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GENETIC VARIATION AND STRUCTURE IN AN ENDEMIC ISLAND OAK, *QUERCUS TOMENTELLA*, AND MAINLAND CANYON OAK, *QUERCUS CHRYSOLEPIS*

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Premise of research. *Quercus tomentella* is a tree species endemic to the California Channel Islands and Isla Guadalupe. Given its distribution across six widely separated islands, significant genetic structure would be expected, despite the propensity of oaks for long-distance pollen dispersal. In comparison, its close mainland relative, *Quercus chrysolepis*, has a more continuous range and fewer barriers to gene flow.

Methodology. We sampled *Q. tomentella* from all the islands in its range ($N = 345$) and *Q. chrysolepis* from five mainland sites and on the islands where it occurs ($N = 100$) and genotyped the trees using eight polymorphic microsatellite loci. Genetic differentiation within and between species was examined using genetic distances, analysis of molecular variance, Bayesian clustering (both spatial and nonspatial approaches), a neighbor-joining tree, and genetic discontinuities indicative of barriers to gene flow. We also looked for evidence of population bottlenecks.

Pivotal results. A high level of clonality was found in *Q. tomentella* on Santa Catalina Island and Santa Rosa Island, but genetic variability was high in both species and at all sites, including the tiny surviving population on Isla Guadalupe. Genetic distance measures were significant between most populations of both species. The most surprising result is that the two species were not clearly differentiated, and genetic clusters identified through both spatial and nonspatial analyses were shared between species.

Conclusions. The island endemic *Q. tomentella* and the widespread *Q. chrysolepis* are not well-differentiated species. Further work is needed to clarify the relationships within and among these species. Insular populations of *Q. tomentella* are genetically diverse and distinct; the remaining population found on Isla Guadalupe warrants protection and management to support recruitment.

Keywords: *Quercus tomentella*, *Quercus chrysolepis*, island endemic, conservation, California Channel Islands.

Introduction

Allopatric isolation on islands has long been appreciated as a driver of evolutionary diversification, with many examples of adaptive radiations occurring on island archipelagos. The role of isolation on islands in promoting divergence would seem particularly important for plants because it would limit gene flow occurring through both seed dispersal and pollen dispersal. Well-known diversifications of island plant taxa include the Hawaiian silversword alliance (Robichaux et al. 1990; Baldwin and Sanderson 1998; Barrier et al. 1999), species of *Aeoniumon* on the Canary Islands (Lems 1960; Jorgensen and Olesen 2001; Mort et al. 2002), and species of *Dendroseris* on the Juan Fernández Islands (Crawford et al. 1992; Sang et al. 1994). The California Channel Islands offer a setting for studying insular diversification that is quite distinct from these well-studied examples. Like these oceanic archipelagos, the California Channel Islands have never been connected to the mainland (Junger and Johnson 1980); however, they are relatively close to their continental source (~30–100 km). Indeed, some of the islands are closer to the mainland than to each other (fig. 1). Thus, the history of colonization and subsequent patterns of gene flow might be quite complex and involve multiple island and mainland populations. This situation may also create difficulties in distinguishing between origins occurring through allopatric speciation on the islands versus persistence as a relict population of a species that has disappeared from the mainland (Moody 2000).

Quercus tomentella Engelm., or island oak, is one of about 20 endemic plant species shared among at least some of the California Islands. It occurs on five of the California Channel Islands, with an additional isolated population on Isla Guadalupe, Mexico, the type locality for the species. It was first described on Isla Guadalupe by Edward Palmer (Jepson 1910) and named for the dense tomentose hairs that cover the lower surfaces of its leaves. Some researchers have argued that *Q. tomentella* is a relictual species because fossils of a similar species

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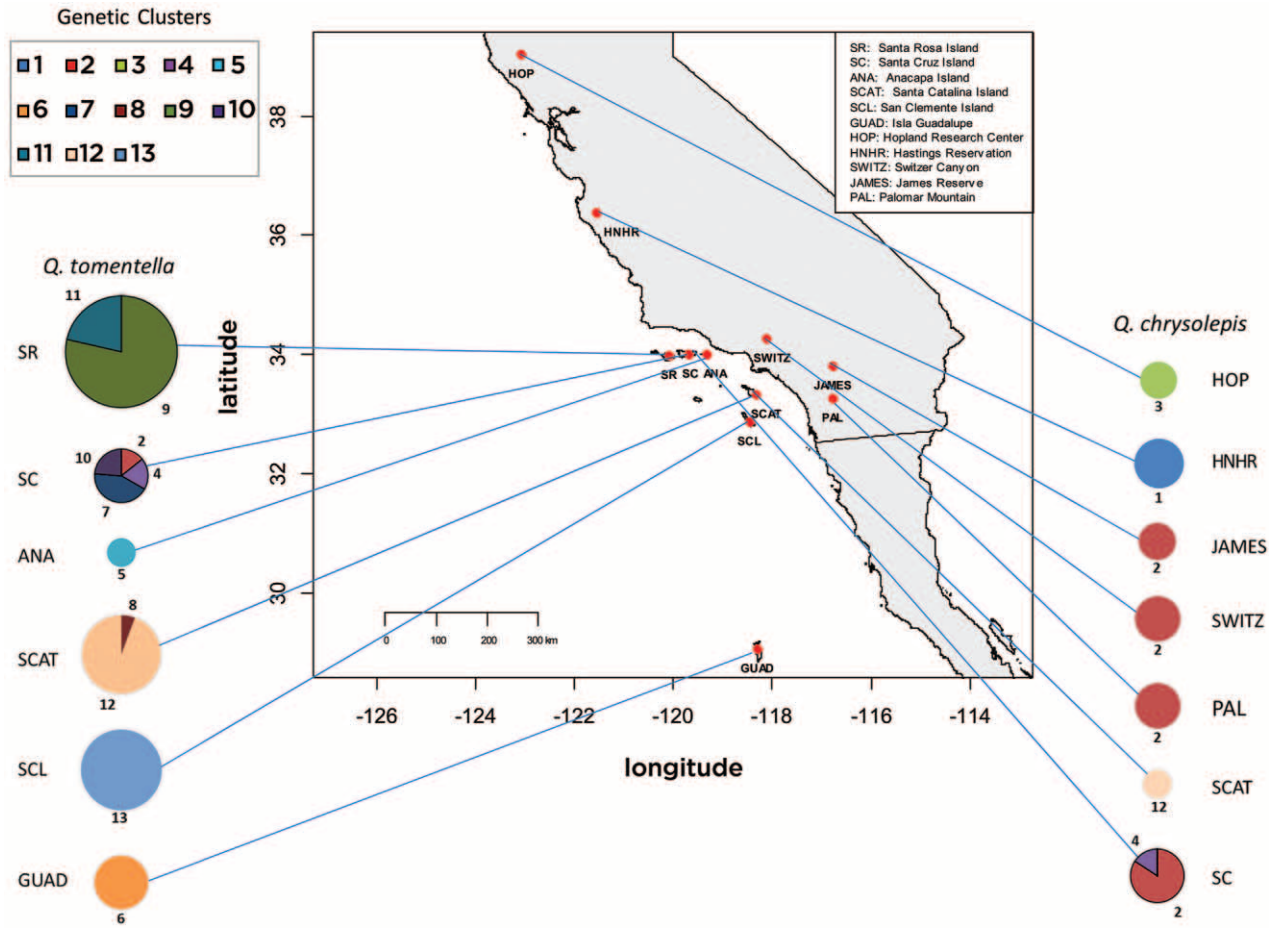

