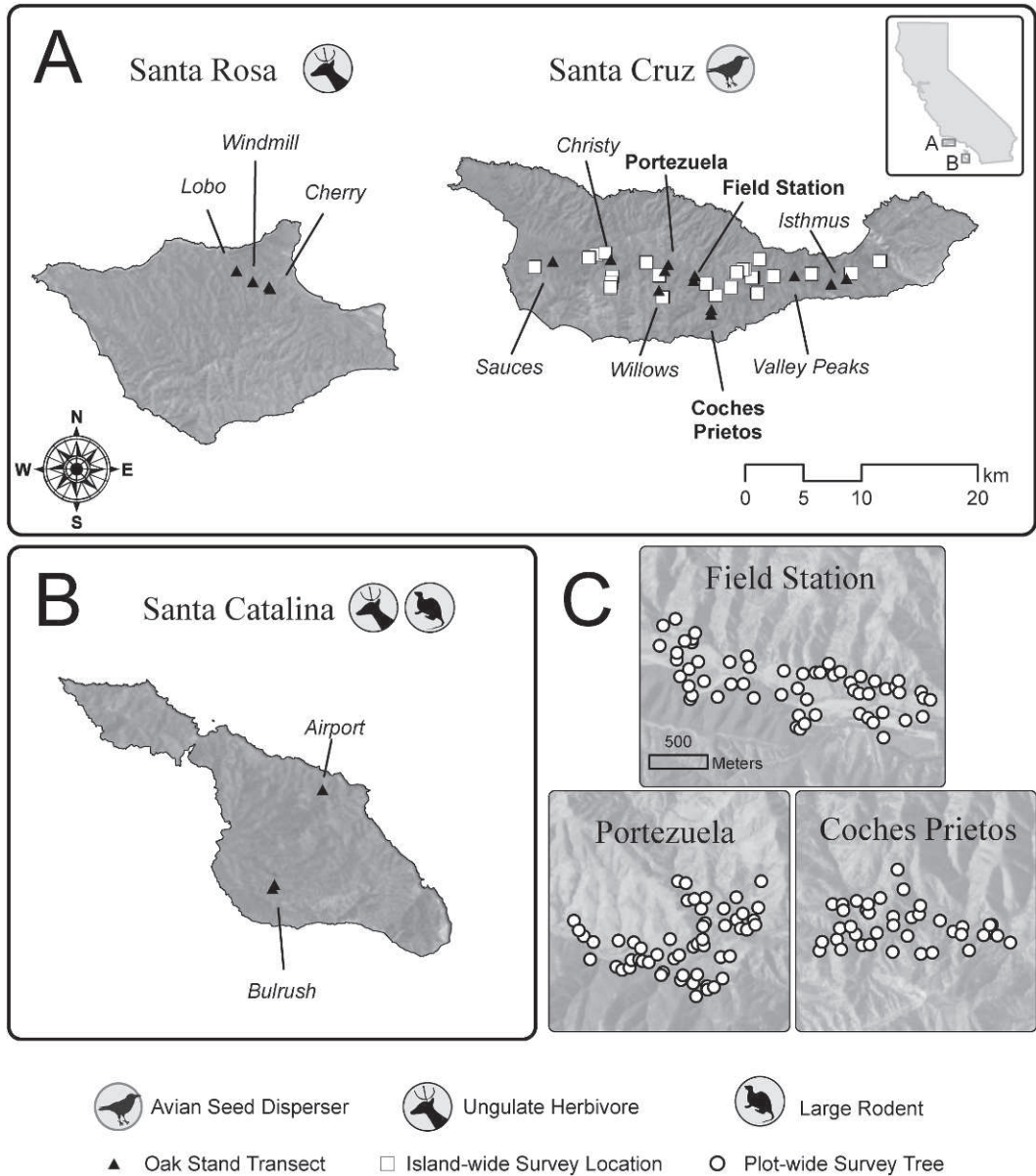


Fig. 1. Map of transect and survey locations in the 3 *Quercus pacifica* populations: A, Santa Rosa and Santa Cruz islands; B, Santa Catalina Island; C, plot-wide survey trees on Santa Cruz Island. Inset shows location of study area in relation to California.

and 5 on Santa Rosa (147 trees) islands. We conducted 3 PCQT on Santa Catalina Island (96 trees) in September 2011. For each tree, we determined species, measured longest crown diameter, and made visual estimates of crown cover (0–9 scale), brown leaves (in 5% increments), acorn size (0–9 scale, 9 representing extremely large acorns), acorn abundance

(0–4 scale; Koenig et al. 1994), level of insect seed predation (proportion of a tree’s acorns with oviposition holes; Espelta et al. 2009), and the presence or absence of oak galls. Galls are induced by oak gall wasps (Hymenoptera: Cynipidae) that lay their eggs into meristematic tissue of branches; the effect of these galls on host trees is unclear (Stone et al. 2002).

