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For the Special Issue: Evolutionary Insights from Studies of Geographic Variation

Association of genetic and phenotypic variability with geography and climate in three southern California oaks[1]

Erin C. Riordan[2], Paul F. Gugger[2], Joaquín Ortego[3], Carrie Smith[2], Keith Gaddis[2], Pam Thompson[2], and Victoria L. Sork[2,4,5]

PREMISE OF THE STUDY: Geography and climate shape the distribution of organisms, their genotypes, and their phenotypes. To understand historical and future evolutionary and ecological responses to climate, we compared the association of geography and climate of three oak species (*Quercus engelmannii*, *Quercus berberidifolia*, and *Quercus cornelius-mulleri*) in an environmentally heterogeneous region of southern California at three organizational levels: regional species distributions, genetic variation, and phenotypic variation.

METHODS: We identified climatic variables influencing regional distribution patterns using species distribution models (SDMs), and then tested whether those individual variables are important in shaping genetic (microsatellite) and phenotypic (leaf morphology) variation. We estimated the relative contributions of geography and climate using multivariate redundancy analyses (RDA) with variance partitioning.

KEY RESULTS: The modeled distribution of each species was influenced by climate differently. Our analysis of genetic variation using RDA identified small but significant associations between genetic variation with climate and geography in *Q. engelmannii* and *Q. cornelius-mulleri*, but not in *Q. berberidifolia*, and climate explained more of the variation. Our analysis of phenotypic variation in *Q. engelmannii* indicated that climate had more impact than geography, but not in *Q. berberidifolia*. Throughout our analyses, we did not find a consistent pattern in effects of individual climatic variables.

CONCLUSIONS: Our comparative analysis illustrates that climate influences tree response at all organizational levels, but the important climate factors vary depending on the level and on the species. Because of these species-specific and level-specific responses, today's sympatric species are unlikely to have similar distributions in the future.

KEY WORDS California; climate; Fagaceae; genetic variation; geography; isolation by distance; isolation by environment; microsatellite markers; morphology; *Quercus*; species distribution modeling

Climate impacts plant species on multiple levels of biological organization and scale—geographic distribution, genetic composition, and phenotype. At the broadest scales, physiological tolerances to climatic conditions define global patterns of species distribution (e.g., Woodward, 1987). Climate also affects historical demographic events, such as population expansion, contraction, and migration (Avise, 2000), which in turn influence fine scale patterns of species distributions. In a similar manner, the genetic composition of a population can be shaped by both climate and evolutionary history (Avise, 2000). For example, Gugger et al. (2013) found evidence that current and historical climate at the last glacial maximum (~20,000 yr ago) was associated with the genetic composition of valley oak, *Quercus lobata*, more than its geographic location. They propose that climate could have influenced gene flow through local expansion–contraction dynamics and flowering phenology and/or reinforced local adaptation by selecting against immigrants from populations with different climates. In fact, in a recent survey of papers examining gene flow, over 70% of the studies indicated that the environment was important in determining gene flow (Sexton et al., 2014). Finally, climate and history can both shape phenotypic variation within a species (Stebbins, 1950). Populations found in the same climate may share phenotypes because of local adaptation, phenotypic plasticity, or common ancestry (West-Eberhard,

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[2] Department of Ecology and Evolutionary Biology, University of California Los Angeles, Box 957239, Los Angeles, California 90095-7239 USA;

[3] Department of Integrative Ecology, Estación Biológica de Doñana (EBD-CSIC), Avenida Américo Vespucio s/n 41092 Seville, Spain; and

[4] Institute of the Environment and Sustainability, University of California Los Angeles, Box 951496, Los Angeles, California 90095-1496 USA

[5] Author for correspondence (e-mail: vlsork@ucla.edu)

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1989; Des Marais et al., 2013). At all three levels, the movement of individuals and genes determines the range of species, their genetic composition, and their phenotypes.

The geographic distribution of a species reflects the complex interplay of evolutionary and ecological processes influenced by limiting environmental conditions as well as dispersal and extinction dynamics (Brown et al., 1996; Gaston, 2003). The strength and type of environmental influences on species distribution varies with scale, often hierarchically, with abiotic factors such as climate dominating at coarse scales and biotic interactions at fine scales (Woodward and Williams, 1987; Pearson and Dawson, 2003; Guisan and Thuiller, 2005; Soberón, 2007). Species distribution modeling (SDM), which relates species occurrence data with environmental information, allows the prediction of species' geographic distributions (Guisan and Thuiller, 2005; Elith and Leathwick, 2009; Franklin, 2009) and can be used to test hypotheses about the important climatic factors influencing various ecological and evolutionary processes on the landscape. However, it is critical that the scale of modeling and data match the scale of processes under investigation, as the nature and shape of species–environment relationships are scale dependent (Guisan and Thuiller, 2005). Furthermore, because populations within a species can also vary in their response to climate (Rehfeldt et al., 2002), species with broad ranges that cross many climatic regions may exhibit different relationships with climate when modeled at regional vs. species-wide scales (e.g., Sork et al., 2010). Thus, it may be more appropriate to focus on regional patterns of species distribution when examining climatic influences across multiple biological processes, especially in areas of high environmental heterogeneity.

Recently, SDM has been applied to landscape genetics (also referred to as ecological niche modeling, ENM) to investigate the association of genetic variation with environmental gradients and make inference about the role of gene flow and selection (Kozak and Wiens, 2006; Freedman et al., 2010; Sork et al., 2010; Ortego et al., 2012; Poelchau and Hamrick, 2012). These studies often use model predictions to describe habitat or climatic suitability as a single integrated measure of multiple complex environmental factors, which is then assessed in terms of its influence on genetic patterns. At a regional level, genetic patterns are determined either through restricted gene flow, creating isolation by distance (IBD) (Wright, 1943; Slatkin, 1993) or isolation by environment (IBE) whereby gene flow is higher among similar environments due to selective forces or ecological barriers restricting movement (Andrew et al., 2012; Shafer and Wolf, 2013; Sexton et al., 2014; Wang and Bradburd, 2014). For example, climate can influence mating patterns when phenological differences among populations lead to assortative mating, as has been shown in some tree species (Soularue and Kremer, 2014). Alternatively, immigrants not adapted to local climatic conditions may be selected against, resulting in a positive relationship between adaptive divergence and genetic differentiation, a pattern also known as isolation by adaptation (IBA) (Nosil et al., 2008 and citations therein; Andrew et al., 2012).

Geographic patterns of phenotypic variation also reflect the influence of the environment (Stebbins, 1950). Many traits have diverged across sites in response to environmental gradients, creating locally adaptive genetic differences driven by selective forces (e.g., Clausen et al., 1947; Endler, 1986; Savolainen et al., 2007). For example, Ramírez-Valiente et al. (2009) showed differentiation in ecophysiological traits related to drought stress (specific leaf area, leaf size, and nitrogen leaf content) among populations of cork oak (*Quercus suber*) along a climatic gradient. Differentiation in such traits likely has a genetic basis, but may also reflect phenotypic plasticity (Bradshaw, 1965; West-Eberhard, 1989; Scheiner, 1993; Nicotra et al., 2010). In a study of candidates genes associated with response to climate found in *Quercus lobata*, several genes showed a correlation with climate gradients (Sork et al., 2016 in this issue). Thus, an association of phenotypic or genotypic variation with environmental gradients provides initial evidence that traits may be under selection (Endler, 1986; Linhart and Grant, 1996), although conclusive evidence of natural selection requires both an underlying genetic basis and demonstration that the trait leads to improved plant performance (Anderson et al., 2011).

