Short title: Genetic and phenotypic spatial patterns in California oaks

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

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ABSTRACT

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 SDM 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 impact due to the same climate variable.

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 unlike to have similar distributions in the future.

Key words: California; climate; 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 and contraction, and migration (Avise, 2000), which in turn influence the fine scale structure 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, Ikegami, and Sork (2013) found evidence that current and historical climate at the last glacial maximum (~20,000 years ago) was associated with the genetic composition of valley oak, *Quercus lobata*, more ~~that~~ 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, over 70% of the studies indicated that the environment was important in ~~the movement of genes~~ (Sexton, Hangartner, and Hoffmann, 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 or phenotypic plasticity or because of their common ancestry (West-Eberhard, 1989a; Marais, Hernandez, and Juenger, 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, Stevens, and Kaufman, 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; Soberon, 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 versus 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 (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, referred to as 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, Hangartner, and Hoffmann, 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, Egan, and Funk, 2008 and citations therein; Andrew et al., 2012).

Geographic patterns of phenotypic variation also reflect the influence of the environment (Stebbins, 1950). Many traits will have diverged across sites in response to environmental gradients, creating locally adaptive genetic differences driven by selective forces (e.g., Clausen, Keck, and Hiesey, 1947; Endler, 1986; Savolainen, Pyhajarvi, and Knurr, 2007). For example, Ramírez-Valiente et al. (2009) show 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. Such traits are likely to have ~~genes underlying those traits~~, but they may also reflect phenotypic plasticity (Bradshaw, 1965; West-Eberhard, 1989b; Scheiner, 1993; Nicotra et al., 2010). Therefore, while an association of phenotype with environmental gradients provides initial evidence that traits may be under selection (Endler, 1986; Linhart and Grant, 1996), additional evidence is needed to identify an underlying genetic basis (Anderson, Willis, and Mitchell-Olds, 2011).

The overall goal of this study is to analyze the association of climate in 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 use SDM to identify the climatic variables important in shaping regional distribution patterns for each of the three species. Second, we assess 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 investigate 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 add morphological data to our analyses and utilize different 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 roles of climate and geography 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 (USA). *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, Goldman, and Vorobik, 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, including the two other study species (J Ortego and VL Sork, unpublished data). *Quercus berberidifolia* (California scrub oak) and *Q. cornelius-mulleri* (Muller's oak) 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 to *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 in Ortego et al. (2012) and Ortego et al. (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.

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 downloaded from the Consortium of California Herbaria on January 18, 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 geo-referenced 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*.

We obtained 30-year 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, Neilson, and Phillips, 1994). We selected a subset of variables to use in SDMs 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 (Tmin), calculated as the average minimum temperature over the coldest months (December-February); summer maximum temperature (Tmax), 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, Anderson, and Schapire, 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, Jimenez-Valverde, and Real, 2008) averaged over five-fold cross-validation replicates. Predicted climatic habitat suitability maps were produced for each species using MaxEnt's logistic output, which provide an estimate of probability of presence ranging from 0 (low suitability) and 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, applying laboratory methods commonly used in our lab (Sork et al., 2002; Grivet et al., 2008), we used nine polymorphic microsatellite markers 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 (SAS Institute 1989) 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 the results based on STRUCTURE (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 multi-locus 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 (see below) 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, Glor, and Turelli, 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, Glor, and Turelli, 2008) with 100 pseudoreplicates to determine if 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 v9). 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, and 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 AMOVA and calculated pairwise F_{ST} among sites in 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 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, versus pair-wise 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 the SDM modeling. Each test was performed ~~in~~ in R 3.1.2 (R Core Development Team) 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 in SDMs, 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, Legendre, and Borcard (2008) double stopping criterion to individual models of geographic and climatic explanatory matrices for each species (Borcard, Gillet, and Legendre, 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 (climate + geography), (2) a partial model of climatic variables controlling for geographic effects (climate | geography), and (3) a partial model of geographic variables controlling for climatic effects (geography | 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, Legendre, and Drapeau, 1992; Peres-Neto et al., 2006). The pure climatic contribution was calculated as the proportion of explained variance in the full RDA (climate + geography) and also explained by the partial (climate | geography) RDA. The pure geographic contribution was calculated as the proportion of explained variance in the full RDA, also explained by the partial (geography | climate) RDA. Finally, we calculated the geographic component of climatic influence, or joint contribution of climate and geography (climate ∩ geography), 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, Blanchet, and Legendre, 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 non-normality. All morphological variables were centered and standardized prior to RDA.

RESULTS

Species distribution models—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 ± standard deviation) 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~~ indicate that the habitat suitability of each species is climatically distinct (*D*: $P < 0.001$; *I*: $P < 0.001$ for all pairwise species tests), suggesting 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 (Bio 4) 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 (Bio 18) 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 is expected because we pre-screened 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 to variation in genotype, with some individuals falling within the 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 isolation by distance—Overall, each species had low values of population differentiation ($F_{\mathrm{ST}} = 0.03$ for *Q. engelmannii*; $F_{\mathrm{ST}} = 0.02$ for *Q. berberidifolia*; and $F_{\mathrm{ST}} = 0.05$ 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). In the first two species, we found significant unique associations between genetic variation and 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 to geography (53.6% versus 33.2% for *Q. engelmannii* and 48.3% versus 35.4% for *Q. cornelius-mulleri*). We found a similar trend of greater contribution of climate to genetic variation compared to geography in *Q. berberidifolia*, though the individual unique contributions were not statistically significant ($P > 0.20$). Precipitation seasonality significantly associated with genetic variation in *Q. berberidifolia*, but not after controlling for geography. 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; $R^2_{adj} = 0.127$, $P = 0.001$) and *Q. berberidifolia* (RDA; $R^2_{adj} = 0.058$, $P = 0.005$) 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*: $R^2_{adj} = 0.014$, $P = 0.04$; *Q. berberidifolia*: $R^2_{adj} = 0.026$, $P = 0.028$). 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 to geography (37.8%) in *Q. berberidifolia*, however, the unique contribution of geography, was not 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 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 species. Precipitation seasonality (Bio15) was significantly associated with genetic variation in all three species but had low contribution to species distribution models.