TABLE 1. Temperatures and precipitation on Santa Cruz Island from 2008 to 2012^a.

Year	Precip ^b (mm)	Temp _{dry} ^c (°C)	Temp _{wet} ^d (°C)
2008	511	17.7 (2.7)	13.3 (2.6)
2009	254	18.4 (2.0)	14.1 (3.0)
2010	479	17.0 (2.4)	12.5 (2.2)
2011	651	15.6 (1.8)	12.9 (1.9)
2012	319	16.1 (1.8)	12.7 (2.3)

^aData from WRCC (2013)

^bTotal precipitation June–May preceding annual acorn survey

^cMean (SD) monthly temperature for April–September preceding annual acorn survey

^dMean (SD) monthly temperature for October–March preceding annual acorn survey

In 2011, we collected 10 acorns from trees with sufficient crop sizes on all 3 islands (total $n = 1090$), measured their width and length using calipers, and weighed them using a Mettler Toledo digital scale. We assessed insect predation by searching the acorns for oviposition holes (Espelta et al. 2009).

Acorn Crop Surveys on Santa Cruz Island

We conducted both island-wide and plot-wide surveys of acorn productivity on Santa Cruz in an effort to examine spatial and temporal variation. The island-wide survey that started in 2008 ranges from the Montañon range to the western end of the island's south ridge, near Saucos Canyon (Fig. 1A). Oak stands were selected within 100 m of a road while maximizing the variation of potential predictors such as distance from shore, elevation, geology, soil, and presence of fog (Cohen et al. 2009). Multiple trees were chosen on arrival at each location by using randomly selected compass bearings. Of the 200 selected trees, 140 were *Q. pacifica* and 58 were *Q. agrifolia*. We augmented the island-wide survey in 2009 with additional surveys in 3 study plots (Coches Prietos Canyon, Portezuela, and the area around the University of California Santa Barbara Field Station in the central valley of the island; Fig. 1C) used since 2008 to monitor Island Scrub-Jays (see Caldwell et al. 2013). We selected 150 trees throughout the total area of the Island Scrub-Jay research plots (~300 ha) by generating random GPS points a minimum distance of 20 m apart using Hawth's tools for ArcGIS 9.2 (Beyer 2004, ESRI 2009). From each point, we located the nearest oak tree, unless it was in a hazardous location. Of the 150 trees, 131 were *Q. pacifica* and 19 were *Q. agrifolia*. Both surveys were conducted annually within the last 2

weeks of October: the island-wide survey starting in 2008 and the plot-wide survey in 2009. Here, we report results of data collected up to fall 2012: 5 years of island-wide and 4 years of plot-wide surveys.

Acorn productivity was quantified annually using the canopy survey method (Koenig et al. 1994). Two researchers counted acorns simultaneously for a duration of 15 s on separate areas of the crown. The 2 counts were then summed, providing the 30-s acorn count. Koenig et al. (1994) found this method to yield results equivalent to trap methods (i.e., methods that collect acorns after they have fallen from the tree) and found that the counts provide a reliable measure of relative acorn abundance, independent of tree size. The location of each sampled tree in both surveys was recorded with a GPS unit, and all trees were marked with a numbered identification tag to facilitate locating them in subsequent years.

Statistical Analysis

One goal of this study was to describe how species interactions and abiotic factors shape oak populations by comparing *Q. pacifica* stands, trees, and acorns among all 3 islands. To estimate absolute stand density and the relative density of *Q. pacifica* and *Q. agrifolia*, we used PCQT methods (Mitchell and Evans 2006, Siepielski and Benkman 2008). Estimates were corrected when no tree was within 25 m in a quadrant (Warde and Petranka 1981). Due to low sample sizes on Santa Catalina and Santa Rosa islands, we did not use statistical tests to compare density estimates, and we summarized the results of the density transects in Table 2. To compare crown size distributions, we pooled the data from trees in the stand-density transects with the data from our 2 longitudinal acorn surveys on Santa Cruz Island (total $n = 1190$ trees) and used the Kolmogorov–Smirnov test with a Bonferroni correction for multiple testing to determine whether the distributions differed significantly between the islands.

To compare acorn sizes across islands, we calculated acorn volume from length and width by using the formula for the volume of an ellipsoid. Volume predicted wet mass of weevil-free acorns well ($R^2 = 0.93$), which allowed us to include acorns with weevil damage in the comparison. We constructed linear mixed models (LMMs) in the *lme4* package

TABLE 2. Stand-density transects. Location (general aspect), number of sampling points, overall and partial density for *Quercus pacifica* and *Quercus agrifolia* (trees · ha⁻¹), and percentage of *Q. pacifica* trees with acorns.