Fig. 1 Map of the study region and results of Geneland clustering analysis. Genetic clusters are identified by color and the numbers 1–13. Pie charts show the proportion of membership assigned to each genetic cluster for samples of each species from each site, as indicated. The size of each pie chart is proportional to sample size.

named *Q. declinata* E. Dorf have been found on the mainland at several locations, dated from 2–20 Myr old (Axelrod 1944, 1967; Muller 1967). In any case, the current limited island range of *Q. tomentella* makes this species one of the rarest oaks, and it is listed as vulnerable on the International Union for Conservation of Nature Red List of Threatened Species and as critically imperiled in Mexico (Oldfield et al. 2007). Like much of the vegetation of these islands, *Q. tomentella* populations declined severely as a result of introduced livestock (sheep, pigs, goats, etc.) during the nineteenth and twentieth centuries, when the islands were overgrazed and experienced extensive erosion (Knowlton et al. 2007). Isla Guadalupe has been practically denuded of vegetation by feral goats, and only 25 or so *Q. tomentella* individuals remain (de la Luz et al. 2003). On the California Channel Islands, most of the nonnative herbivores have been removed, and the vegetation, including oak woodlands, is recovering (Beltran et al. 2014).

Quercus tomentella belongs to section *Protobalanus*, the intermediate or golden-cup oaks. *Protobalanus* is a small clade of five species restricted to the southwestern United States, northwestern Mexico, and the islands off the Pacific coast (Manos 1993*a*, 1997). One species, *Q. chrysolepis* Liebm., is widespread, and the other four species have narrow, largely allopatric ranges. Other members of section *Protobalanus* are *Q. palmeri* Engelm., found in scattered parts of southern California, northern Baja California, Arizona, and New Mexico; *Q. vaccinifolia* Kellogg, widespread in the mountains of northern and central California and extending into Nevada and Oregon; and *Q. cedrosensis* C. H. Mull., found in Baja California and on Cedros Island. Relative to the other North American oaks, section *Quercus* sensu stricto (white oaks) and section *Lobatae* (red and black oaks), phylogenetic analysis of morphology (Nixon 1993) and molecular characters (Manos et al. 1999; Pearse and Hipp 2009; Hipp et al. 2014, 2017) supports the relationship [*Lobatae* – (*Protobalanus* + *Quercus* sensu stricto)]. While a comprehensive phylogenetic study of *Protobalanus* has not been undertaken, a study of foliar trichome characters found support for the current taxonomy (Manos 1993*b*), and recent restriction site associated DNA sequencing (RAD-seq) studies of North American oaks suggest that *Q. tomentella*, *Q. chrysolepis*, and *Q. vaccinifolia* may comprise a recent and poorly resolved subclade (Hipp et al. 2017; McVay et al. 2017).

Like all oaks, *Q. tomentella* is monoecious and wind pollinated. It produces large acorns with a period of 13 mo between pollination and fertilization, a characteristic of section *Protobalanus*. In addition to sexual reproduction, *Q. tomentella* also

regenerates via vegetative reproduction; clonal stems may grow in close, circular clusters or be widely spaced (Ashley et al. 2010). Individual trees can grow up to 20 m in height, but *Quercus tomentella* also grows as a shrub under pressure from grazing or limited water resources. *Quercus tomentella* occurs in a variety of plant communities, including mixed oak woodlands, pine forest, and chaparral (Kindsvater 2010). *Quercus chrysolepis* grows up to 24 m in height and occurs in several types of communities in California, including mixed conifer, chaparral, and mixed oak woodlands at elevations from 20 to 1500 m (Allen-Diaz et al. 2007).

Among the islands that comprise the range of *Q. tomentella*, Isla Guadalupe is the most remote, lying 240 km west of Baja California and more than 400 km from the closest Channel Island, San Clemente Island. Isla Guadalupe is estimated to be approximately 7 Myr old (Hubbs 1967). The uplift of the Channel Islands began about 5 Myr ago (Atwater 1998; Schumann et al. 2012), and geological evidence suggests there were no land bridges between the islands and the mainland nor between the northern and southern islands (Junger and Johnson 1980; Vedder and Howell 1980). However, the northern islands (San Miguel, Santa Rosa, Santa Cruz, and Anacapa) were joined as a larger landmass known as Santarosae as recently as the Last Glacial Maximum (LGM) 18,000 yr ago (Vedder and Howell 1980). At that time, Santarosae was still more than 100 km from Santa Catalina Island, so any gene flow occurring among *Q. tomentella* populations on northern and southern islands required movement of pollen or acorns across a large expanse of ocean. In contrast to that of *Q. tomentella*, the range of *Q. chrysolepis* is largely continuous in California, forming a ring around the California Central Valley and extending south into ridges and canyons in the Transverse and Peninsular Ranges of Southern California. Its range also extends north into southern Oregon, south into Baja California, and east into New Mexico. It is also found in very restricted areas on Santa Cruz, Santa Rosa, and Santa Catalina Islands, cooccurring and possibly hybridizing with *Q. tomentella* (Muller 1967). Although the current range of *Q. chrysolepis* is topographically complex and partially fragmented in the southern regions, there are no large geographical breaks in its distribution. Ecological niche modeling suggests that populations of *Q. chrysolepis* were more connected during the LGM, and the distribution of suitable habitat has remained relatively stable since that time (Ortego et al. 2015).