The overall goal of this study was to analyze the influence of climate within three levels of biological organization—the species distribution, its genetic composition, and its phenotypic variation for one tree oak, *Quercus engelmannii* Greene, and two scrub oaks, *Q. berberidifolia* Liebm. and *Q. cornelius-mulleri* Nixon & K.P.Steele (Fagaceae). First, we used SDMs to identify the climatic variables important in shaping regional distribution patterns for each of the three species. Second, we assessed the relative impacts of climate and geography on genetic and phenotypic variation using redundancy and partial redundancy models (Legendre and Fortin, 2010; Legendre and Legendre, 2012). Third, we investigated whether the climate variables important in defining regional patterns of species distribution also shape landscape-level patterns of genetic and phenotypic variation. Given that these three species co-occur in an environmentally heterogeneous region of southern California, each has an opportunity to be shaped by strong environmental differences at relatively fine spatial scales. Previous work has shown that environmental heterogeneity promoted genetic differentiation in *Q. engelmannii* (Engelmann oak) (Ortego et al., 2012) and that climate plays a role in the persistence of hybrids between *Q. engelmannii* and co-occurring scrub oaks (Ortego et al., 2014). Here we added morphological data to our analyses and used multivariate statistical approaches to investigate how much climate, independent of geography, shapes genetic and phenotypic differences between these species. We discuss similarities and differences in the relative influence of climate and geography in shaping variation among species, lending insight into the response of these currently co-occurring species to future climates.

MATERIALS AND METHODS

Study species and field sampling—We focus our study on three oak species in southern California (United States). *Quercus engelmannii* (Engelmann oak) is a rare oak species found in southern California and northwestern Baja California (Mexico) and has one of the smallest ranges of any California oak species (Scott, 1991; Roberts, 1995). These large, single-stemmed trees grow to 5–25 m and have leaves that are oblong to ovate, abaxially pubescent, and pale blue-green in color (Baldwin et al., 2012). Additionally, *Q. engelmannii* is drought-tolerant, occurring in dry, open oak woodlands and mostly interior cismontane foothills below 1300 m (Scott, 1991; Roberts, 1995). This oak hybridizes with sympatric species in the scrub oak complex (J. Ortego and V. L. Sork, unpublished), including *Quercus berberidifolia* (California scrub oak) and *Q. cornelius-mulleri* (Muller's oak). Both scrub oak species are multi-stemmed with spiny or very pubescent leaves with fewer spines (Roberts, 1995). The abaxial leaf surface of *Q. cornelius-mulleri* has particularly

dense stellate trichomes. *Quercus berberidifolia* is widespread in southern California, tending to occur in more mesic habitats compared with *Q. cornelius-mulleri*, which is restricted to dry washes and slopes, typically on granitic soils, in the interior desert margins and juniper–piñon woodlands of southern California and northern Baja California (Nixon, 2002). Both scrub oak species are considered drought-tolerant (Pavlik et al., 1991).

Oaks were sampled across southern California where the ranges of all three species partially overlap from southern Los Angeles County to the international border with Mexico. During 2008–2011, we sampled leaf tissues from 343 total adult trees, 2–15 trees across 31 localities (Table 1, Fig. 1) as described by Ortego et al. (2012, 2014). Spatial coordinates of each individual tree were recorded using a global positioning system (GPS) unit. Leaf samples for genetic analyses were stored frozen (–20°C), and samples for morphological measurements were dried. We selected 291 individual trees genetically assigned to one of the three study species (see below) for subsequent analysis, 174 of which were also measured for morphological leaf traits (Appendix S1, see Supplemental Data with the online version of this article).

Species distribution modeling—We used SDM to identify the climatic factors influencing regional patterns of oak species distribution and predict the geographic distribution of climatically suitable habitat. Occurrence data were obtained from oak sampling sites and digitized herbarium records collected since 1900 and downloaded from the Consortium of California Herbaria on 18 January 2015 (CCH; http://ucjeps.berkeley.edu/consortium/). For *Q. berberidifolia*, which is broadly distributed throughout the state, we only modeled the southern portion of the species range that partially overlaps with *Q. engelmannii* and *Q. cornelius-mulleri*. To ensure high quality of herbarium record data, we excluded records of planted or cultivated individuals and any records having ≥2.5 km error or uncertainty associated with the georeferenced location. We also excluded obvious species misidentifications. Occurrences were then thinned to one record per grid cell of the climatic data. The final numbers of occurrence records used for modeling were 367 for *Q. engelmannii*, 497 for *Q. berberidifolia*, and 238 for *Q. cornelius-mulleri*.

TABLE 1. Geographic location of oak sampling sites in southern California. The number of genetically defined *Quercus engelmannii* (N_{ENG}), *Quercus berberidifolia* (N_{BER}), and *Quercus cornelius-mulleri* (N_{CMU}) individuals are indicated for each locality.

Locality	Code	Latitude	Longitude	N_{ENG}	N_{BER}	N_{CMU}
Glendora	GLE	34.177483	−118.0950	2	0	0
Pasadena	PAS	34.134079	−118.0989	16	0	0
Yucaipa	YUC	34.038817	−117.0217	0	2	1
Joshua Tree N. P.	JOS	34.017380	−116.1674	0	0	4
Beaumont	BEA	33.909783	−116.9832	0	0	5
Hemet	HEM	33.628262	−117.0129	18	3	0
Avocado Mesa	AVO	33.513735	−117.3089	10	5	1
Pauba Ranch	PAU	33.508552	−117.0882	8	26	0
De Luz	LUZ	33.423553	−117.3214	5	9	0
Pala Reservation	PAL	33.390607	−117.0393	8	5	1
Harold's	HAR	33.302025	−116.8930	5	1	0
Oak Knoll	OAK	33.298210	−116.9221	10	0	0
Lake Henshaw	HEN	33.276442	−116.8550	5	0	0
Warner Springs	WAR	33.275230	−116.6241	2	7	0
Ranchita	RAN	33.211081	−116.4855	0	0	18
Daley Ranch	DAL	33.165990	−117.0470	2	0	0
Santa Ysabel	YSA	33.102790	−116.6694	8	6	0
Julian	JUL	33.074770	−116.5491	12	3	0
Lake Hodges	HOD	33.07470	−117.1181	3	0	0
Ramona	RAM	33.029917	−116.8231	7	0	0
Louis A. Stelzer Co. P.	LOU	32.881655	−116.9012	2	1	1
Laguna Mountain	LAG	32.849683	−116.4852	0	5	0
Japatul	JAP	32.823380	−116.6275	1	2	0
Alpine	ALP	32.814090	−116.7724	7	0	0
Cleveland N. F.	CLE	32.776504	−116.4948	5	5	0
McCain Valley Road	CAI	32.770260	−116.2586	0	0	6
Lawson Valley Road	LAW	32.744610	−116.8057	9	6	0
Jamul	JAM	32.730587	−116.8757	3	0	0
North Tecate/Dulzura	DUL	32.631651	−116.7615	8	0	0
Jacumba	JAC	32.622233	−116.2183	0	0	6
Potrero	POT	32.597267	−116.5549	1	5	0

Notes: Co. = County; F. = Forest; N. = National; P = Park.