For *Q. engelmannii*, variables related to water balance (AET, CWD) and temperature seasonality had important contributions to both habitat suitability and genetic variation, whereas precipitation seasonality 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 ~~habitat suitability~~, with particularly a 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 different ways. Species differed notably in the specific climatic variables influencing regional patterns of distribution, despite a high degree of geographic overlap. Our use of SDMs identified individual climate variables that shaped habitat suitability, and we utilized 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 geographic variation in genetic and phenotypic variation and that different climate variables were important at each level of biological organization.

Species Distribution Models—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 SDMs and single habitat suitability metrics to landscape genetic studies.

Genetic structure--geography versus 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 in 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, the genetic structure we find is significant among localities for each of the species, suggesting climate could have an influence 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. For example, 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, for *Q. berberidifolia*, the most widely and continuously distributed of the three species, F_{ST} = 2% and in the RDA, the association between genetic variation and climate and geography was not significant. It is possible that *Q. berberidifolia* may maintain large effective population sizes and/or high gene flow among populations, which could 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. Because our interests lie in the explainable variation, the explained constrained variance is of greater interested. 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, Ikegami, and Sork, 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 correlates with climate variables.

The life histories and habitat distributions of *Quercus 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 are 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 versus climate—We anticipated that leaf morphology would be correlated with climate, as several leaf traits in oaks improve drought response

(Abrams, 1990). Moreover, given that some leaf traits respond with phenotypic plasticity to the environment, morphological variation could have both genetic and non-genetic associations with climate that could be even stronger than those found for genetic variation. Indeed, the overall percent of variation explained by the two full RDA models of morphology was greater than was explained for the genetic RDA models for both *Q. engelmannii* and *Q. berberidifolia*. In *Q. engelmannii*, geography had a greater unique contribution to leaf morphology relative to climate. Additionally, the proportion of variance explained by climate that was spatially structured was relatively large. 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). In contrast, climate had a greater unique contribution to morphological variation in *Q. berberidifolia* relative to geography.

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 micro-climatic variability 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 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, the three species showed very species' specific patterns.

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) predict shifts in suitable habitat for California's endemic flora that could result in multiple extinctions. Our comparative analysis here indicates that we will be unable to make predictions based on habitat suitability and regional distribution patterns about whether the critical climate variables for habitat suitability will be the same ones 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 regional SDMs to make inferences about landscape genetic patterns of populations or about 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; Rehfeldt et al., 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 eco-physiological limiting factors for the species) (Guisan and Thuiller, 2005), and that the spatial resolution of our environmental data is 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 climate can affect species interactions, soil biochemistry, and many other environmental factors 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 environment shapes contemporary distributions, genetic variation, and phenotypic variation in these species imply that different patterns of local adaptation and therefore different local to regional responses to projected climate change are likely. 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 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, models exist that will allow spatial modeling that combines genomic data and SDM approaches that will generate predictions about the geographic distribution of genetic data in response to climate change (Fitzpatrick and Keller, 2015). The 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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TABLES

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}) are indicated for each locality.

Locality	Code	Latitude	Longitude	N_{ENG}	N_{BER}	N_{CMU}
Glendora	GLE	34.177483	-118.095	2	0	0
Pasadena	PAS	34.134079	-118.0989	16	0	0
Yucaipa	YUC	34.038817	-117.0217	0	2	1
Joshua Tree National Park	JOS	34.01738	-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	-116.893	5	1	0
Oak Knoll	OAK	33.29821	-116.9221	10	0	0
Lake Henshaw	HEN	33.276442	-116.855	5	0	0
Warner Springs	WAR	33.27523	-116.6241	2	7	0
Ranchita	RAN	33.211081	-116.4855	0	0	18
Daley Ranch	DAL	33.16599	-117.047	2	0	0
Santa Ysabel	YSA	33.10279	-116.6694	8	6	0
Julian	JUL	33.07477	-116.5491	12	3	0

Locality	Code	Latitude	Longitude	N_{ENG}	N_{BER}	N_{CMU}
Lake Hodges	HOD	33.0747	-117.1181	3	0	0
Ramona	RAM	33.029917	-116.8231	7	0	0
Louis A. Stelzer County Park	LOU	32.881655	-116.9012	2	1	1
Laguna Mountain	LAG	32.849683	-116.4852	0	5	0
Japatul	JAP	32.82338	-116.6275	1	2	0
Alpine	ALP	32.81409	-116.7724	7	0	0
Cleveland National Forest	CLE	32.776504	-116.4948	5	5	0
McCain Valley Road	CAI	32.77026	-116.2586	0	0	6
Lawson Valley Road	LAW	32.74461	-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

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

Climate Variable	*Q. engelmannii*		*Q. berberidifolia*		*Q. cornelius-mulleri*	
	Percent Contribution	Permutation Importance	Percent Contribution	Permutation Importance	Percent 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	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 Tmin	2	2	4.5	17.6	20.6	5.8
Summer Tmax	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 genetic (A) and morphological (B) differences among *Q. 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 text.