Given the insular distribution of *Q. tomentella*, genetic structure across its range might be expected to be much greater than that of *Q. chrysolepis* because of restricted gene flow. However, long-distance pollen-mediated gene flow in oaks has repeatedly been shown, and even small, isolated stands receive substantial immigrant pollen (Muir et al. 2004; Craft and Ashley 2010; Buschbom et al. 2011). Among insular oaks, a molecular and morphological study of Cuban oak (*Q. sagraeana* Nuttall) supported an origination from Pleistocene dispersal of *Q. virginiana* from Florida to Cuba (Gugger and Cavender-Bares 2013). A study of island scrub oak (*Q. pacifica*, K. Nixon and C. H. Muller) suggested that some gene flow among populations on three of the California Channel Islands occurred following a Pleistocene origin (Backs and Ashley 2016). *Quercus tomentella* provides a unique system to compare patterns of genetic differentiation and genetic cohesion for an island endemic and a comparison to a closely related mainland species. The goals of this study were to (1) determine whether the island endemic *Q. tomentella* comprises a genetically cohesive evolutionary lineage, (2) describe the genetic variation and structure across the range of *Q. tomentella* and compare these patterns to that found in *Q. chrysolepis*, (3) infer the demographic history of the island populations of *Q. tomentella*, and (4) use the patterns of genetic diversity and structure to inform conservation management of this threatened species.

Material and Methods

Sampling and Genotyping

Leaf samples from a total of 345 *Quercus tomentella* trees were collected from all six islands where it occurs (fig. 1). Sample sizes ranged from four on Anacapa Island, where all trees from the only small grove were sampled, to 165 on Santa Rosa Island (table 1). We collected leaves from clearly separate stems at each site and, to the extent possible, locations across each island. Trees identified in the field as *Q. chrysolepis* occur on Santa Catalina Island and Santa Cruz Island, and we sampled five of these trees on Santa Catalina Island and 19 on Santa Cruz Island. We also obtained 100 samples of *Q. chrysolepis* from five mainland sites, two in Northern California and three in Southern California (fig. 1; table 1).

Eight microsatellite loci were used in this study: QpZAG1/5, QpZag 110, and QpZag 9 developed in the European oak *Q. petraea* (Steinkellner et al. 1997); MSQ4 developed in the North American *Q. macrocarpa* (Dow and Ashley 1996, 1998); QpZAG11, QpZAG15, and QrZAG58 developed in *Q. robur* (Kampfer et al. 1998); and QM69-2M1 developed in the Asian *Q. myrsinifolia* (Isagi and Suhandono 1997). These loci were selected based on their utility for studying population structure in several species of section *Quercus* (e.g., Craft and Ashley 2010; Abraham et al. 2011; Backs and Ashley 2016). PCR was carried out using 50–100 ng genomic DNA in 10 μL PCR mix with the following reagents: 0.5 mM of 10 mM dNTP mix (Denville Scientific, Holliston, MA), 0.04 μM of the forward primer with the fluorescent-labeled M13 (−21) universal primer, 0.6 −0.8 μM reverse primer, 1.0 μg/μL bovine serum albumin, and 0.25 U Taq polymerase. PCR conditions are described in Abraham et al. (2011). PCR products (1.5 μL) were analyzed in a capillary DNA sequencing machine (Applied Biosystems 3730) using a LIZ500 ladder (Applied Biosystems). All microsatellite genotypes were scored by analyzing the raw data, using Applied Biosystems' GeneMapper software, version 3.7.

Genetic Diversity

Identical multilocus genotypes (MLGs) were identified in the database, and if they occurred at the same sampling location, they were assumed to be derived from clones. After removing duplicates of MLGs (clones), genetic diversity was estimated by the mean number of alleles per locus (N_A), number of private alleles, mean effective number of alleles (N_E), observed heterozygosity (H_O), and expected heterozygosity (H_E), using GenAlEx, version 6.5.1 (table 1; Peakall and Smouse 2006). Fixation indexes (F_{IS}) were also calculated using GenAlEx. Allelic richness (AR) and private allelic richness (PAR) for each

Table 1

Sample Sizes and Descriptive Statistics for *Quercus tomentella* and *Quercus chrysolepis* Used for This Study

Species and site (abbreviation)	N	MLG	N_A	N_E	AR	PA	PAR	H_O (SE)	H_E (SE)	F_{IS} (SE)
Quercus tomentella:										
Santa Rosa Island	165	98	9.5	4.2	3.75	4	.21	.512 (.067)	.662 (.070)	.194 (.102)
Santa Cruz Island	23	21	4.9	2.6	3.08	0	.04	.422 (.071)	.573 (.060)	.222 (.135)
Anacapa Island	4	4	2.6	2.2	2.25	0	.04	.313 (.132)	.356 (.107)	.163 (.213)
Santa Catalina Island	75	53	10.1	5.2	4.45	5	.40	.573 (.081)	.766 (.035)	.256 (.097)
San Clemente Island	56	55	10.0	4.7	4.23	7	.24	.647 (.066)	.752 (.032)	.151 (.064)
Isla Guadalupe	22	22	7.5	4.1	4.00	9	.59	.650 (.090)	.668 (.083)	.030 (.051)
Overall (mean)	345	253	16.3	5.1	(3.63)		(.25)	.557	.756	.262
Quercus chrysolepis:										
Santa Cruz Island	19	19	7.9	5.2	4.43	1	.15	.634 (.069)	.761 (.043)	.182 (.078)
Santa Catalina Island	5	5	5.4	4.6	4.74	0	.41	.788 (.061)	.760 (.020)	−.032 (.069)
Hopland Research Station	11	11	5.6	4.0	3.80	2	.31	.616 (.070)	.666 (.070)	.052 (.069)
Hastings Reservation	21	21	7.75	5.0	4.24	0	.57	.639 (.071)	.733 (.051)	.117 (.090)
Switzer Canyon	16	16	9.0	5.6	4.90	2	.49	.782 (.040)	.800 (.023)	.015 (.061)
James Reserve	12	12	8.9	5.7	5.13	2	.37	.759 (.051)	.807 (.022)	.050 (.078)
Palomar Mountain	16	16	10.1	6.5	5.15	6	.62	.791 (.030)	.809 (.033)	.015 (.043)
Overall (mean)	100	100	16.4	7.3	(4.63)		(.42)	.705	.829	.146