Island	Transect (aspect)	Points	Density			<i>Q. pacifica</i> w/acorns
			Total	<i>pacifica</i>	<i>agrifolia</i>	
Santa Rosa	Cherry Canyon (W)	9	307.8	307.8	—	36%
	Cherry Canyon (E)	11	566.9	276.9	158.2	77%
	Windmill Canyon (S)	11	252.0	76.2	—	62%
	Lobo Canyon (S)	8	87.9	10.3	43.9	95%
	Lobo Canyon (N)	7	164.4	—	127.8	50%
Santa Catalina	Bulrush Canyon (S)	8	217.0	217.0	—	75%
	Bulrush Canyon (N)	8	84.4	84.4	—	88%
	Airport (N)	8	182.3	182.3	—	41%
Santa Cruz	Field Station (S)	8	170.4	165.1	5.3	41%
	Field Station (N)	10	816.3	816.3	—	10%
	Portezuela (S)	10	97.8	97.8	—	80%
	Portezuela (N)	10	398.4	309.0	16.3	53%
	Coches Prietos (S)	10	58.3	58.3	—	68%
	Coches Prietos (N)	9	76.0	76.0	—	15%
	Isthmus (S)	10	46.4	46.4	—	23%
	Isthmus (N)	10	465.5	465.5	—	45%
	Christy Canyon (N)	10	468.5	468.5	—	49%
	Sauces (W)	10	1164.8	1164.8	—	26%
	Willows Canyon (S)	10	218.8	131.3	49.2	33%
Valley Peaks	10	103.3	103.3	—	28%	

in R (Bates et al. 2012, R Core Team 2012) with *Island* as fixed effect, and *Tree* nested in *Transect* as a random effect to account for sampling multiple acorns from the same tree and to control for variation within transects. For all models with trees as replicates, rather than within-tree counts, we used *Transect* as a random effect to control for local effects (Zuur et al. 2009, Bates et al. 2012).

We used generalized linear mixed models (GLMMs) for comparison of data that could not be transformed to meet model assumptions of LMMs. To compare the proportions of parasitized acorns, we used a beta error distribution; for the presence or absence of oak galls, we used a binomial distribution. Acorn size scores and abundance scores are ordinal scales, best compared using GLMMs with Poisson error distributions (Zuur et al. 2009, Hox 2010). All models contained the same random effect, *Transect*. If the overall island comparison indicated significant differences, we used the Tukey HSD post hoc comparison in the *glht* function of the R package *multcomp* (Hothorn et al. 2008). Significance tests (i.e., χ^2 for GLMMs, *F* values for LMMs, and *P* values associated with fixed effects) were obtained from Type II Wald tests in the *car* package (Fox and Weisberg 2011). This procedure is based solely on the estimated parameter coefficients and their covariance

matrix and does not report the degrees of freedom (Bolker et al. 2009).

We analyzed acorn counts from our annual surveys to test (1) whether year, elevation, and canopy size predicted acorn production and (2) whether acorn production showed spatial or temporal synchrony. The 2 surveys were each analyzed separately, with 5 years (2008–2012) of data for the island-wide survey and 4 years (2009–2012) for the plot-wide survey. We constructed GLMMs with Poisson error distributions—the fixed effects being *Crown Diameter*, *Elevation*, and *Year*—while controlling for repeated sampling by using *Tree* nested within *Point* (island-wide survey) or *Plot* as random effects (Zuur et al. 2009). The comparison of the summed squared residuals to the residual degrees of freedom indicated that the data were overdispersed ($\chi^2 = 4335.8$, $P < 0.0001$). Therefore, we included observation number (*Obs_nmbr*) as a random effect for each unit of replication, thereby effectively eliminating overdispersion (Elston et al. 2001, Bolker et al. 2009).

To test for spatial autocorrelation of acorn counts, we performed a Mantel test in the R package *ncf* (Bjornstad 2012). In this procedure, annual acorn counts for each possible pairwise combination of trees are compared with a linear regression, and the Pearson's regression coefficients are then correlated to