	Canonical correlation	Adjusted Canonical correlation	Squared Canonical Correlation	Eigen-value	Approximate F Value	Numerator Degrees of Freedom	Denominator Degrees of Freedom	Pr > F
A. Genetic								
1	0.9488	0.9316	0.9003	9.03	14.26	200	418	<.0001
2	0.9144	0.8871	0.8362	5.11	10.83	99	210	<.0001
B. Morphological								
1	0.8759	0.8701	0.7672	3.30	31.76	16	328	<.0001
2	0.5822	0.5649	0.3390	0.51	12.09	7	165	<.0001

Table 4. (A) Results of redundancy analyses (RDAs) on microsatellite genetic variation for *Q. engelmannii* (Q_{ENG}), *Q. berberidifolia* (Q_{BER}), and *Q. cornelius-mulleri* (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. Bold face 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*-Value
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: (Tmax+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

Species	Microsatellite genetic variation	Partitioned Variance	Proportion Constrained	R^2_{adj}	*P*-Value
Q_{CMU}	Total Variance	4.183			
	Full Model: Spatial + Climate (constrained variance)	0.954	1	0.074	0.001
	Pure Climate: (Tmax+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	Percent Constrained	*F*	*P*-value
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 Tmax	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 Tmax	**3.61**	**24.5**	**1.610**	**0.004**

Table 5. (A) Results of redundancy analyses (RDAs) on morphological leaf trait variation for *Q. 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. Bold face 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*-value
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: (Tmax) | 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	Percent Constrained	*F*	*P*-value
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 Tmax**	**5.85**	**100**	**3.166**	**0.003**

Table 6. Importance of climatic variables in oak habitat suitability, genetic, and morphological trait models. Species are abbreviated as follows: *Q. 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 non-significant values are blank. Data is summarized from Tables 2, 4B, and 5B. (Q_{CMU} has no test for leaf morphology.)

		Habitat Suitability		Genetic Variation	Leaf Morphology
Species	Climate Variable	Percent Contribution	Permutation Importance		
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 Tmin				
	Summer Tmax	X	X		
Q_{BER}	T_{seas} (Bio4)		X		
	PPT_{seas} (Bio15)	X		X	
	Summer PPT (Bio18)				
	Winter PPT (Bio19)				
	AET	X			

		Habitat Suitability		Genetic Variation	Leaf Morphology
Species	Climate Variable	Percent Contribution	Permutation Importance		
	CWD	X	X		
	Winter Tmin		X		
	Summer Tmax	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 Tmin	X			
	Summer Tmax	X		XX	

Appendices

Appendix 1. Climatic variables at oak sampling localities. Climate variables were extracted using sampling site latitude and longitude from 30-year averages of recent historical (1951–1980) climate data from the California Basin Characterization Model (BCM; Flint and Flint, 2012; Flint et al., 2013).