Note. N = number stems sampled; MLG = number of unique multilocus genotypes; N_A = average number of alleles per locus; N_E = effective number of alleles per locus; AR = average allelic richness; PA = number of private alleles; PAR = average private allele richness; H_O = observed heterozygosity; H_E = expected heterozygosity; F_{IS} = fixation index.

population of both species, as well for each species overall, were calculated using Hp-Rare 1.0 (Kalinowski 2004, 2005).

Genetic Differentiation and Clustering

With duplicate clones removed, we used the R package DEMEtics (Gerlach et al. 2010) to calculate G_{ST} (Nei and Chesser 1983) and D_{JOST} (Jost 2008) as measures of species and population differentiation. The degree of genetic differentiation between populations has traditionally been measured by the fixation index G_{ST}; however, differentiation at highly polymorphic loci may be better reflected by the D value (Jost 2008; Gerlach et al. 2010). The DEMEtics package allows locus-by-locus (and averaged over loci) pairwise G_{ST} and D values for codominant markers between populations and their averages over all populations. P values (indicating the strength of evidence against the null hypothesis of no genetic differentiation) and 95% confidence limits are obtained from bootstrap methods. Depending on whether all populations are in Hardy-Weinberg equilibrium for a given locus, either alleles or genotypes are randomized over populations, respectively. We used analysis of molecular variance (AMOVA; Excoffier et al. 1992) in Arlequin V3.5.2 (Excoffier and Lischer 2010) to examine hierarchical F statistics using 20,000 permutations. Results are the average over eight loci.

We used two different Bayesian approaches to identify genetic clusters among samples of both species, Structure, version 2.3.4 (Pritchard et al. 2000), and Geneland (Guillot et al. 2005). Structure implements a nonspatial approach that ignores geographic information, while Geneland uses georeferenced individuals or populations. We ran Structure under the admixture model using no priors and also with two different Locprior options, using first species as location identifiers and again with sampling locations as location identifiers. The use of prior information may help detect weak population structure (Hubisz et al. 2009). The number of assumed genetic clusters (K) was set from 1 to 15, and 10 runs with a 100,000 burn-in and 250,000 Markov chain Monte Carlo (MCMC) were run for each K. Best K was determined by calculating $\ln(K)$ and ΔK (Evanno et al. 2005), using Structure Harvester, version 0.6.93 (Earl and Vonholdt 2012). Consensus analyses were performed using Clumpp 1.1.2 (Jakobsson and Rosenberg 2007) to group individuals into genotypes on the average scores for the inferred K value. Structure Plot 2.0 (Ramasamy et al. 2014) was used to visualize the Structure output.

We chose Geneland over other spatial Bayesian methods because it has been reported to have the highest power when tested with simulated data (Safner et al. 2011; Blair et al. 2012). For Geneland, the graphical user interface was used to run the correlated frequency, spatial model at 100,000 MCMC, thin rate 100, and burn-in 200 for 10 runs at K of 1–15. This procedure was repeated five times. For each repetition, the run with the highest posterior probability was chosen, and from these five results, best K was inferred from the modal value of K with the highest posterior probability. For the mainland samples of *Q. chrysolepis*, only a single set of spatial coordinates was collected at each sampling site (not for each tree). Therefore, we set uncertainty on coordinate to 0.0005 (about 75 m) to prevent individuals from being automatically assigned to the same inferred group by Geneland.

To further visualize the relationships among the populations of both species, we constructed a neighbor-joining tree with the program Populations (Langella 1999), using the Cavalli-Sforza and Edwards (1967) chord distance.

Demographic History

To look for evidence of recent population bottlenecks, we tested for excess heterozygosity in each population (Cornuet and Luikart 1996). We used values for observed and expected heterozygosity for each locus as computed in GenAlEx 6.501 (table 1) and conducted a one-tailed Wilcoxon signed-rank test

with a significance level of 0.05 to check for significant differences between these two values for the eight loci in the populations at each island or mainland site. We also tested for bottlenecks using the *M* ratio (Garza and Williamson 2001; Excoffier et al. 2005), where $M = K/R$ with K = total number of alleles and R = overall range in allele size. The *M* ratio is less sensitive to effects of null alleles or Wahlund effects than heterozygosity comparisons and retains indications of a bottleneck over longer periods of time (Garza and Williamson 2001; Spear et al. 2006; Peery et al. 2012). We used Arlequin v3.5.1.2 (Excoffier and Lischer 2010) to determine the *M* ratio (Garza-Williamson index). A ratio below 0.68 is indicative of a bottleneck.

Results

Genotypic and Genetic Diversity

Despite our efforts to sample independently growing trees at all sites, a surprisingly high level of clonal growth was detected for *Quercus tomentella* on Santa Rosa and Santa Catalina Islands. On Santa Rosa Island, 24 identical MLGs were found in multiple samples from the same site, with two to eight samples per MLG (data not shown). The sites with clones were widely scattered on the island. Eight MLGs were found in multiple samples on Santa Catalina Island. As previously reported, 14 trees sampled at one site on Santa Catalina Island, Lone Tree Grove, had only two MLGs (Ashley et al. 2010). A couple of clones of *Q. tomentella* were found on Santa Cruz Island and San Clemente Island, but none were found on Anacapa Island, San Clemente Island, or Isla Guadalupe. No clones were detected among *Q. chrysolepis* samples. All but one representative of each MLG was removed from the data set for all subsequent analyses. This reduced the overall sample size for *Q. tomentella* from 345 to 253 (table 1).