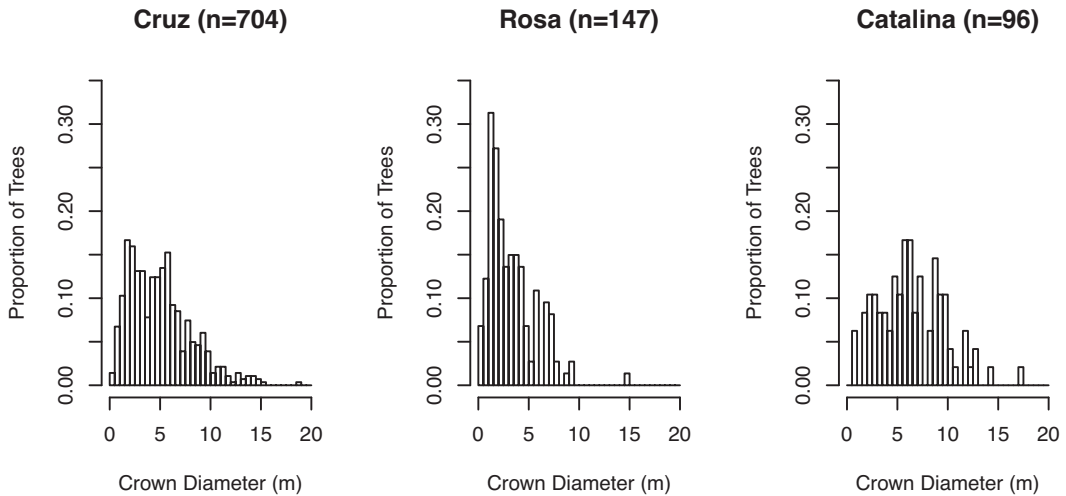


Fig. 2. Frequency distribution of crown diameters for *Quercus pacifica* trees in the 3 island populations.

the distance between the trees. We investigated temporal synchrony in acorn production with Kendall's concordance coefficient W in the R package *vegan* (Oksanen et al. 2012), and we tested whether the synchrony was stronger than expected by chance by permutating the acorn counts for each tree and year 999 times to generate a null distribution of W values.

RESULTS

Comparison of Island Populations

Stand densities of *Q. pacifica* varied broadly within islands but did not reveal a systematic difference between islands. Overall, stand densities spanned 3 orders of magnitude, ranging from 10 to 1164 trees per hectare (Table 2). On Santa Cruz and Santa Rosa islands, stands on south-facing slopes generally occurred in lower densities and had higher proportions of trees with acorns than their north-facing counterparts (Table 2). Crown diameters differed significantly between islands (GLMM: $F_{2,957} = 7.91$, $P = 0.02$, Fig. 2), as trees on Santa Rosa Island (mean \pm SE: 3.38 ± 0.19 m, $n = 147$) were significantly smaller than on Catalina (6.49 ± 0.34 m, $n = 96$) and Santa Cruz (5.07 ± 0.13 m, $n = 704$). The distributions of crown diameters also varied significantly among all 3 islands (Kolmogorov-Smirnoff test with Bonferroni-adjusted P values: Catalina vs. Cruz: $D = 0.2274$, $P = 0.00124$; Rosa vs Cruz: $D = 0.282$, $P > 0.0001$;

Catalina vs Rosa: $D = 0.4775$, $P > 0.0001$). Acorn abundance index scores on the individual trees in 2011 were similar for all islands ($\chi^2 = 2.697$, $P = 0.26$), and trees on Catalina had significantly fewer oak galls than trees on Santa Cruz ($\chi^2 = 19.49$, $P > 0.0001$; Tukey HSD: $z = 4.2$, $P > 0.001$) and Santa Rosa islands ($z = 2.7$, $P = 0.02$).

Acorns varied in size, but not in weevil infestation, across the islands. The volumes and size scores of acorns were significantly smaller on Santa Rosa Island than on the other 2 islands (volume: $\chi^2 = 7.20$, $P = 0.03$; size scores: $\chi^2 = 18.13$, $P < 0.001$; all post hoc tests with Rosa: $P < 0.05$). *Quercus pacifica* acorns on Santa Cruz (mean \pm SE: 1913.0 ± 35.8 mm³) and Santa Catalina islands (1991.6 ± 57.2 mm³) had, respectively, 18.9% and 23.8% larger mean volumes than acorns from Santa Rosa Island (1608.2 ± 41.8 mm³). Weevils infested between 36% and 40% of acorns, and infestation rate did not differ significantly between islands ($\chi^2 = 0.24$, $df = 2$, $P = 0.887$) and was not affected by acorn volume ($\chi^2 = 0.04$, $P = 0.841$).

Acorn Production on Santa Cruz Island

Acorn production varied widely between years. *Quercus agrifolia* trees in the island-wide survey had only one year of high productivity (2009), with only a few acorns produced in the other 4 years (Fig. 3). Year explained the most variance of *Q. pacifica* acorn counts in both the island-wide (Fig. 3,