We obtained 30-yr averages of contemporary (1951–1980) climate data from the California Basin Characterization Model (BCM; Flint and Flint, 2012; Flint et al., 2013), which applies a regional water-balance model to simulate hydrologic responses to climate at high (270 m) resolution. We calculated 19 bioclimatic variables (Nix, 1986) from the monthly BCM temperature and precipitation data, which are downscaled from the parameter–elevation regressions on independent slopes model (PRISM; Daly et al., 1994). We selected a subset of variables to use in SDM that (1) are important drivers of western US plant distributions (Stephenson, 1998; Rehfeldt et al., 2006), (2) maximize model performance, and (3) minimize correlations between variables (Pearson's $r < 0.8$). These eight climatic variables were minimum winter temperature (T_{min}), calculated as the average minimum temperature over the coldest months (December–February); summer maximum temperature (T_{max}), calculated as the average maximum temperature over the hottest months (June–August); temperature seasonality (Bio4); precipitation seasonality (Bio15); summer precipitation (precipitation of the warmest quarter; Bio18); winter precipitation (precipitation of the coldest quarter; Bio19); climatic water deficit (CWD); and actual evapotranspiration (AET). Climatic water deficit is the evaporative demand exceeding soil moisture, or the difference between potential and actual evapotranspiration, and can be interpreted as a measure of drought stress (Stephenson, 1998; Flint et al., 2013). Because the BCM climate data does not include Mexico, we were unable to include the southernmost distributional limit of the three species in northwestern Baja California.

We modeled the contemporary species–climate relationship for each oak species using MaxEnt (Phillips et al., 2006), a maximum-entropy modeling method tailored for presence-only species data that is robust to irregularly sampled data, such as herbarium records (Elith et al., 2006; Loiselle et al., 2008; Phillips et al., 2009). Models were run using linear, quadratic, and product features in MaxEnt. We used a targeted background consisting of CCH herbarium records for all California plant taxa to control for the effects of sampling bias from occurrence records and to improve model performance (Phillips et al., 2009; Kramer-Schadt et al., 2013). To limit our models to the environmental conditions likely sampled by the species and thus most relevant in driving distributional patterns (VanDerWal et al., 2009; Barbet-Massin et al., 2012), we used a 100 km buffer around species occurrences as the spatial domain. We evaluated overall model performance using the area under the receiver operator curve (AUC) statistic (Fielding and Bell, 1997; but see Lobo et al., 2008) averaged over 5-fold cross-validation replicates. Predicted climatic habitat suitability maps were produced for each species using MaxEnt's logistic output, which provides an

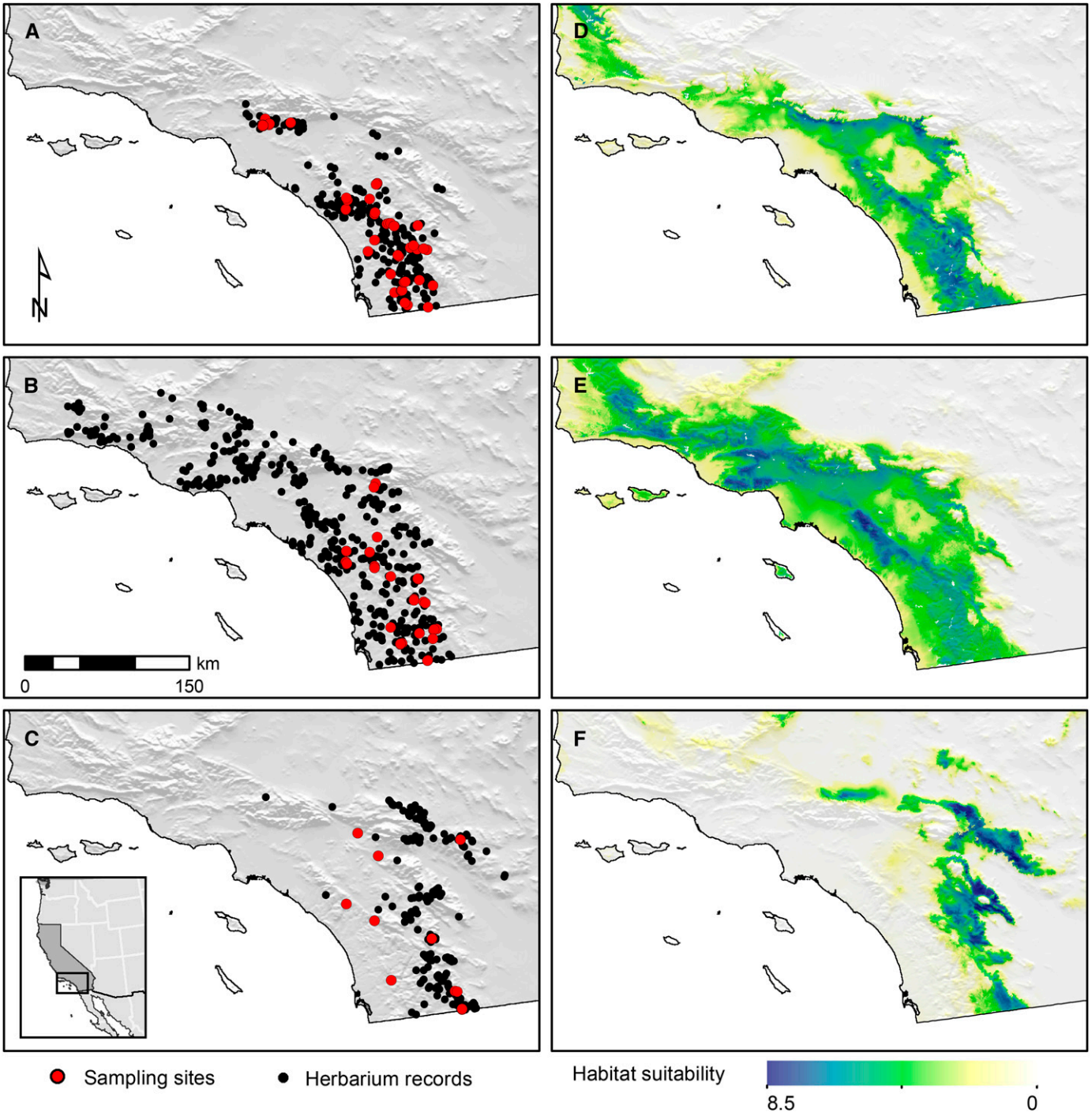

FIGURE 1 (A–C) Localities of sampling sites (red) and herbarium records (black) and (D–F) modeled habitat suitability maps for *Quercus engelmannii* (A, D), *Q. berberidifolia* (B, E), and *Q. cornelius-mulleri* (F, C).

estimate of probability of presence ranging from 0 (low suitability) to 1 (high suitability) in geographic space. We identified important climatic variables using MaxEnt's metrics of variable contribution and permutation importance. Because these metrics are sensitive to correlations among variables, we also used MaxEnt's jackknife tests of variable importance, which calculate the (1) predictive power measured as the model gain of individual variables when used in isolation and (2) the unique contribution of individual variables measured as the drop in model gain when a variable is excluded from the model.

Genotyping—To confirm the species classification of our 343 samples with putative field identifications, we used a set of nine microsatellite genetic markers that were commonly used in our laboratory (Sork et al., 2002; Grivet et al., 2008) and developed for other *Quercus* species: QpZAG7, MSQ4, QpZAG9, QpZAG36, QpZAG110,

QrZAG20, QM69-2M1, QpZAG1/5, and QrZAG1 (Steinkellner et al., 1997; Kampfer et al., 1998).