The eight microsatellite loci were highly variable in both species (table 1), with an overall H_E of 0.756 for *Q. tomentella* and 0.829 for *Q. chrysolepis*. These values are typical for oak microsatellite studies using these loci, which have been widely used for studies of white oaks, section *Quercus* (e.g., Craft et al. 2002; Craft and Ashley 2010; Abraham et al. 2011; Backs et al. 2015; Backs and Ashley 2016). Although the total number of alleles per locus in each species is nearly identical, for other measures of diversity, including N_E, AR, and PAR, *Q. chrysolepis* generally showed higher levels of variation than *Q. tomentella* (table 1). Nine of the populations sampled had private alleles, ranging from one for Santa Cruz Island *Q. chrysolepis* to nine for Isla Guadalupe *Q. tomentella* (table 1). All private alleles were at frequencies of <0.10 (data not shown).

Genetic Differentiation and Clustering

Most pairwise values of G_{ST} and D_{JOST} for populations of both species were significant (table 2). In fact, the only nonsignificant comparisons were those among *Q. chrysolepis* on Santa Cruz and Santa Catalina Islands and the three Southern California mainland populations of *Q. chrysolepis*. For *Q. tomentella*, very high levels of differentiation were found for comparisons involving Anacapa Island, but this may be a result of the small number of trees (four) on that island. Isla Guadalupe had especially higher levels of differentiation than the other islands, particularly for D_{JOST}, ranging from 0.34 for San Clemente Island to 0.54 for Anacapa Island. Notably, interspecific differentiation levels were not consistently or markedly higher than intraspecific differentiation levels.

AMOVA results for genetic variation among groups (i.e., species *Q. tomentella* and *Q. chrysolepis*; $F_{CT} = 0.02025$, $P = 0.00819$) indicate low differentiation between the two species (table 3). Variation among populations within groups (six populations within *Q. tomentella* and seven within *Q. chrysolepis*; $F_{SC} = 0.08074$, $P = 0.00000$) indicates more variation than within the species. There is more genetic variation among individuals within populations ($F_{IS} = 0.17840$, $P = 0.00000$), and,

Table 2

G_{ST} (Nei and Chesser 1983) Values above Diagonal and D_{JOST} (Jost 2008) Values below Diagonal

	Quercus tomentella						*Quercus chrysolepis*						
	SR	SC	ANA	SCAT	SCL	GUAD	SC	SCAT	HOP	HNHR	SWITZ	JAMES	PAL
Q. tomentella:													
SR		.04	.12	.03	.05	.12	.05	.05	.08	.08	.06	.05	.04
SC	.24		.15	.04	.04	.12	.07	.07	.08	.07	.07	.06	.07
ANA	.32	.32		.12	.15	.19	.16	.16	.20	.20	.14	.13	.13
SCAT	.18	.20	.31		.03	.07	.03	.01	.06	.04	.03	.02	.03
SCL	.27	.21	.40	.20		.07	.03	.03	.06	.04	.04	.02	.03
GUAD	.45	.44	.54	.36	.34		.06	.08	.14	.10	.05	.04	.05
Q. chrysolepis:													
SC	.23	.32	.42	.24	.20	.33		.02	.06	.04	.00	.00	.00
SCAT	.27	.30	.49	.12	.25	.45	.16		.06	.04	.02	.01	.02
HOP	.40	.36	.55	.44	.33	.57	.32	.37		.04	.06	.07	.07
HNHR	.42	.37	.64	.40	.36	.53	.36	.32	.26		.04	.04	.04
SWITZ	.33	.39	.42	.29	.32	.37	.06	.17	.35	.36		.00	.00
JAMES	.25	.33	.43	.20	.18	.25	.00	.17	.40	.33	.08		.00
PAL	.30	.37	.51	.24	.28	.32	.05	.15	.42	.39	.07	.01	

Note. Significant values ($P < 0.01$) are underlined. For site abbreviations, see figure 1.

Table 3

Analysis of Molecular Variance

Source of variation	Variance components	Percentage of variation	Fixation index	*P* value
Among species	.066	2.025	.020 F_{CT}	<.01
Among populations within species	.256	7.911	.081 F_{SC}	<.01
Among individuals within populations	.521	16.068	.178 F_{IS}	<.01
Within individuals	2.399	73.996	.260 F_{IT}	<.01

Note. F_{CT} = among species; F_{SC} = among populations within species; F_{IS} = among individuals within populations; F_{IT} = within individuals.

finally, the most variation (74%) is among individuals (F_{IT} = 0.26004, P = 0.00000).

Both the Structure run that used no priors and the run with species identifications used to inform the prior showed that the peak distribution of ΔK (Evanno et al. 2005) occurred at $K = 2$ for 10 simulations at K values from 1 to 15. The cluster assignments were very similar for both runs. Even when species identifications were used to inform priors, the two clusters did not correspond to the two species, *Q. tomentella* and *Q. chrysolepis* (fig. 2*A*). Rather, there was a northern cluster including most *Q. tomentella* individuals from Santa Rosa, Santa Cruz, and Anacapa Islands and a southern cluster including most *Q. tomentella* from San Clemente Island and Isla Guadalupe. Santa Catalina *Q. tomentella* were a mix of clusters 1 and 2. *Quercus chrysolepis* from all sampling locations were assigned to the second cluster (with the exception of one individual from Santa Cruz Island).

When sampling location was used to inform the prior in the Structure runs, the peak distribution of ΔK (Evanno et al. 2005) occurred at $K = 5$. Again, the two species did not cluster separately, nor did islands form distinct clusters. Many *Q. tomentella* trees from Santa Rosa Island had high assigned ancestry in one cluster (shown in yellow in fig. 2*B*), while trees from Santa Cruz, Anacapa, Santa Catalina, and San Clemente Islands had mixed ancestry. Interestingly, trees from Isla Guadalupe had high assigned ancestry in another cluster (shown in red in fig. 2*B*), which was also the predominant genetic cluster for *Q. chrysolepis* trees from the Southern California sampling sites.