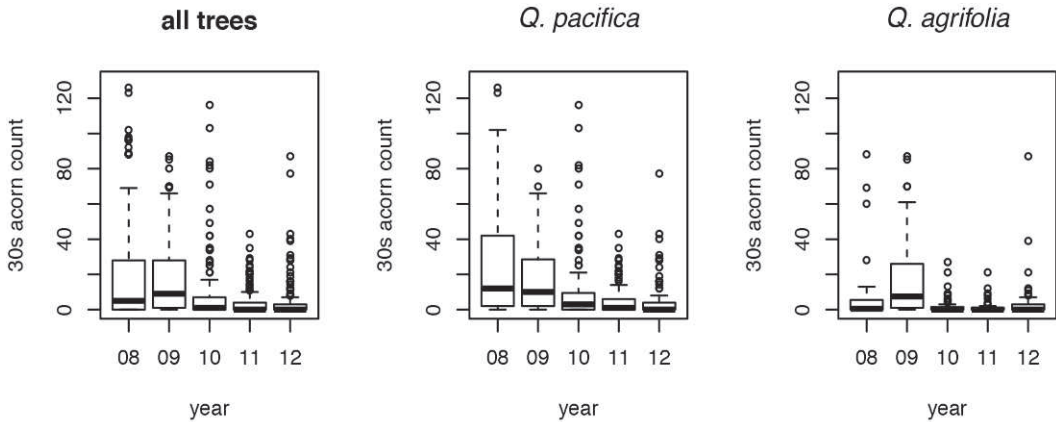


Fig. 3. Acorn productivity of all trees ($n = 198$), *Quercus pacifica* ($n = 141$), and *Quercus agrifolia* ($n = 57$) in the island-wide survey on Santa Cruz Island, 2008–2012. Black horizontal bars indicate the mean; boxes, the interquartile range; and whiskers extend to 1.5 times that range.

TABLE 3. Island-wide acorn counts on Santa Cruz Island. The role of year, elevation, crown diameter, and their interactions in predicting acorn counts on specific trees. Type II ANOVA for island-wide acorn count GLMM with Poisson error distribution ($n = 123$ trees; 5 years).

Fixed effect	df	χ^2	P
Year	4	134.8	<0.001
Elevation	1	15.6	<0.001
Crown	1	7.3	0.007
Crown : elevation	1	0.1	0.820
Crown : year	4	5.8	0.214
Elevation : year	4	21.9	<0.001
Crown : elevation : year	4	3.7	0.446
RESIDUALS	528		

Table 3) and plot-wide (Fig. 4, Table 4) surveys. In the island-wide survey, acorn counts declined from 23.8 ± 2.8 (mean \pm SE) acorns per tree in 2008 to 4.9 ± 1.1 acorns per tree in 2012 (Fig. 3). Throughout the 5-year study period, 135 of 140 *Q. pacifica* trees (96.4%) produced acorns at least once, but only 87 (63.1%) did so in 2012 (Fig. 5). Plot-wide counts declined from 20.3 ± 2.7 acorns per tree in 2009 to 5.1 ± 1.0 acorns in 2012 (Fig. 4). Of the 131 *Q. pacifica* trees in the plot-wide survey, 111 (84.7%) produced acorns at some point throughout the study period. In 2009 and 2010, 73% of trees produced acorns, whereas $<60\%$ of trees carried any acorns in 2011 and 2012. The Coches Prietos plot had the lowest productivity: 30% of trees never produced acorns and only 12% had acorns in 2012. The years preceding the 2 years (2008 and 2009) of higher acorn productivity experi-

TABLE 4. Plot-wide acorn counts on Santa Cruz Island. The role of year, elevation, plot, crown diameter, and their interactions in predicting acorn counts on specific trees. Type II ANOVA for island-wide acorn count GLMM with Poisson error distribution ($n = 150$ trees; 4 years).

Fixed effect	df	χ^2	P
Year	3	111.4	<0.001
Plot	2	57.3	<0.001
Crown	1	7.6	0.006
Elevation	1	13.0	<0.001
Year : plot	6	24.9	<0.001
Year : crown	3	6.7	0.083
Year : elevation	3	11.6	0.009
Plot : crown	2	2.3	0.332
Plot : elevation	2	9.6	0.008
Crown : elevation	1	2.0	0.153
Year : crown : plot	6	4.0	0.680
Year : elevation : plot	6	8.7	0.193
Year : crown : elevation	3	1.8	0.618
Plot : crown : elevation	2	1.8	0.415
RESIDUALS	451		

enced higher mean temperatures in both the wet (October–March) and dry (April–September) seasons compared to low productivity years. The amount of precipitation, however, was the highest in 2008 and only half that amount in 2009 (Table 1).