Figures

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

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

Figure 1

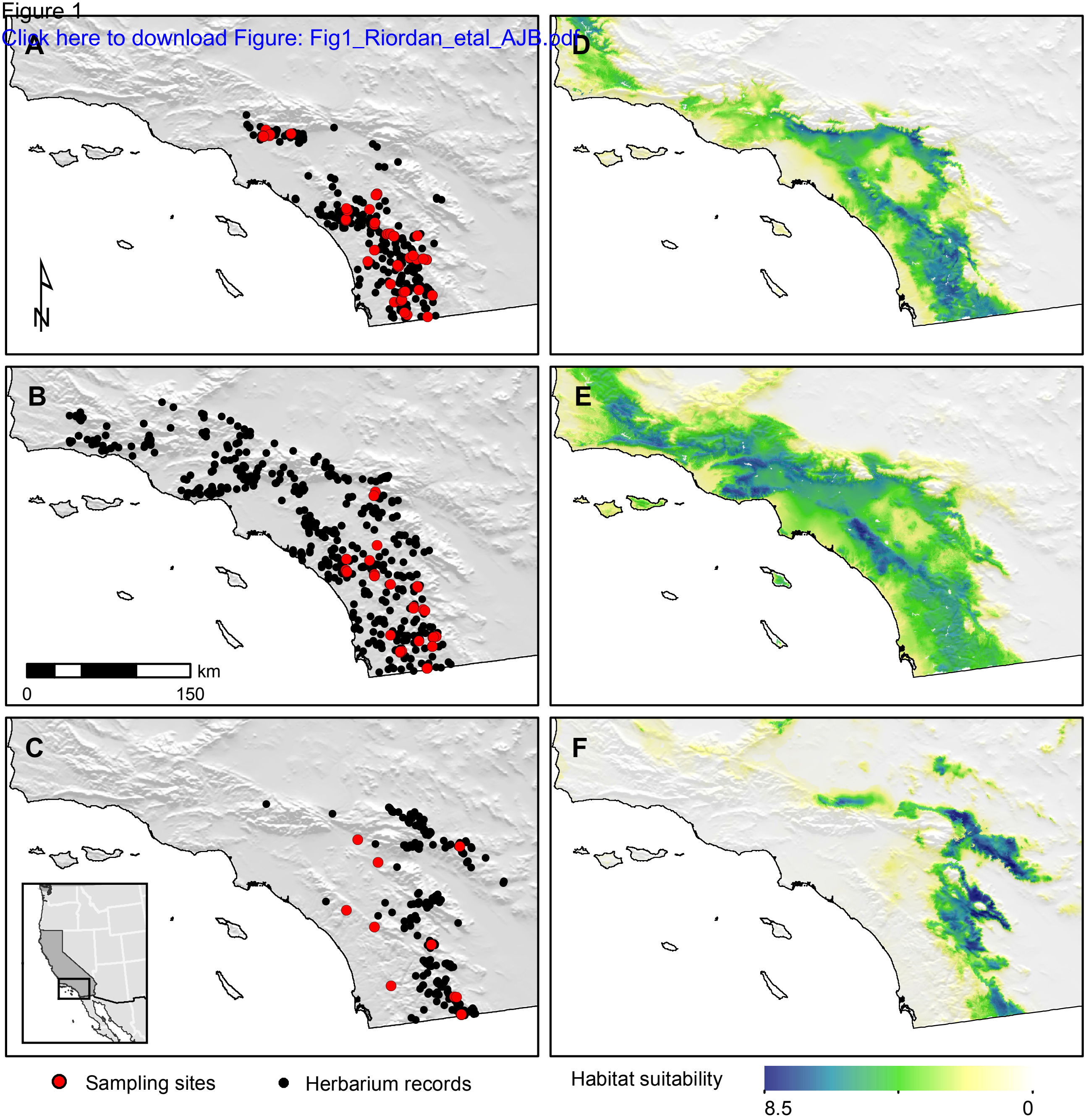
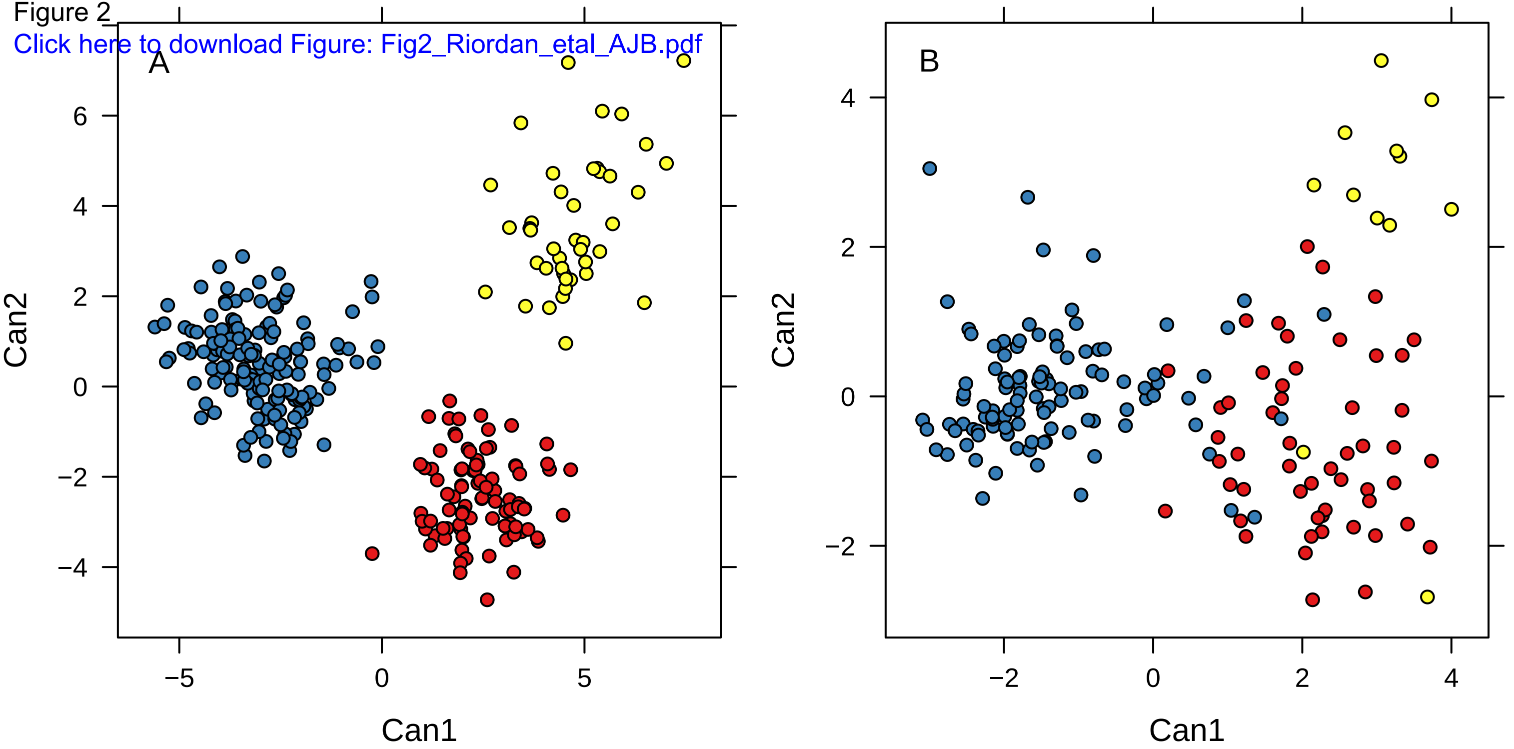

A
N
D
B
km
0
150
E
C
F
Sampling sites
Herbarium records
Habitat suitability
8.5
0