To conduct our multivariate analyses, we transformed single-locus genotypes into allelic variables by assigning a score of 0, 0.5, or 1, depending on whether the individual possessed homozygous or heterozygous alleles at that locus (Westfall and Conkle, 1992). The number of single variables created at each locus is the number of alleles minus one, which yielded 248 allelic variables. We then used principal component analysis implemented in PROC PRINCOM in SAS version 9 (SAS Institute, Cary, North Carolina, USA) to reduce the 248 variables into a smaller set of 50 orthogonal axes. With these data, we reassigned the field species identifications of all individuals based on assignments of canonical discriminant analysis (CDA) implemented in PROC DISCRIM, which also estimated the percentage of each individual's genotype that was assignable to one of the three species. We assigned an individual to a single species if its genetic assignment was at least 90% associated with that species. This classification, which resulted in 157 *Q. engelmannii*, 91 *Q. berberidifolia*, and 43 *Q. cornelius-mulleri* individuals, did not differ notably from previous clustering results (Ortego et al., 2014), except that we divided the scrub oaks into separate species as justified by our CDA, and excluded hybrids from analyses. These multilocus genotypes were used in subsequent statistical analyses (as described below).

Morphological traits—We analyzed phenotypic variation in leaf morphology of 174 individuals assigned to a single species (109 *Q. engelmannii*, 53 *Q. berberidifolia*, and 12 *Q. cornelius-mulleri*). Leaf measurements included lamina width, lamina length, petiole length, lamina thickness, number of veins, number of leaf lobes, leaf spines, abaxial leaf trichome density, and adaxial leaf pubescence density. Lamina width was measured as the widest part of the leaf for entire leaves or the width from the largest lobe to the main vein for leaves with lobed or toothed margins. Lamina length was measured from the bottom of the leaf (excluding the petiole) to the end of the blade. Petiole length was measured from the bud to the base of the leaf. Lamina thickness was measured in a portion of the leaf without veins using a micrometer. Number of veins was measured abaxially and only included the first veins expanding from the main vein. Number of leaf lobes was a summation of curved or rounded projections occurring along the leaf margin. We recorded the presence or absence of teeth surrounding the leaf (leaf spines). We used an index of trichome density, which was quantified under a dissecting scope, using a scale from 1 (few trichomes) to 6 (high trichome density), following other studies in oaks (Kissling, 1977; Kremer et al., 2002). We calculated an additional variable, petiole ratio [petiole length/(petiole length + lamina length)] to normalize for differences in leaf size across individuals. We averaged measurements across three mature leaves collected per individual tree. For statistical analyses (described next), we $\log_{10}$-transformed the variables lamina width, lamina length, lamina thickness, and petiole ratio to correct for skew.

Statistical analyses—We measured the similarity between predictions of climatic habitat suitability between pairs of oaks species using two estimates of niche overlap, Schoener's *D* (Schoener, 1968) and Warren's *I* statistic (Warren et al., 2008). Both measures range from 0 (completely discordant SDMs) to 1 (identical SDMs) and were calculated from MaxEnt's raw suitability scores. We then used the niche identity test statistic (Warren et al., 2008) with 100 pseudoreplicates to determine whether the SDMs of species pairs were more different than expected if they were drawn from the same underlying distribution (i.e., the pooled sample of occurrence points from both species). A rejection of the null hypothesis indicates species models are climatically distinct and is suggestive of distinct climatic niches. Niche overlap calculations and identity tests were implemented in R with the niche.equivalency.test function in the phyloclim package (Heibl, 2011).

To test the genetic and morphological differences among species, we conducted two separate canonical discriminant analyses (Proc CANDISC, SAS version 9). First, we examined the genetic differences using the 291 multilocus genotypes assigned to a given species. Then, we tested whether the three species differed morphologically based on eight leaf traits: lamina width, lamina length, petiole ratio, lamina thickness, number of leaf veins, number of leaf lobes, adaxial leaf pubescence, and abaxial leaf trichome density measured for 174 individuals.

To examine genetic structure within each species, we first conducted an AMOVA and calculated pairwise F_{ST} among sites in the program GenAlEx 6.5 (Peakall and Smouse, 2012) using the nine microsatellite markers. A few sample sites had one or two samples and were grouped following the method of Ortego et al. (2014) or otherwise discarded from these analyses. We then tested for isolation by distance using Mantel tests of geographic distance, calculated assuming the WGS84 spherical model of the Earth, vs. pairwise genetic distance of subpopulations estimated by F_{ST}. We tested for isolation by environment for each species individually using partial Mantel tests of genetic distance with environmental distance controlling for geographic distance. Environmental distance was calculated as Euclidean distance among pairs of sample sites based on the centered and scaled climate variables used in SDM. Each test was performed in R version 3.1.2 (R Core Team, 2013) based on 1000 permutations, except for *Q. cornelius-mulleri*, which was based on 120 permutations due to small sample size.

We further investigated the effects of climate and geography on neutral genetic structure for each species using a series of full and partial redundancy analyses (RDA) with variance partitioning. Redundancy analysis, a form of constrained ordination, is the canonical extension of multiple linear regression to multivariate response data in which the canonical axes built from linear combinations of response data are also constrained to be linear combinations of the explanatory variables (Legendre and Legendre, 2012). Redundancy analysis has proven more powerful in detecting complex species–environment relationships and spatial structures in multivariate genetic data than Mantel tests or regression on distance matrices when response and explanatory variables are not limited to distance measures (Legendre and Fortin, 2010; Guillot and Rousset, 2013). We used the 248 allelic variables created from the nine microsatellite loci as the response matrix (Smouse and Williams, 1982) for RDA models of genetic structure. We divided explanatory variables into two matrices (1) climatic, consisting of the same eight variables identified from SDM, and (2) geographic, consisting of the five variables of first- and second-order orthogonal polynomials calculated from the centered latitude and longitude of the oak sampling localities using the poly function in the R package stats. To reduce geographic and climatic matrices to their most relevant and significant components, we applied a stepwise forward model selection process with the Blanchet et al. (2008) double stopping criterion to individual models of geographic and climatic explanatory matrices for each species (Borcard et al., 2011).

To disentangle the effects of geography and climate on genetic structure, we ran three different RDAs for individual species: (1) a full model including both climatic and geographic explanatory variables identified in the forward selection procedure (spatial + climate), (2) a partial model of climatic variables controlling for geographic effects (climate | spatial), and (3) a partial model of geographic variables controlling for climatic effects (spatial | climate). We then used variance partitioning to calculate the proportions of variation in genetic structure that are explained by the independent contributions of climate and geography (Borcard et al., 1992; Peres-Neto et al., 2006). The pure climatic contribution was calculated as the proportion of explained variance in the full RDA (spatial + climate) and also explained by the partial (climate | spatial) RDA. The pure geographic contribution was calculated as the proportion of explained variance in the full RDA, also explained by the partial (spatial | climate) RDA. Finally, we calculated the geographic component of climatic influence, or joint contribution of climate and geography (spatial ∩ climate), as the remaining explained variance in the full RDA not contributed to either pure climatic or geographic effects. For each model, we determined the overall model significance and marginal significance of individual explanatory variables using permutation tests with a minimum of 1000 permutations. We calculated the adjusted coefficient of multiple determination (R^2_{adj}) for full models and the individual geographic and climatic components of variance (Peres-Neto et al., 2006). Mantel tests, RDA, and tests for the significance of explanatory variables were implemented in R using the vegan package (Oksanen et al., 2015). Stepwise forward selection with the Blanchet et al. (2008) double stopping criterion was implemented in R with the forwardsel function in the packfor package (Dray et al., 2013).