Elevation above sea level also explained significant variation in acorn counts in both surveys. Trees at higher elevations produced more acorns, especially during high productivity years (Figs. 3, 4). In the plot-wide survey, elevations were not equally distributed between plots, but the plot at lowest elevation always recorded the lowest acorn production. The

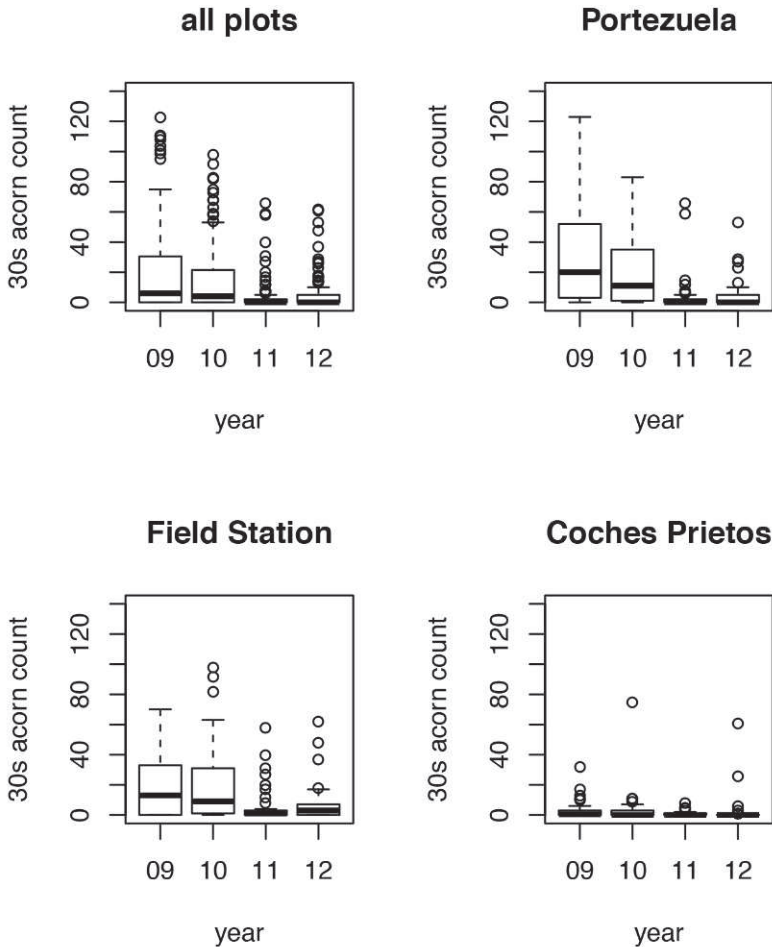


Fig. 4. Acorn productivity of *Quercus pacifica* trees ($n = 131$) in the plot-wide survey on Santa Cruz Island from 2009 to 2012, overall and by plot. Black horizontal bars indicate the mean; boxes, the interquartile range; and whiskers extend to 1.5 times that range.

effect of crown diameter was significant in the plot-wide survey but explained little variation (Table 3) and was not significant in the island-wide data (Table 2). Visual inspection of the data suggested that the smallest trees drove the effect of crown diameter. Therefore, we reran models on the 2 datasets but excluded the lowest 10% of values. The effect of crown was no longer significant for the island-wide survey ($n = 110$ trees, 5 years, $\chi^2 = 1.67$, $P = 0.196$) and was much weaker for the plot-wide survey ($n = 132$ trees, $\chi^2 = 5.58$, $P = 0.018$).

Acorn counts showed weak yet significant signatures of temporal and spatial synchrony. Kendall's concordance coefficient for temporal synchrony of counts over 5 years was very low

($n = 123$, $W = 0.13$, $P < 0.001$) in the island-wide counts. Plot-wide counts, in contrast, had a moderate degree of temporal synchrony over 4 years ($n = 131$, $W = 0.49$, $P < 0.001$). However, the Mantel test for spatial autocorrelation indicated no significant effect of distance on the synchrony of acorn counts between tree pairs in the island-wide survey (Mantel statistic $r = -0.050$, $P = 0.963$) or the plot-wide survey ($r = -0.008$, $P = 0.334$).

DISCUSSION

Island Comparison

Our comparison of *Q. pacifica* stands provides new information on a keystone chaparral