Figure 2



Tree ID	**Scientific Name**	**Locality Name**	**Latitude**	**Longitude**	**Elevation (meters)**	**Morphology data (0=missing)**
1--3	*Quercus berberidifolia*	De Luz	33.431967	-117.322733	114	1
1--4	*Quercus berberidifolia*	De Luz	33.432100	-117.322700	114	1
1--6	*Quercus berberidifolia*	De Luz	33.417783	-117.311983	139	1
1--9	*Quercus berberidifolia*	De Luz	33.417200	-117.312800	139	1
1--11	*Quercus berberidifolia*	De Luz	33.416300	-117.318383	96	1
1--12	*Quercus berberidifolia*	De Luz	33.415850	-117.318167	96	1
1--15	*Quercus engelmannii*	De Luz	33.421050	-117.320267	112	1
1--16	*Quercus engelmannii*	De Luz	33.421250	-117.320467	112	1
1--17	*Quercus berberidifolia*	De Luz	33.422383	-117.321333	106	1
1--18	*Quercus berberidifolia*	De Luz	33.422833	-117.321583	106	1
1--19	*Quercus engelmannii*	De Luz	33.424533	-117.322233	93	1
1--20	*Quercus engelmannii*	De Luz	33.424517	-117.322183	93	0
1--22	*Quercus engelmannii*	De Luz	33.426417	-117.321750	104	1
1--25	*Quercus berberidifolia*	De Luz	33.426617	-117.321583	104	1
2--2	*Quercus berberidifolia*	Pala Reservation	33.375217	-117.044967	249	1
2--4	*Quercus engelmannii*	Pala Reservation	33.379617	-117.044800	273	1
2--5	*Quercus engelmannii*	Pala Reservation	33.394683	-117.036100	495	1
2--6	*Quercus engelmannii*	Pala Reservation	33.394283	-117.036533	495	0
2--7	*Quercus engelmannii*	Pala Reservation	33.392783	-117.037817	495	1
2--9	*Quercus engelmannii*	Pala Reservation	33.391950	-117.038467	475	1
2--10	*Quercus berberidifolia*	Pala Reservation	33.391550	-117.040217	475	1
2--11	*Quercus engelmannii*	Pala Reservation	33.391533	-117.040783	475	1
2--12	*Quercus engelmannii*	Pala Reservation	33.391400	-117.041033	475	1
2--13	*Quercus engelmannii*	Pala Reservation	33.389400	-117.040250	410	1
2--15	*Quercus berberidifolia*	Pala Reservation	33.377067	-117.045600	263	1
2--16	*Quercus berberidifolia*	Pala Reservation	33.376833	-117.045667	263	1
2--17	*Quercus cornelius-mulleri*	Pala Reservation	33.375833	-117.045300	263	1
2--18	*Quercus berberidifolia*	Pala Reservation	33.375633	-117.045167	263	1
3--1	*Quercus engelmannii*	Harolds	33.302200	-116.910467	774	0
3--3	*Quercus engelmannii*	Harolds	33.301967	-116.886200	1168	0
3--4	*Quercus engelmannii*	Harolds	33.301967	-116.886200	1168	1
3--5	*Quercus engelmannii*	Harolds	33.301950	-116.887517	1168	0
3--6	*Quercus engelmannii*	Harolds	33.301983	-116.887650	1168	0
3--7	*Quercus berberidifolia*	Harolds	33.302800	-116.885817	1168	1
4--1	*Quercus engelmannii*	Lake Henshaw	33.276817	-116.853300	719	1
4--2	*Quercus engelmannii*	Lake Henshaw	33.276150	-116.853967	719	1
4--3	*Quercus engelmannii*	Lake Henshaw	33.275767	-116.853617	719	1
4--4	*Quercus engelmannii*	Lake Henshaw	33.277417	-116.858433	721	1
4--5	*Quercus engelmannii*	Lake Henshaw	33.277033	-116.859267	721	1
5--2	*Quercus berberidifolia*	Warner Springs	33.275067	-116.622900	1074	1
5--4	*Quercus berberidifolia*	Warner Springs	33.275033	-116.622400	1099	0
5--6	*Quercus berberidifolia*	Warner Springs	33.275050	-116.621817	1099	0
5--8	*Quercus berberidifolia*	Warner Springs	33.275230	-116.624060	1074	1
5--9	*Quercus berberidifolia*	Warner Springs	33.275360	-116.624340	1074	1
5--10	*Quercus berberidifolia*	Warner Springs	33.275360	-116.624340	1074	0
5--11	*Quercus engelmannii*	Warner Springs	33.275510	-116.624410	1074	1
5--12	*Quercus engelmannii*	Warner Springs	33.273670	-116.620640	1099	1
5--13	*Quercus berberidifolia*	Warner Springs	33.272250	-116.619720	1107	1
6--1	*Quercus engelmannii*	Lake Hodges	33.074400	-117.118100	91	1
6--2	*Quercus engelmannii*	Lake Hodges	33.074750	-117.118017	91	1
6--3	*Quercus engelmannii*	Lake Hodges	33.074950	-117.118100	91	1
7--1	*Quercus engelmannii*	Ramona	33.027867	-116.820017	501	1
7--2	*Quercus engelmannii*	Ramona	33.028700	-116.819733	525	1
7--3	*Quercus engelmannii*	Ramona	33.026583	-116.820833	501	1
7--4	*Quercus engelmannii*	Ramona	33.026000	-116.820783	501	1