We repeated full and partial RDAs on morphological data for *Q. engelmannii* and *Q. berberidifolia*, but excluded *Q. cornelius-mulleri* due to a small sample size of individuals with morphological measurements. As in the CDA, we $\log_{10}$-transformed variables of lamina width, lamina length, petiole ratio, and lamina thickness to correct for skew and excluded the variable for leaf spines due to correlation with other morphological variables and issues with nonnormality. All morphological variables were centered and standardized before the RDA.

RESULTS

Species distribution modeling—Predicted climatic habitat suitability maps were consistent with the known distributions of each oak in southern California. High AUC scores for all three species—0.890 ± 0.0098 (mean ± SD) for *Q. engelmannii*, 0.791 ± 0.0176 for *Q. berberidifolia*, and 0.931 ± 0.0101 for *Q. cornelius-mulleri*—indicated overall high model performance. Although species have high geographic overlap (Fig. 1), the results from pairwise niche identity tests indicated that the habitat suitability of each species is climatically distinct (*D*: $P < 0.001$; *I*: $P < 0.001$ for all pairwise species tests), suggesting species have distinct climatic niches. Overlap in climatic suitability was high between *Q. engelmannii* and *Q. berberidifolia* ($D = 0.612$; $I = 0.864$), and low between *Q. berberidifolia* and *Q. cornelius-mulleri* ($D = 0.180$; $I = 0.409$) and *Q. engelmannii* and *Q. cornelius-mulleri* ($D = 0.138$; $I = 0.327$). The contribution of individual climatic variables to SDMs varied across species (Table 2). Jackknife tests identified temperature seasonality (Bio4) as highly important in determining *Q. engelmannii* and *Q. berberidifolia* habitat suitability, having both the greatest predictive power when used in isolation and the greatest unique information not present in the other climatic variables. Climatic water deficit and AET also had high contributions to habitat suitability models for both species. In contrast, summer precipitation (Bio18) was the single most important variable for *Q. cornelius-mulleri*, having greatest predictive power when used in isolation and the greatest information not present in the other climatic variables.

Genetic and morphological differences among oak species—Canonical discriminant analysis revealed that the three species differed based on multilocus genotypes for both canonical axes (Table 3, Fig. 2A). This result was expected because we prescreened these genotypes to be 90% assignable to one of three species, although we obtained the same result using field identifications and not omitting hybrid individuals. Using the genetically based species assignments, we found that the multivariate leaf morphology differed significantly among the three species for both canonical axes (Table 3). For morphology, there was much greater variation within the species compared with variation in genotype, with some individuals falling within the morphological distribution of a different species (Fig. 2B). The first CDA axis distinguished between *Q. engelmannii* and *Q. cornelius-mulleri* and was most highly correlated with abaxial leaf trichome density and lamina length. The second CDA axis separated *Q. cornelius-mulleri* from the other two oaks and was most highly correlated with adaxial leaf pubescence.

Genetic structure and tests of IBD and IBE—Overall, each species had low values of population differentiation ($F_{ST} = 0.03$ for

TABLE 2. Importance of climatic variables in species distribution models in three southern California oak species. Italicized text indicates the variable with the greatest predictive power and boldface text indicates the variable with the greatest unique contribution, determined from jackknife tests of variable importance in MaxEnt (see methods for further details).

	Quercus engelmannii		*Quercus berberidifolia*		*Quercus cornelius-mulleri*	
Climate variable	**Contribution %**	**Permutation importance**	**Contribution %**	**Permutation importance**	**Contribution %**	**Permutation importance**
T_{seas} (Bio4)	***14.5***	***40.8***	***8.2***	***17.8***	1.5	0.9
PPT_{seas} (Bio15)	4.1	7.2	10.3	8.5	7.7	11.2
Summer PPT (Bio18)	3.7	15.4	2.2	9.7	***32***	***52.1***
Winter PPT (Bio19)	7.8	13.5	9.6	8.6	8	18.5
AET	30.1	1.3	28.4	7.7	0.9	2.8
CWD	24.3	2.7	26.3	18.9	10.2	0.3
Winter T_{min}	2	2	4.5	17.6	20.6	5.8
Summer T_{max}	13.5	17.1	10.6	11.2	19.2	8.3

TABLE 3. Summary of three canonical discriminant function analyses (Proc CANDISC, SAS V9) testing the (A) genetic and (B) morphological differences among *Quercus engelmannii*, *Q. berberidifolia*, and *Q. cornelius-mulleri*. The genetic differences are based on nine microsatellite loci and the morphological differences are based on leaf traits described in the text.

Differences	Canonical correlation	Adjusted canonical correlation	Squared canonical correlation	Eigen value	Approximate *F* value	Numerator df	Denominator df	Pr > *F*
A) Genetic								
1	0.9488	0.9316	0.9003	9.03	14.26	200	418	<0.0001
2	0.9144	0.8871	0.8362	5.11	10.83	99	210	<0.0001
B) Morphological								
1	0.8759	0.8701	0.7672	3.30	31.76	16	328	<0.0001
2	0.5822	0.5649	0.3390	0.51	12.09	7	165	<0.0001

Q. engelmannii; F_{ST} = 0.02 for *Q. berberidifolia*; and F_{ST} = 0.05 for *Q. cornelius-mulleri*). We found evidence for isolation by distance and isolation by environment in only one species, *Q. cornelius-mulleri*, which exhibited significant correlation between genetic distance (F_{ST}) and geographic distance (Mantel test; r = 0.54, P = 0.05), and between environmental distance defined by climate variables and genetic distance controlling for geographic distance (partial Mantel test: r = 0.76, P = 0.04). We did not find significant correlations in the other two species ($-0.17 < r < 0.09$; $P > 0.26$).

Effect of geography and climate on genetic structure—Full RDA models of combined geographic and climatic variables explained a small but significant portion of variation in allelic frequencies for *Q. engelmannii* (RDA; R^2_{adj} = 2.8%, P = 0.001) and *Q. cornelius-mulleri* (RDA; R^2_{adj} = 7.4%, P = 0.001), but not for *Q. berberidifolia* (RDA; R^2_{adj} = 0.6%, P = 0.064) (Table 4A). For the first two species, we found significant unique associations between genetic variation and both climate (climate | spatial) and geography (spatial | climate) (partial RDA; all $P < 0.01$). For *Q. engelmannii*, five climatic variables were significantly associated with genetic variation, temperature seasonality, precipitation seasonality, winter precipitation, AET, and CWD, with both precipitation seasonality and AET retaining significance after controlling for geography (Table 4B). For *Q. cornelius-mulleri*, precipitation seasonality, winter precipitation, AET, and summer maximum temperature were significantly associated with genetic variation, with all but AET retaining significance after controlling for geography. Additionally, climate had a greater unique contribution to genetic variation compared with geography (53.6% vs. 33.2% for *Q. engelmannii* and 48.3% vs. 35.4% for *Q. cornelius-mulleri*). We found a similar trend of greater contribution of climate to genetic variation compared with geography in *Q. berberidifolia*, though the individual unique contributions were not statistically significant ($P > 0.20$). The proportion of genetic variation explained by climate that was also spatially structured (spatial ∩ climate) was similar across all three oaks (12–16%) (Table 4A).