Geneland identified 13 genetic clusters (fig. 1). For *Q. tomentella*, trees from Anacapa Island, San Clemente Island, and Isla Guadalupe each comprised a different, unique genetic cluster. Trees from Santa Rosa Island comprised two unique genetic clusters. For Santa Cruz Island, trees were placed in four different genetic clusters, two unique to the island and two shared with *Q. chrysolepis* (clusters 2 and 4 in fig. 1). One of these, cluster 2 shown in red in figure 1, is especially notable because it contains *Q. tomentella* from Santa Cruz Island, *Q. chrysolepis* from Santa Cruz Island, and all the *Q. chrysolepis* trees sampled from the Southern California sites. On Santa Catalina Island, most of the *Q. tomentella* individuals (50 of 53) and all trees identified as *Q. chrysolepis* comprised a single genetic cluster. The neighbor-joining tree (fig. 3) supports several aspects of the cluster analyses. For example, *Q. chrysolepis* from the southern mainland and Santa Cruz Island group together, and Isla Guadalupe *Q. tomentella* again groups more closely with these populations than with *Q. tomentella* from the other islands. The neighbor-joining tree shows a grouping of the northern island *Q. tomentella* not revealed in the cluster analysis.

Demographic History

While the Wilcoxon signed-rank tests of excess heterozygosity showed significant differences between observed and expected heterozygosity for some populations of both species (*Q. tomentella* on Santa Rosa, Santa Catalina, and San Clemente Islands and *Q. chrysolepis* on Santa Cruz Island), in these cases the observed heterozygosity was lower than the expected heterozygosity. Thus, the data show no evidence of recent population bottlenecks. In contrast, the *M* ratio (Garza-Williamson index) was below 0.4 for all populations for both species and significantly below the 0.68 cutoff ratio for a bottleneck, suggesting that bottlenecks have occurred for both species at some time in the past.

Discussion

Many species of oaks reproduce both sexually through seeds (acorns) and asexually through vegetative sprouting. Clones may sometimes grow in connected clusters; however, cryptic clonal growth has also been reported in some oak species, with widely separated stems sharing identical multilocus genotypes (Backs et al. 2015). For rare or threatened plant species, such as *Quercus tomentella*, it is important to characterize clonal structure, because it will influence the genetic diversity of the population and the effective population size. Within section *Protobalanus*, a remarkable clone of *Q. palmeri* in the Jurupa Mountains of Southern California was estimated to be more than 13,000 yr old (May et al. 2009). A study of clone formation in *Q. chrysolepis* reported that most trees had unique multilocus genotypes but spatially clustered clonal trees were also common, with most clones consisting of three to five trees (Montalvo et al. 1997). In our study, none of our samples of *Q. chrysolepis* shared MLGs. We did, however, find extensive clonal growth of *Q. tomentella* on two islands, Santa Catalina and Santa Rosa. Cloning on Santa Catalina Island had been previously reported (Ashley et al. 2010). On Santa Rosa Island, a sample of 165 trees yielded only 98 MLGs. Trees with identical MLGs were always found growing in the same stands but were not growing in tight clumps or with any apparent connections. Pressure from overgrazing and subsequent erosion may have contributed to a shift to asexual reproduction on these two islands. These pressures certainly occurred on the other islands as well, but only a few clones were found on the other islands. It was reassuring that all individuals sampled on Isla Guadalupe, which included nearly all remaining trees, were each genetically unique. Despite extensive clonal growth on Santa Catalina and Santa Rosa, both islands still har-

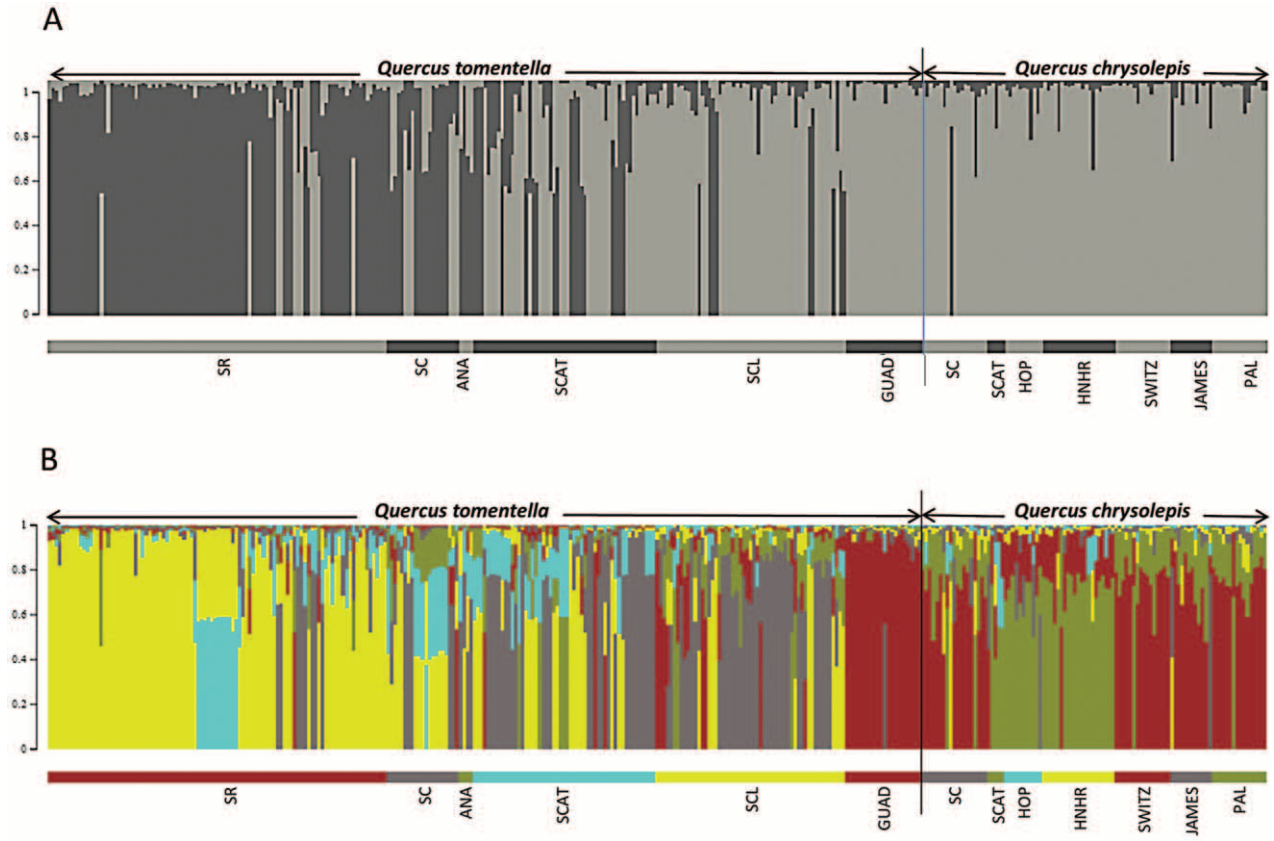

Fig. 2 Results of Structure analysis. *A*, Assigned ancestry of individual trees at $K = 2$, the number of clusters inferred when species identification was used to inform the priors. *B*, Assigned ancestry of individual trees at $K = 5$, the number of clusters inferred when sample location was used to inform priors.

bored high allelic and genotypic diversity, and opportunities for outcross pollination remain high.