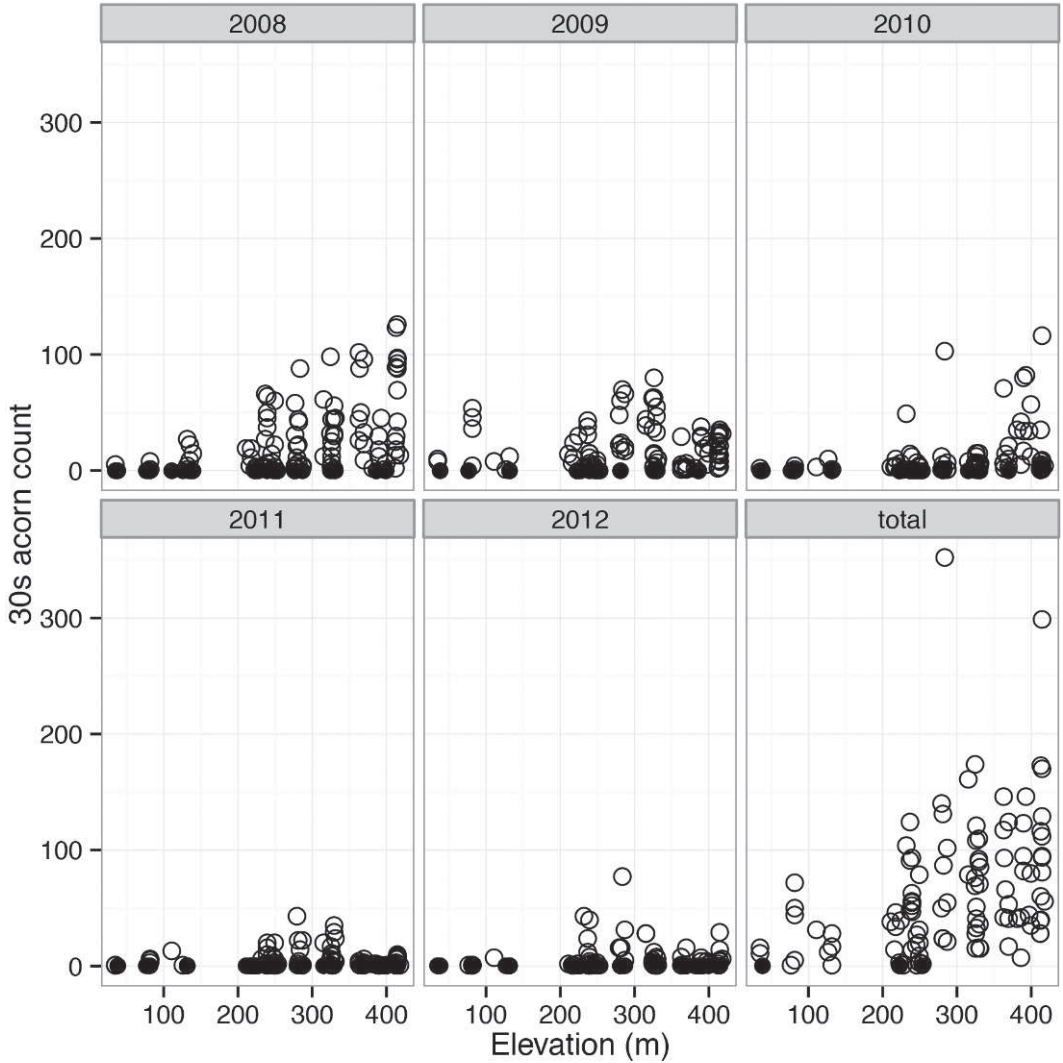


Fig. 5. The influence of elevation on acorn counts of *Quercus pacifica* trees ($n = 140$) in the island-wide survey on Santa Cruz Island, 2008–2012, by year and for all years combined. Filled circles indicate zero counts.

species on the Channel Islands. Stand structure, characterized by crown diameter distributions, acorn size, and gall infestation, all differ between islands. The trees we sampled on Santa Rosa Island were generally smaller in crown diameter. Despite similar acorn abundances in all 3 populations, acorns on Santa Rosa Island had up to 25% less volume. Finally, we observed that the 3 stands we visited on Santa Catalina Island had a low occurrence of oak galls. Only 3% of trees had galls, compared to 35% on Santa Cruz and 19% on Santa Rosa Islands. The effect of galls

on trees is poorly understood, but gall wasps can be important indicators of ecosystem condition and diversity (Stone et al. 2002, Hayward and Stone 2005). We will thus continue recording their presence but hesitate to speculate about the observed patterns at this point.

The smaller crown sizes on Santa Rosa Island could lead to less acorn availability than on Santa Catalina and Santa Cruz Islands but reveal little about different stand structures. Acorn counts and abundance index scores describe the relative density of acorns on the

canopy, and less canopy area would therefore result in fewer available acorns overall. Crown diameters tell us little about different age structures across populations. *Quercus pacifica* occurs in 2 main growth forms, a shrubby form (<2 m height) and an arborescent form (<10 m), which makes age determination using trunk diameter difficult (de Gouvenain and Ansary 2010). It is also unclear how ungulate herbivory and subsequent sprouting contributed to this effect. Nevertheless, crown diameter tends to correlate strongly with tree biomass or volume and is increasingly applied in remote sensing studies (Dubayah and Drake 2000, Popescu et al. 2011). Furthermore, recent work shows that crown area, estimated from crown diameter, is a reliable predictor of overall acorn production in 5 common oak species of the eastern United States (Rose et al. 2012).