Effects of geography and climate on morphological traits—Full RDA models of combined geographic and climatic variables explained a significant portion of variation in leaf morphology for both *Q. engelmannii* (RDA; R^2_{adj} = 12.7%, P = 0.001) and *Q. berberidifolia* (RDA; R^2_{adj} = 5.8%, P = 0.005) and explained a higher portion of morphological variation compared to genetic variation (Table 5A).

Partial RDAs identified unique, significant associations between climate and morphological variation in both species after controlling for geographic effects (climate | spatial) (*Q. engelmannii*: R^2_{adj} = 1.4%, P = 0.04; *Q. berberidifolia*: R^2_{adj} = 2.6%, P = 0.028). Precipitation seasonality and summer precipitation were significantly associated with morphological variation in *Q. engelmannii*, but only summer precipitation remained significant after controlling for geography (Table 5B). In *Q. engelmannii*, geography (51.3%) had a greater unique contribution relative to climate (19.0%). Additionally, a large (29.7%) proportion of the morphological variation in *Q. engelmannii* explained by climate was also spatially structured (spatial ∩ climate). In contrast, climate had a greater contribution (45.9%) to morphological variation compared

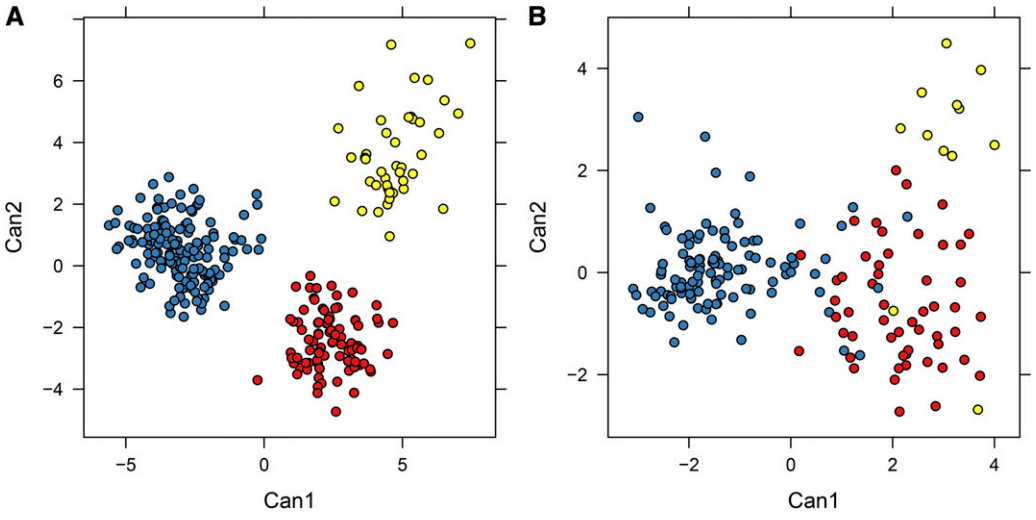

FIGURE 2 (A) Genetic and (B) morphological differentiation of oaks species. Axes correspond to the first and second canonical discriminant functions. Species are represented by colors as follows: *Quercus engelmannii* (blue), *Q. berberidifolia* (red), and *Q. cornelius-mulleri* (yellow).

TABLE 4. (A) Results of redundancy analyses (RDAs) on microsatellite genetic variation for *Quercus engelmannii* (Q_{ENG}), *Q. berberidifolia* (Q_{BER}), and *Q. corneliusmulleri* (Q_{CMU}). Partitioning of variance into pure climatic (Climate | Spatial) and pure spatial (Spatial | Climate), and joint (Spatial ∩ Climatic) components are shown. Proportion constrained corresponds to the partitioned variance relative to the constrained variance of the full RDA model (Spatial + Climate). (B) Significance of individual climatic variables in simple RDAs of genetic variation and climate. Boldface text indicates variables that are still significantly associated with genetic variation after controlling for geography in partial RDAs.

A) Summary of RDA results for genetic variation.

Species	Microsatellite genetic variation	Partitioned variance	Proportion constrained	R^2_{adj}	*P*
Q_{ENG}	Total Variance	3.912			
	Full Model: Spatial + Climate (constrained variance)	0.303	1	0.028	0.001
	Pure Climate: (CWD+Bio19+AET+ Bio4+Bio15) | Spatial	0.162	0.536	0.011	0.001
	Pure Spatial: (XY+Y+Y^2) | Climate	0.097	0.322	0.006	0.004
	Spatial ∩ Climate	0.043	0.142	0.011	NA
Q_{BER}	Total Variance	3.919			
	Full Model: Spatial + Climate (constrained variance)	0.154	1	0.006	0.064
	Pure Climate: (T_{max}+Bio15) | Spatial	0.095	0.614	0.002	0.220
	Pure Spatial: (X^2) | Climate	0.041	0.267	−0.001	0.607
	Spatial ∩ Climate	0.018	0.119	0.005	NA
Q_{CMU}	Total Variance	4.183			
	Full Model: Spatial + Climate (constrained variance)	0.954	1	0.074	0.001
	Pure Climate: (T_{max}+Bio19+AET+Bio15) | Spatial	0.461	0.483	0.024	0.001
	Pure Spatial: (XY+Y+Y^2) | Climate	0.338	0.354	0.016	0.031
	Spatial ∩ Climate	0.156	0.163	0.034	NA

B) Significance of individual climatic variables.

Species	Climate variable	Total variance	Constrained %	*F*	*P*
Q_{ENG}	T_{seas} (Bio4)	0.98	18.7	1.565	0.010
	PPT_{seas} (Bio15)	**0.95**	**18.0**	**1.513**	**0.017**
	Winter PPT (Bio19)	1.16	22.1	1.851	0.001
	AET	**1.06**	**20.2**	**1.694**	**0.002**
	CWD	1.21	23.1	1.936	0.001
Q_{BER}	PPT_{seas} (Bio15)	1.72	59.7	1.555	0.006
	Summer T_{max}	1.25	43.5	1.134	0.235
Q_{CMU}	**PPT_{seas} (Bio15)**	**3.13**	**21.2**	**1.395**	**0.035**
	Winter PPT (Bio19)	**3.59**	**24.3**	**1.600**	**0.001**
	AET	3.59	24.4	1.601	0.005
	Summer T_{max}	**3.61**	**24.5**	**1.610**	**0.004**

to geography (37.8%) in *Q. berberidifolia*; however, the unique contribution of geography was not statistically significant (Table 5A, $P = 0.068$) after controlling for climate. Only one climatic variable, maximum summer temperature significantly contributed to morphological variation (Table 5B).

Contribution of individual climate variables to habitat suitability, genetic structure, and morphology—We found all three oak species differed in the contribution of individual climatic variables to habitat suitability, genetic structure, and leaf morphology (Table 6). Variables most important in defining climatic suitability

TABLE 5. (A) Results of redundancy analyses (RDAs) on morphological leaf trait variation for *Quercus engelmannii* (Q_{ENG}) and *Q. berberidifolia* (Q_{BER}). Partitioning of variance into components and significance of levels are the same as Table 4. (B) Significance of individual climatic variables in simple RDAs of morphology and climate. Boldface text indicates variables that are still significantly associated with morphological variation after controlling for geography in partial RDAs.

A) Summary of RDA results for leaf trait variation.