Even with a restricted, isolated distribution and some clonal reproduction, genetic diversity of *Q. tomentella* was relatively high for all island populations (table 1). An overall expected heterozygosity of 0.756 for *Q. tomentella* was lower than that for *Q. chrysolepis* (0.829) in this study but higher than that reported for the widespread valley oak, *Q. lobata* (0.703; Ashley et al. 2015). Isolated or rare oaks seem to be able to maintain high heterozygosity, with high values also reported for the endangered *Q. hinckleyi* (0.853; Backs et al. 2015) and the endemic island scrub oak, *Q. pacifica* (0.851; Backs and Ashley 2016). While these studies all used the same or nearly the same set of microsatellite loci, comparisons across species must be made with caution because of the possibility of ascertainment bias (Ellegren et al. 1995). Nevertheless, the data suggest that genetic decline in the form of increased homozygosity is not an immediate concern for threatened oak species. Allelic diversity, though, may be somewhat eroded through genetic drift or other factors, with populations of *Q. tomentella* having lower values for the effective number of alleles and allelic richness than *Q. chrysolepis*, despite more thorough sampling of *Q. tomentella* diversity (table 1). However, the data showed no evidence of excess heterozygosity that might be expected from recent population bottlenecks and the loss of rare alleles (Cornuet and Luikart 1996). *M* ratio results showed evidence for historical bottlenecks; however, they included populations of both species so seem to reflect neither founder events nor genetic drift in island populations but rather some other process that applies to both species.

Quercus tomentella showed genetic structure across islands, with all pairwise comparisons between island populations significant for both G_{ST} and D_{JOST} (table 2). In particular, trees from Isla Guadalupe had higher levels of pairwise differentiation than the other island populations, especially the northern Channel Islands. The Isla Guadalupe population also had nine private alleles, the highest of any population (table 1). Although significant, G_{ST} values among the Channel Islands *Q. tomentella* were low (0.03–0.07; table 2), with the exception of Anacapa Island, which has only four individuals. For *Q. chrysolepis*, most intraspecific pairwise comparisons were significant, but G_{ST} values were consistently low (0.01–0.07; table 2). Genetic distances among the three Southern California sampling sites, and between these sites and the Santa Cruz Island *Q. chrysolepis* population, were not significant.

All interspecific comparisons between *Q. tomentella* and *Q. chrysolepis* were significant, except for trees identified as *Q. chrysolepis* on Santa Catalina Island, which were not significantly different from *Q. tomentella* on that island for G_{ST}.

This suggests that the trees may have been misidentified as *Q. chrysolepis* or that introgression was extensive between the two species on Santa Catalina Island. We sampled the trees at the only site (Mt. Orizaba) where *Q. chrysolepis* has been reported on Santa Catalina Island (Thorne 1967). Certainly, oaks are well known for their propensity to hybridize. Muller (1967) reported that the few *Q. chrysolepis* trees on Santa Catalina Island show evidence of introgression by *Q. tomentella*, and Thorne (1967) doubted the existence of pure *Q. chrysolepis* on the island.

Although interspecific comparisons between populations showed significant genetic differentiation (with the exception noted above), *Q. tomentella* and *Q. chrysolepis* are poorly resolved species with our set of microsatellite markers. AMOVA revealed that only ~2% of the genetic variation is partitioned between species, compared to ~8% for populations within species (table 3). Similarly, even when species identification was used to inform priors for Structure analysis, the two species did not form separate clusters (fig. 2*A*). Rather, there was a broad north-south transition in *Q. tomentella*, with *Q. tomentella* from the southern islands of San Clemente and Guadalupe primarily clustering with *Q. chrysolepis*. Most *Q. tomentella* individuals from Santa Rosa, Santa Cruz, and Anacapa Islands showed high ancestry in a second genetic cluster, while trees from Santa Catalina Island were divided between the two clusters. When sampling island/location was used to inform priors, five clusters were identified, but again clusters were shared between species (fig. 2*B*). Note that in this analysis, trees from Isla Guadalupe formed a cluster with *Q. chrysolepis* trees from Santa Cruz Island and the Southern California sampling sites (the red cluster in fig. 2*B*).

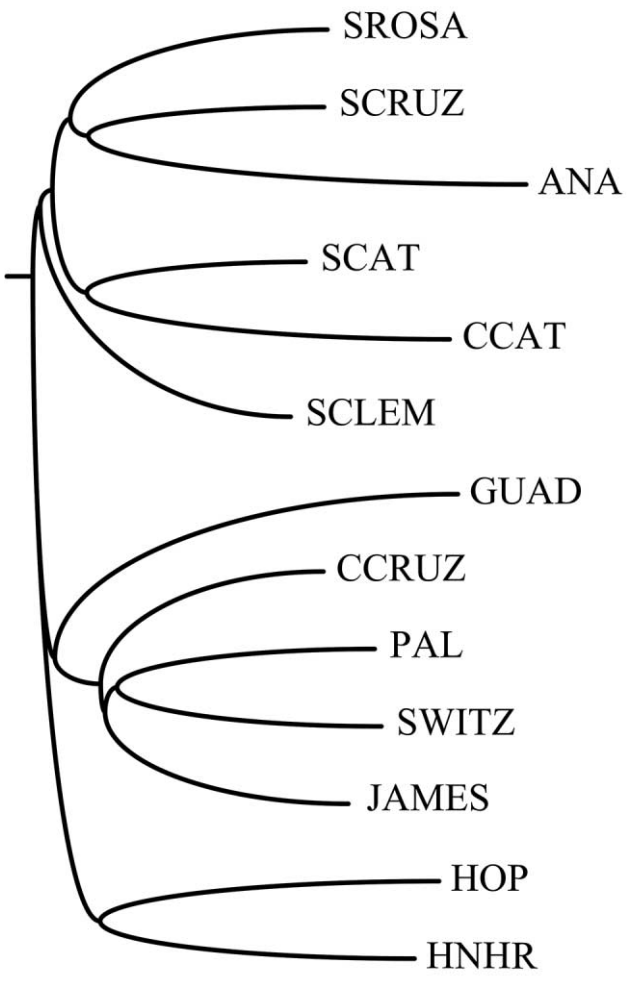

Fig. 3 Neighbor-joining tree of populations of both species based on chord distance. Abbreviations are given in figure 1.