7--5	*Quercus engelmannii*	Ramona	33.026317	-116.820733	501	1
7--7	*Quercus engelmannii*	Ramona	33.037450	-116.829817	529	1
7--8	*Quercus engelmannii*	Ramona	33.036500	-116.829433	529	1
8--1	*Quercus engelmannii*	Santa Ysabel	33.093333	-116.702067	889	1
8--2	*Quercus engelmannii*	Santa Ysabel	33.110217	-116.670150	928	1
8--3	*Quercus engelmannii*	Santa Ysabel	33.109300	-116.669300	963	1
8--4	*Quercus engelmannii*	Santa Ysabel	33.109367	-116.669133	963	1
8--6	*Quercus engelmannii*	Santa Ysabel	33.108833	-116.668983	931	1
8--7	*Quercus berberidifolia*	Santa Ysabel	33.109133	-116.668933	963	1
8--8	*Quercus engelmannii*	Santa Ysabel	33.108783	-116.669000	931	1
8--9	*Quercus engelmannii*	Santa Ysabel	33.108633	-116.668900	931	1
8--10	*Quercus berberidifolia*	Santa Ysabel	33.108550	-116.668850	931	1
8--11	*Quercus berberidifolia*	Santa Ysabel	33.108033	-116.668617	931	1
8--12	*Quercus berberidifolia*	Santa Ysabel	33.107667	-116.668467	931	1
8--13	*Quercus berberidifolia*	Santa Ysabel	33.107317	-116.668300	931	1
8--15	*Quercus berberidifolia*	Santa Ysabel	33.098300	-116.664983	962	1
8--17	*Quercus engelmannii*	Santa Ysabel	33.079850	-116.637083	1142	1
9--1	*Quercus berberidifolia*	Julian	33.080450	-116.572150	960	1
9--2	*Quercus engelmannii*	Julian	33.080400	-116.572550	960	1
9--3	*Quercus engelmannii*	Julian	33.080883	-116.572767	960	1
9--4	*Quercus engelmannii*	Julian	33.081133	-116.572233	960	1
9--5	*Quercus engelmannii*	Julian	33.081817	-116.572067	979	1
9--6	*Quercus berberidifolia*	Julian	33.080333	-116.571983	960	1
9--12	*Quercus berberidifolia*	Julian	33.072583	-116.558467	873	1
9--16	*Quercus engelmannii*	Julian	33.071250	-116.542650	922	1
9--17	*Quercus engelmannii*	Julian	33.071617	-116.541900	922	1
9--18	*Quercus engelmannii*	Julian	33.071700	-116.541667	922	1
9--19	*Quercus engelmannii*	Julian	33.072233	-116.540717	835	1
9--20	*Quercus engelmannii*	Julian	33.072500	-116.539983	835	1
9--21	*Quercus engelmannii*	Julian	33.073000	-116.539050	835	1
9--22	*Quercus engelmannii*	Julian	33.073250	-116.538767	835	1
9--23	*Quercus engelmannii*	Julian	33.073817	-116.538300	797	1
11--1	*Quercus berberidifolia*	Laguna Mountain	32.853817	-116.454283	1745	1
11--4	*Quercus berberidifolia*	Laguna Mountain	32.857467	-116.457467	1683	1
11--6	*Quercus berberidifolia*	Laguna Mountain	32.849683	-116.485150	1509	1
11--9	*Quercus berberidifolia*	Laguna Mountain	32.849517	-116.485567	1509	1
11--11	*Quercus berberidifolia*	Laguna Mountain	32.849450	-116.485967	1509	1
12--1	*Quercus engelmannii*	Cleveland National Forest	32.776250	-116.494517	1041	1
12--2	*Quercus engelmannii*	Cleveland National Forest	32.776350	-116.494683	1041	1
12--3	*Quercus engelmannii*	Cleveland National Forest	32.776500	-116.494767	1041	1
12--4	*Quercus berberidifolia*	Cleveland National Forest	32.776650	-116.494850	1041	1
12--5	*Quercus berberidifolia*	Cleveland National Forest	32.776733	-116.494933	1041	1
12--6	*Quercus engelmannii*	Cleveland National Forest	32.776917	-116.495167	1041	1
12--7	*Quercus berberidifolia*	Cleveland National Forest	32.777033	-116.495250	1044	1
12--8	*Quercus engelmannii*	Cleveland National Forest	32.776117	-116.494483	1041	1
12--9	*Quercus berberidifolia*	Cleveland National Forest	32.776250	-116.494317	1041	1
12--11	*Quercus berberidifolia*	Cleveland National Forest	32.776317	-116.494150	1041	1
13--2	*Quercus cornelius-mulleri*	Jacumba	32.622833	-116.218883	938	1
13--4	*Quercus cornelius-mulleri*	Jacumba	32.622633	-116.218600	938	1