Species	Morphological leaf variation	Partitioned variance	Proportion constrained	R^2_{adj}	*P*
Q_{ENG}	Total Variance	8.000			
	Full Model: Spatial + Climate	1.271	1	0.127	0.001
	Pure Climate: (Bio15+Bio18) | Spatial	0.241	0.190	0.014	0.040
	Pure Spatial: (XY+Y) | Climate	0.652	0.513	0.067	0.001
	Spatial ∩ Climate	0.378	0.297	0.046	NA
Q_{BER}	Total Variance	8.000			
	Full Model: Spatial + Climate	0.752	1	0.058	0.005
	Pure Climate: (T_{max}) | Spatial	0.345	0.459	0.026	0.028
	Pure Spatial: (X) | Climate	0.284	0.378	0.018	0.068
	Spatial ∩ Climate	0.123	0.163	0.014	NA

B) Significance of individual climatic variables.

	Climate Variable	Total variance	Constrained %	*F*	*P*
Q_{ENG}	PPT_{seas} (Bio15)	4.55	58.8	5.231	0.001
	Summer PPT (Bio18)	**1.98**	**25.6**	**2.276**	**0.048**
Q_{BER}	**Summer T_{max}**	**5.85**	**100**	**3.166**	**0.003**

TABLE 6. Importance of climatic variables in oak habitat suitability, genetic variation, and morphological trait models. Species are abbreviated as follows: *Quercus engelmannii* (Q_{ENG}), *Q. berberidifolia* (Q_{BER}), and *Q. cornelius-mulleri* (Q_{CMU}). XX = Variables with high values for habitat suitability or that retain significance in genetic variation and leaf morphology after controlling for geography. X = variables with moderate values. Low and nonsignificant values are blank. Data are summarized from Tables 2, 4B, and 5B. Q_{CMU} has no test for leaf morphology.

		Habitat suitability			
Species	**Climate variable**	**Contribution %**	**Permutation importance**	**Genetic variation**	**Leaf morphology**
Q_{ENG}	T_{seas} (Bio4)	X	XX	X	
	PPT_{seas} (Bio15)			XX	X
	Summer PPT (Bio18)		X		XX
	Winter PPT (Bio19)		X	X	
	AET	XX		XX	
	CWD	X		X	
	Winter T_{min}				
	Summer T_{max}	X	X		
Q_{BER}	T_{seas} (Bio4)		X		
	PPT_{seas} (Bio15)	X		X	
	Summer PPT (Bio18)				
	Winter PPT (Bio19)				
	AET	X			
	CWD	X	X		
	Winter T_{min}		X		
	Summer T_{max}	X	X	X	XX
Q_{CMU}	T_{seas} (Bio4)				
	PPT_{seas} (Bio15)		X	XX	
	Summer PPT (Bio18)	XX	XX		
	Winter PPT (Bio19)		X	XX	
	AET		X	X	
	CWD	X			
	Winter T_{min}	X			
	Summer T_{max}	X		XX	

were not necessarily significantly associated with genetic structure or leaf morphology. For example, summer precipitation (Bio18), which was the single-most important variable contributing to habitat suitability in *Q. cornelius-mulleri*, was not significantly associated with genetic variation in the other species. Precipitation seasonality (Bio15) was significantly associated with genetic variation in all three species but had low contribution to habitat suitability.

For *Q. engelmannii*, variables related to water balance (AET, CWD) and temperature seasonality (Bio4) had important contributions to both habitat suitability and genetic variation, whereas precipitation seasonality (Bio15) and summer precipitation (Bio18) had the greatest contributions to leaf morphology. For *Q. berberidifolia*, the contribution of individual climate variables to habitat suitability was similar to that of *Q. engelmannii*—temperature seasonality and water balance variables (AET, CWD). Climatic influences on genetic variation, however, were weak and lost entirely after controlling for geographic effects. The species also differed in climatic associations with morphology with summer maximum temperature having a strong contribution to variation in leaf morphology. *Quercus cornelius-mulleri* was most distinct in its climatic requirements for habitat suitability, with a particularly high contribution of summer precipitation, and to a lesser extent winter minimum and summer maximum temperatures. Summer maximum temperature also contributed to genetic variation in the species, along with precipitation seasonality, winter precipitation, and AET. Thus, the climatic factors influencing habitat suitability and regional distribution patterns differed from those influencing genetic and morphological variation in all three oaks, indicating species-specific responses to different climatic factors.

DISCUSSION

Climate shaped regional patterns of geographic distribution, neutral genetic variation, and morphological variation of the three southern California oak species in various ways. Species differed notably in the specific climatic variables influencing regional patterns of distribution, despite a high degree of geographic overlap. Our use of SDM identified individual climate variables that shaped habitat suitability, and we used the climate variables directly to assess the association of climate with species' distributions. As we examined the importance of climate variables to genetic and morphological spatial patterns, controlling for geography, we found that climate has an independent role in shaping patterns of variation in genetic and phenotypic variation and that distinctive climate variables were important at each level of biological organization.

Species distribution modeling—SDM revealed species-specific differences in the climatic factors influencing regional patterns of distribution of the three oak species in southern California. Not surprisingly, the two species with the greatest geographic overlap also had the greatest similarity in the importance of individual climatic variables to habitat suitability (e.g., shared importance of temperature seasonality, CWD, and AET for both *Q. engelmannii* and *Q. berberidifolia*). In contrast, summer precipitation was most important in defining habitat suitability for *Q. cornelius-mulleri*, which has the most interior distribution of all three oaks, occurring in dry washes and slopes in desert margins and juniper–piñon woodlands of inland southern California. We found the use of individual climatic variables identified by SDMs was much more

informative in identifying important climatic associations with genetic and morphological variation than a single, integrated measure like that of habitat suitability. Indeed, partial Mantel tests and constrained ordinations where habitat suitability scores were substituted for individual climatic variables failed to explain significant variation in either genetic structure or leaf morphology (results not shown). These findings suggest careful consideration is necessary before applying SDM and single habitat suitability metrics to landscape genetic studies.

Genetic structure–geography vs. climate—Despite the fact that southern California is a topographically and climatically complex region (Vandergast et al., 2008), we found only subtle genetic structure across populations within each species (all three species have $F_{ST} < 0.05$). These values are lower than those observed for other California oak studies. For example, *Quercus lobata* (valley oak) had higher levels of genetic differentiation using microsatellite markers ($F_{ST} = 0.12$) (Grivet et al., 2008), possibly due to a species-wide rather than regional focus for sampling. However, higher levels of genetic structure ($F_{ST} = 0.16$) in *Q. lobata* were also found using randomly sampled single nucleotide polymorphisms (SNPs) of three populations sampled on a similar geographic scale to this study, though those populations were separated by mountain ranges (Platt et al., 2015). The pattern of low genetic differentiation in southern California oaks found in our current study could reflect long-distance pollen flow or recent expansions from a common ancestral population in the region. Nonetheless, we observed sufficient genetic structure to indicate that gene flow would not swamp out the impact of climate factors on the distribution of genotypes.