Geneland analysis, which utilizes both spatial and genetic data, identified 13 clusters, and most islands/sampling sites formed one or more unique clusters (fig. 1). Three clusters were shared between species. On Santa Catalina Island, the five trees identified as *Q. chrysolepis* clustered with *Q. tomentella* from that island, suggesting either misidentification or introgression, as also indicated above by the nonsignificant genetic distances between them. The same may be true for some trees identified as *Q. tomentella* on Santa Cruz Island that were placed in two clusters shared by *Q. chrysolepis* sampled on that island. One of these clusters also included all the *Q. chrysolepis* from Southern California and most of the Santa Cruz *Q. chrysolepis* individuals.

While the set of eight microsatellite loci used in this study is limited, variation at these loci has been useful for delineating other closely related oak species, including the California scrub oaks *Q. pacifica*, *Q. dumosa*, and *Q. berberidifolia* (Backs and Ashley 2016), as well as *Q. lobata* and *Q. douglasii* (Craft et al. 2002; Abraham et al. 2011). In other studies, microsatellite markers have been less successful in distinguishing oak species (e.g., Aldrich et al. 2003; Craft and Ashley 2006). To date, there is little or no genetic evidence supporting the current species boundaries and relationships within section *Protobalanus*. This group has not been thoroughly or recently investigated, but a study using chloroplast DNA (cpDNA) restriction sites and internal transcribed spacers (ITS) also found little support for current species delineations (Manos et al. 1999). The cpDNA data identified two distinct clades, but *Q. chrysolepis* individuals were placed in both clades. *Quercus tomentella* did form a monophyletic group in the Manos et al. (1999) study, but it included samples from only three islands. Our results raise the possibility that *Q. tomentella* may have arisen from multiple colonizations of the islands and may not represent a single independent lineage. Populations on Isla Guadalupe are genetically more similar to *Q. chrysolepis* on the Southern California mainland than *Q. tomentella* from the northern Channel Islands (fig. 3). Our results also do not provide evidence in support of *Q. tomentella* as a relictual species (Axelrod 1944, 1967), as this hypothesis would predict strong differentiation from extant mainland species and some genetic cohesion among *Q. tomentella* populations.

We identified genetic structure within *Q. chrysolepis*, with a strong genetic discontinuity between our Northern California and Southern California sampling sites. Another recent study of *Q. chrysolepis* (Ortego et al. 2015) reported significant genetic differentiation among geographical regions, although most populations sampled in the study showed greater evidence for genetic admixture. Morphological variability of *Q. chrysolepis* has long been noted in the literature, with highly variable acorns, leaves, and growth forms and historical recognition of several varieties (Sudworth 1908; Jepson 1910; Tucker 1993). Recently, RAD-seq data have proved useful for resolving problematic phylogenetic relationships among American oaks (Hipp et al. 2014,

2017) and might be better able to resolve relationships within *Protobalanus* than previous approaches.

As described in the introduction, it is expected that the evolutionary history of biota on the nearshore California Islands would be different and more varied compared to biota on distant, isolated archipelagos. Proximity to the mainland and varying interisland distances have undoubtedly resulted in patterns of mainland-to-island colonization and interisland dispersal that vary among taxa. For more than 10,000 yr, the islands have also been occupied by humans, who have likely played a role as dispersal agents for numerous species (Erlandson et al. 2004, 2008; Hofman and Rick 2017). Several notable floristic studies of the California Islands have been published (Raven 1967; Thorne 1967; Philbrick 1980; Moody 2000), and a number of conservation genetics studies focusing on endemic species of San Clemente Island have been conducted by Helenurm and colleagues (e.g., Helenurm and Hall 2005; Helenurm et al. 2005; Furches et al. 2009). While there have been relatively few phylogeographic or population genetic studies of California island plants with multi-island distributions to date, the studies that have been conducted have revealed complex and varied relationships among island and mainland taxa. A recent study of the island scrub oak, *Q. pacifica*, found on Santa Rosa, Santa Cruz, and Santa Catalina Islands, reported that it was a genetically cohesive lineage, differentiated from mainland scrub oaks but connected by historical gene flow among islands (Backs and Ashley 2016). Mainland and island varieties of *Acmispon argophyllus* (A. Gray) and *Acmispon dendroideus* (Greene) Brouillet (Fabaceae) have strikingly different phylogeographic patterns (Wallace et al. 2017). *Acmispon argophyllus* is described as a complex of divergent mainland and island populations with a history of multiple colonists between mainland and islands, while island varieties of *A. dendroideus* were monophyletic. The botanically diverse California Islands remain a rich system for evolutionary studies of diversification and divergence in a nearshore island system.

Our final goal was to use the patterns of genetic diversity and structure to inform conservation management of *Q. tomentella*. Island endemics such as *Q. tomentella* are particularly vulnerable because of their restricted range and small population sizes. Natural factors such as disease, fire, and hurricanes, as well as human impacts, particularly introduction of nonnative species, make island endemics more likely to face extinction than their mainland counterparts. Although the status of *Q. tomentella* as a single evolutionary lineage was not confirmed by our analysis, the data presented here suggest that the island populations are genetically diverse and differentiated from each other. In particular, the tiny remaining population found on Isla Guadalupe harbors unique genetic diversity that merits continuing protection and increased efforts to support recruitment. Overall, our results lead us to recommend continuing efforts to promote the recovery to island oak ecosystems on the Channel Islands and to promote increased efforts to protect the remaining trees on Isla Guadalupe.

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