13--6	*Quercus cornelius-mulleri*	Jacumba	32.622233	-116.218267	938	1
13--8	*Quercus cornelius-mulleri*	Jacumba	32.621900	-116.217817	938	1
13--9	*Quercus cornelius-mulleri*	Jacumba	32.621717	-116.217817	938	1
13--10	*Quercus cornelius-mulleri*	Jacumba	32.621700	-116.217967	938	1
14--1	*Quercus engelmannii*	Potrero	32.598100	-116.551133	761	1
14--2	*Quercus berberidifolia*	Potrero	32.599717	-116.552817	757	1
14--3	*Quercus berberidifolia*	Potrero	32.597217	-116.554550	731	1
14--4	*Quercus berberidifolia*	Potrero	32.597267	-116.554867	731	1
14--5	*Quercus berberidifolia*	Potrero	32.597267	-116.557017	741	1
14--6	*Quercus berberidifolia*	Potrero	32.597283	-116.557200	741	1
15--1	*Quercus engelmannii*	Jamul	32.730700	-116.874340	254	1
15--2	*Quercus engelmannii*	Jamul	32.730530	-116.876400	275	1
15--3	*Quercus engelmannii*	Jamul	32.730530	-116.876400	275	1
16--1	*Quercus engelmannii*	Lawson Valley Road	32.743030	-116.810740	581	1
16--2	*Quercus engelmannii*	Lawson Valley Road	32.743030	-116.810740	581	1
16--3	*Quercus engelmannii*	Lawson Valley Road	32.743030	-116.810740	581	1
16--4	*Quercus engelmannii*	Lawson Valley Road	32.743030	-116.810740	581	1
16--7	*Quercus engelmannii*	Lawson Valley Road	32.746880	-116.797650	609	1
16--8	*Quercus engelmannii*	Lawson Valley Road	32.746720	-116.798620	609	1
16--11	*Quercus berberidifolia*	Lawson Valley Road	32.746820	-116.799220	609	1
16--12	*Quercus engelmannii*	Lawson Valley Road	32.746820	-116.799220	609	1
16--13	*Quercus berberidifolia*	Lawson Valley Road	32.746820	-116.799220	609	1
16--14	*Quercus engelmannii*	Lawson Valley Road	32.746450	-116.799800	609	1
16--15	*Quercus berberidifolia*	Lawson Valley Road	32.746420	-116.800550	595	1
16--17	*Quercus engelmannii*	Lawson Valley Road	32.745610	-116.802520	595	1
16--21	*Quercus berberidifolia*	Lawson Valley Road	32.738880	-116.813790	551	1
16--23	*Quercus berberidifolia*	Lawson Valley Road	32.739920	-116.812410	551	1
16--25	*Quercus berberidifolia*	Lawson Valley Road	32.739640	-116.811690	563	1
17--1	*Quercus engelmannii*	Alpine	32.811980	-116.778210	537	1
17--2	*Quercus engelmannii*	Alpine	32.811740	-116.778340	537	1
17--3	*Quercus engelmannii*	Alpine	32.811650	-116.778400	537	1
17--5	*Quercus engelmannii*	Alpine	32.813440	-116.772100	577	1
17--6	*Quercus engelmannii*	Alpine	32.815660	-116.771870	557	1
17--8	*Quercus engelmannii*	Alpine	32.816330	-116.764050	581	1
17--9	*Quercus engelmannii*	Alpine	32.816200	-116.764600	581	1
18--1	*Quercus cornelius-mulleri*	Louis A. Stelzer County Park	32.881980	-116.900320	264	1
18--4	*Quercus berberidifolia*	Louis A. Stelzer County Park	32.881760	-116.900860	264	1
18--5	*Quercus engelmannii*	Louis A. Stelzer County Park	32.881800	-116.901170	264	1
18--7	*Quercus engelmannii*	Louis A. Stelzer County Park	32.881510	-116.901280	206	1
20--2	*Quercus cornelius-mulleri*	Beumont	33.909933	-116.982617	784	1

20--3	*Quercus cornelius-mulleri*	Beumont	33.909783	-116.982733	779	1
20--5	*Quercus cornelius-mulleri*	Beumont	33.909467	-116.983250	779	0
20--8	*Quercus cornelius-mulleri*	Beumont	33.910000	-116.983200	784	1
20--11	*Quercus cornelius-mulleri*	Beumont	33.910900	-116.983467	784	1
21--1	*Quercus engelmannii*	Hemet	33.631817	-117.005217	659	1
21--2	*Quercus engelmannii*	Hemet	33.631600	-117.005767	659	1
21--3	*Quercus engelmannii*	Hemet	33.631433	-117.005917	659	1
21--4	*Quercus engelmannii*	Hemet	33.631467	-117.006033	659	0
21--5	*Quercus engelmannii*	Hemet	33.631283	-117.006250	641	1
21--6	*Quercus engelmannii*	Hemet	33.631000	-117.006867	641	1
21--7	*Quercus engelmannii*	Hemet	33.631167	-117.006483	641	1
21--8	*Quercus engelmannii*	Hemet	33.631033	-117.006050	659	1
21--9	*Quercus berberidifolia*	Hemet	33.630983	-117.005850	659	1
21--12	*Quercus berberidifolia*	Hemet	33.630850	-117.005750	659	1
21--20	*Quercus engelmannii*	Hemet	33.631183	-117.005300	659	1
21--21	*Quercus berberidifolia*	Hemet	33.631100	-117.005100	659	1
21--22	*Quercus engelmannii*	Hemet	33.630967	-117.004950	659	1
21--24	*Quercus engelmannii*	Hemet	33.625867	-117.018733	587	1
21--25	*Quercus engelmannii*	Hemet	33.625683	-117.018833	590	1
21--26	*Quercus engelmannii*	Hemet	33.625600	-117.018817	590	1
21--27	*Quercus engelmannii*	Hemet	33.625583	-117.018850	590	1
21--28	*Quercus engelmannii*	Hemet	33.625550	-117.018783	590	1
21--29	*Quercus engelmannii*	Hemet	33.625433	-117.018867	590	1
21--30	*Quercus engelmannii*	Hemet	33.625267	-117.018817	590	1
21--32	*Quercus engelmannii*	Hemet	33.625183	-117.018733	590	1
22--1	*Quercus engelmannii*	Avocado Mesa	33.504630	-117.302040	591	0
22--2	*Quercus engelmannii*	Avocado Mesa	33.504360	-117.302090	591	0
22--3	*Quercus engelmannii*	Avocado Mesa	33.503700	-117.302760	599	0
22--4	*Quercus engelmannii*	Avocado Mesa	33.503860	-117.301230	616	0
23--1	*Quercus berberidifolia*	Avocado Mesa	33.522460	-117.314670	687	0
23--2	*Quercus berberidifolia*	Avocado Mesa	33.521990	-117.315170	687	0
23--6	*Quercus cornelius-mulleri*	Avocado Mesa	33.522310	-117.315300	687	0
23--7	*Quercus berberidifolia*	Avocado Mesa	33.522320	-117.315320	687	0
23--9	*Quercus berberidifolia*	Avocado Mesa	33.523170	-117.315670	656	0
23--10	*Quercus engelmannii*	Avocado Mesa	33.523180	-117.315750	656	0
23--11	*Quercus engelmannii*	Avocado Mesa	33.523270	-117.315710	656	0
23--12	*Quercus berberidifolia*	Avocado Mesa	33.522750	-117.315720	656	0
23--13	*Quercus engelmannii*	Avocado Mesa	33.522990	-117.315800	656	0
23--14	*Quercus engelmannii*	Avocado Mesa	33.523330	-117.315850	656	0
23--15	*Quercus engelmannii*	Avocado Mesa	33.523410	-117.315790	656	0
23--16	*Quercus engelmannii*	Avocado Mesa	33.523740	-117.315790	679	0
24--1	*Quercus engelmannii*	Pauba Ranch	33.508552	-117.088208	384	0
24--2	*Quercus engelmannii*	Pauba Ranch	33.508552	-117.088208	384	0
24--3	*Quercus engelmannii*	Pauba Ranch	33.508552	-117.088208	384	0
24--5	*Quercus engelmannii*	Pauba Ranch	33.508552	-117.088208	384	0
24--6	*Quercus engelmannii*	Pauba Ranch	33.508552	-117.088208	384	0
24--7	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--8	*Quercus engelmannii*	Pauba Ranch	33.508552	-117.088208	384	0
24--9	*Quercus engelmannii*	Pauba Ranch	33.508552	-117.088208	384	0
24--10	*Quercus engelmannii*	Pauba Ranch	33.508552	-117.088208	384	0
24--11	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--12	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--13	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--14	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--15	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--17	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--18	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--19	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--20	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0