Constrained ordinations of combined geographic and climatic variables explained only a small portion of the total genetic variation (2.8%, 0.6%, and 7.41% for *Q. engelmannii*, *Q. berberidifolia*, and *Q. cornelius-mulleri*, respectively). These low adjusted R^2 values are not surprising given the number of other unmeasured factors, such as additional genotypes, localities, environmental variables and stochastic effects, not included in our analyses. More importantly, most genetic variation is likely within sites/samples, as is commonly observed in F_{ST}/AMOVA-type analyses. The low values of F_{ST} that we report in this study reflects that about 5% of variation is among sites, which is what we are partitioning in the RDA. For example, *Q. berberidifolia*, the most widely and continuously distributed of the three species, had only 2% of the genetic variation distributed among populations and nonsignificant associations between genetic variation and both climate and geography. This lack of spatial genetic structure in *Q. berberidifolia* may be caused by large effective population sizes and/or high gene flow among populations, which would homogenize genetic differences among populations and create large genetic variation within populations. Consequently, for this species, we cannot assess the partial associations of climate or geography on genetic variation in microsatellite loci. For the other two species with significant associations between genetic variation and climate/geography (*Q. engelmannii* and *Q. cornelius-mulleri*), we found a greater unique contribution of climate alone (54% and 61%, respectively). This finding suggests that isolation by environment (climate) is influencing the distribution of genetic variation and is similar to what we reported for *Q. engelmannii* previously (Ortego et al., 2012) using causal modeling (Cushman et al., 2006) to analyze the potential influence of climatic factors. In studies examining *Q. lobata*, climate also played a strong role in multivariate genetic gradients (Sork et al., 2010; Gugger et al., 2013). One possible explanation for the impact of climate in this heterogeneous southern California region is that gene flow from neighboring dissimilar habitats may be disfavored (Sexton et al., 2014; Wang and Bradburd, 2014), creating mosaics of genetic variation that correlate with climate variables.

The life histories and habitat distributions of *Q. engelmannii* and *Q. cornelius-mulleri* differ sharply—*Q. engelmannii* is a tree that grows in higher elevations or more mesic slopes while *Q. cornelius-mulleri* is a desert shrub. Interestingly, they shared three climate variables that were significantly associated with multivariate genetic variation: precipitation seasonality, winter precipitation, and actual evapotranspiration. Despite these similarities, there were some differences in climatic relationships: for *Q. engelmannii*, climatic water deficit and temperature seasonality were important, and for *Q. cornelius-mulleri*, maximum temperature was important. Taken collectively, our results suggest that certain climatic factors shape genetic patterns more than spatial factors even in the presence of presumed high gene flow. Variation in the importance of specific climate variables among species suggests different aspects of environmental heterogeneity may influence gene flow and demography differently in each species.

Leaf morphology–geography vs. climate—We anticipated that leaf morphology would be correlated with climate because several leaf traits in oaks improve drought response (Abrams, 1990). Moreover, given that some variation in leaf traits is due to phenotypic plasticity in response to the environment, observed morphological variation could have a stronger association with climate than that found in genetic variation alone. Indeed, for *Q. berberidifolia*, climate alone accounted for more of the variation in leaf morphological than geography alone (46% vs. 28% of the explained variance), although R^2_{adj} values were very small. Unexpectedly, geography had a greater unique contribution to leaf morphology relative to climate (51% vs. 19% of the explained variance) in *Q. engelmannii*. Additionally, the proportion of variance explained by climate that was spatially structured was relatively large (30%). These strong geographic effects may be due to the fact that *Q. engelmannii* has spatially separated subpopulations that are sufficiently distinguishable to be detected as subgroups with Bayesian clustering analyses (Ortego et al., 2012). The contrast in climate effects on morphology between the two species illustrates the way in which climate and geography, including the effects of evolutionary history, can interact differently among sympatric species.

Even though we find for both species that climate is significantly correlated with morphology, the association is not strong, which may be due to multiple factors—weak selection, low plasticity, extensive gene flow, and/or low intraspecific variability for the measured traits. It is also possible that we see a weak association with climate variables because we are not measuring climate at the appropriate spatial scale. Although relatively fine scale with respect to regional distribution patterns, the 270-m climate data downscaled by BCM may not capture topo- and microclimatic variability that influences local patterns of both morphological and genetic variation. Nonetheless, given that phenotypes in natural populations often show larger differences than those measured in common gardens because they include both genetic and environmental effects, our results indicate these traits may not be very genetically differentiated across this heterogeneous region, which is consistent with the low genetic structure we found using the microsatellite markers.

Impacts of climate on species response—Each species varied in its relationship with individual climatic variables with respect to habitat suitability, genetic variation, and morphological variation (see Table 6). In general, the critical climate variables at all three levels of biological organization differed among species, with one exception—precipitation seasonality, which was important in explaining associations between genetic variation and climate for all three species. This finding could indicate a potential common selective pressure for the three species in southern California, where the precipitation regime is highly variable, both within and between years. Otherwise, responses to climate were highly species-specific.

Given concerns about the impact of rapid climate change, it is useful to assess the extent to which certain climate variables will have an impact at multiple levels of biological process. For example, Loarie et al. (2008) predicted shifts in suitable habitat for California's endemic flora that could result in multiple extinctions. Our comparative analysis here indicates that the climatic variables important in shaping regional patters of species distribution are not necessarily the same as those affecting genetic structure or phenotypic patterns. In *Q. berberidifolia,* only one of the variables, maximum summer temperature, played a role in three of the models (habitat suitability, genetic variation, morphology), and for the other species, the role of climate differed across models. Thus, we advise some caution when applying SDM to make inferences about landscape genetic patterns of populations or evolutionary and ecological responses of organisms. Because a species distribution modeling approach applies a single predictive relationship throughout the range of a species or focal region, it is unlikely to take into account local adaptation, IBE, and variable responses among populations within a species range (Rehfeldt et al., 2002, 2006). We assume that the climatic variables included in our species distribution models are limiting factors for our species (e.g., that temperature or water availability are ecophysiological limiting factors for the species) (Guisan and Thuiller, 2005), and that the spatial resolution of our environmental data are relevant to the mechanisms shaping both geographic distribution and genetic and phenotypic responses. Another limitation of any climate study is that it may overlook other important environmental factors influencing ecological and evolutionary processes, such as soil composition and biotic interactions. This problem is relevant to climate change studies because species interactions, soil biochemistry, and many other environmental factors are affected by climate. Thus, the climate variables important in predicting a species distribution do not necessarily indicate high selective pressure on individuals and therefore may not be as important in shaping migration, historical demography, or natural selection.

CONCLUSIONS

Species-specific responses to different environmental factors illustrate that the drivers of genetic and phenotypic differentiation can strongly differ even among related species distributed in similar landscapes. Our findings highlight the importance of integrating genetic, phenotypic, and climatic data across multiple species and spatial scales to better understand the factors that shape demographic trajectories of populations and their responses to climate (Wiens, 1989). Our results showing differences in how the environment shapes contemporary distributions, genetic variation, and phenotypic variation in southern Californian oaks imply that each species has a unique pattern of local adaptation and therefore will also exhibit different local to regional responses to projected climate change. As a result, even currently overlapping species with similar dispersal capabilities will not necessarily share distributions in the future. To better understand the interactions of species with their climate, forthcoming research should attempt to measure climate at the same spatial scale and degree of sensitivity for the SDMs as the individual genotypic and phenotypic samples. Due to the emergence of next-generation sequencing, it is now feasible to examine both neutral genetic variation that distinguishes the impacts of historical demographic processes and climate-associated selection on spatially divergent patterns of genetic variation (Sork et al., 2013). Moreover, emerging techniques in spatial modeling that allow the combination of genomic data and SDM approaches will generate predictions about the geographic distribution of genetic data in response to climate change (Fitzpatrick and Keller, 2015). This incorporation of genetic and phenotypic responses to species distribution models will provide better predictions of the distribution of species, their genetic response to change, and the future composition of communities.

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