Reduced tree sizes on Santa Rosa Island could be due both to species interactions and to abiotic factors. Cooler and windier conditions may have contributed to reduced tree growth. Our transects on Santa Rosa Island also were within the vicinity of the main ranch and could have been affected by human activity over the past 150 years. Basal sprouting in response to ungulate herbivory likely played a major role in shaping the crowns of the existing stands, making inference about the role of acorn availability in shaping stand structure difficult (Knapp 2010a). The presence of ungulates could have exacerbated any anthropogenic effects because both elk and deer feed preferentially on recently emerged leaves and target seedlings and sprouts, thereby stifling regeneration and growth of oak stands (Manuwal and Sweitzer 2010). We would expect to observe such effects mostly on Santa Catalina Island, which is still home to a sizable deer population (Knapp 2010a).

Temperature differences may also be a cause of reduced acorn sizes on Santa Rosa Island. Acorns of *Q. pacifica* mature by early October after pollination in early spring. The maturation process of acorns thus coincides with the span of the largest temperature difference between Santa Rosa and the other islands (WRCC 2013; Table 1). A study of acorn size of valley oaks in the Sierra Nevada of California also found that trees at low elevations (400–600 m) and warmer temperatures had acorns that were almost twice as large as the

acorns on trees at high elevations (1400 m; Phillips 1992). A similar pattern was found for blue oaks: acorns at 1000–1300 m were 35% smaller than acorns at 400–650 m (Phillips 1992). On a broader scale, reduced temperatures during acorn development are the driving factor for the latitudinal decrease in acorn size across 32 North American oak species (Aizen and Woodcock 1992, Koenig and Knops 2013). Additional years of acorn counts on Santa Cruz Island will allow us to address temperature-related hypotheses in more detail, as the western part of that island is cooler and experiences more wind and fog than the eastern and interior parts (Fischer et al. 2009).

Acorn Production on Santa Cruz Island

We observed large variation in acorn production throughout our study period, but our inferences about environmental correlates of annual variation were limited with only 5 years of data. Our study covered one year of high acorn production in 2008, one year of intermediate production (2009), and 3 years of low counts (2010–2012). *Quercus agrifolia* masted in 2009, improving island-wide acorn availability; but thereafter, relatively few acorns have been available to wildlife on Santa Cruz (Fig. 2). The 2 seasons with increased acorn productivity were both preceded by years with relatively higher temperatures. Precipitation showed no pattern of association with our count data, but we found a positive correlation between elevation and acorn abundance (Fig. 5, Tables 3, 4). The annual pattern of the island-wide productivity was mirrored by the overall results of the smaller-scale plot-wide survey. However, the variation between our plots underscores the important role of elevation and local abiotic environment in *Q. pacifica* acorn production: even in good years, trees at low elevation carried few acorns or failed to produce seed crops. The difference between plots also suggests other variables not captured in our study, such as soil composition, moisture, and exposure to solar radiation.

The spatial and temporal synchrony of acorn production on Santa Cruz was low, despite the strong island-wide fluctuation of acorn production. The fact that the temporal synchrony was stronger in our small-scale survey than in the island-wide survey suggests that local conditions, in addition to island-wide influences, affect acorn production. Large

California oaks, such as *Q. lobata*, *Q. douglasii*, and *Q. agrifolia*, exhibit spatial concordance over distances as large as 300 km (Koenig et al. 1996). Interestingly, the temporal masting patterns of these species arise in response to variation in environmental factors such as precipitation and temperature and appear to have an evolved cycling mechanism (Koenig and Knops 2013). This combination of cyclical behavior and a partial dependence on environmental conditions has also been observed in 5 Florida scrub oak species (Abrahamson and Layne 2003). We recorded only one period of high productivity (2008) and are thus likely underestimating the degree of spatial and temporal reproductive synchrony for *Q. pacifica*.

Resprouting will likely affect the ability of existing trees to persist, but the dispersal of acorns may be necessary to convert non-native grassland into chaparral. *Quercus pacifica* readily resprouts, and in the absence of ungulate herbivory, such sprouts may develop into full-grown trees (Knapp 2010a). However, a combination of sprouting and seeding is likely adaptive in regularly disturbed vegetation communities (Bellingham and Sparrow 2000). Restoration trials on Santa Catalina Island suggest that acorns planted in a way similar to scatter-hoarding show high rates of survival, especially during wet years and if protected from herbivory (Stratton 2010). Additional years of acorn counts and oak stand surveys that include seedling and sprout counts will provide a clearer understanding of recruitment in *Q. pacifica*.

The complexity of our results underscores the important role of long-term data collection in understanding the dynamics of oak seed production and stand structure. These data establish a baseline for future monitoring of the Channel Islands' oak populations. Future work should be extended to include detailed stem mapping of oaks at multiple sites per island and quantifying patterns of flowering within and between islands. We also need systematic studies of how endemic animal populations, such as the Catalina California ground squirrels (*Spermophilus beecheyi nesioticus*), interact with island oaks.

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