24--21	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--22	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--23	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--24	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--25	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--27	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
24--016A	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
25--1	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
25--2	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
25--3	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
25--4	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
25--6	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
25--7	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
25--9	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
25--11	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
25--12	*Quercus berberidifolia*	Pauba Ranch	33.508552	-117.088208	384	0
26--1	*Quercus engelmannii*	North Tecate/Dulzura	32.623390	-116.749540	472	0
26--2	*Quercus engelmannii*	North Tecate/Dulzura	32.623440	-116.749420	472	0
26--3	*Quercus engelmannii*	North Tecate/Dulzura	32.623480	-116.748600	472	0
26--4	*Quercus engelmannii*	North Tecate/Dulzura	32.623480	-116.748600	472	0
26--5	*Quercus engelmannii*	North Tecate/Dulzura	32.623480	-116.748600	472	0
26--6	*Quercus engelmannii*	North Tecate/Dulzura	32.642430	-116.777770	333	0
26--7	*Quercus engelmannii*	North Tecate/Dulzura	32.642560	-116.777810	333	0
26--8	*Quercus engelmannii*	North Tecate/Dulzura	32.642780	-116.778920	330	0
27--2	*Quercus engelmannii*	Oak Knoll	33.298210	-116.922127	696	0
27--3	*Quercus engelmannii*	Oak Knoll	33.298210	-116.922127	696	0
27--4	*Quercus engelmannii*	Oak Knoll	33.298210	-116.922127	696	0
27--6	*Quercus engelmannii*	Oak Knoll	33.298210	-116.922127	696	0
27--7	*Quercus engelmannii*	Oak Knoll	33.298210	-116.922127	696	0
27--8	*Quercus engelmannii*	Oak Knoll	33.298210	-116.922127	696	0
27--9	*Quercus engelmannii*	Oak Knoll	33.298210	-116.922127	696	0
27--10	*Quercus engelmannii*	Oak Knoll	33.298210	-116.922127	696	0
27--11	*Quercus engelmannii*	Oak Knoll	33.298210	-116.922127	696	0
27--12	*Quercus engelmannii*	Oak Knoll	33.298210	-116.922127	696	0
28--1	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--2	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--3	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--4	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--5	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--6	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--7	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--8	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--9	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--10	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--11	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--12	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--13	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--14	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--15	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--16	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
28--17	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0

28--18	*Quercus cornelius-mulleri*	Ranchita	33.211081	-116.485548	1233	0
29--1	*Quercus cornelius-mulleri*	Mc Cain Valley Road	32.774040	-116.281570	1222	0
29--2	*Quercus cornelius-mulleri*	Mc Cain Valley Road	32.774220	-116.281050	1222	0
29--3	*Quercus cornelius-mulleri*	Mc Cain Valley Road	32.774210	-116.280960	1222	0
29--4	*Quercus cornelius-mulleri*	Mc Cain Valley Road	32.774390	-116.280720	1187	0
29--5	*Quercus cornelius-mulleri*	Mc Cain Valley Road	32.774430	-116.280620	1187	0
31--1	*Quercus cornelius-mulleri*	Mc Cain Valley Road	32.770260	-116.258620	1061	0
32--3	*Quercus berberidifolia*	Japatul	32.823380	-116.627470	1022	0
32--4	*Quercus berberidifolia*	Japatul	32.823380	-116.627470	1022	0
32--5	*Quercus engelmannii*	Japatul	32.823380	-116.627470	1022	0
34--2	*Quercus cornelius-mulleri*	Joshua Tree National Park	34.017380	-116.167374	1314	0
34--3	*Quercus cornelius-mulleri*	Joshua Tree National Park	34.017380	-116.167374	1314	0
34--6	*Quercus cornelius-mulleri*	Joshua Tree National Park	34.017380	-116.167374	1314	0
34--7	*Quercus cornelius-mulleri*	Joshua Tree National Park	34.017380	-116.167374	1314	0
41--1	*Quercus cornelius-mulleri*	Yucaipa	34.102467	-117.182283	391	0
42--10	*Quercus berberidifolia*	Yucaipa	34.069250	-117.005850	1106	0
43--2	*Quercus berberidifolia*	Yucaipa	34.038817	-117.021700	928	0
45--7	*Quercus engelmannii*	Glendora	34.185567	-118.095283	396	0
45--13	*Quercus engelmannii*	Glendora	34.153133	-117.846033	319	0
50--2	*Quercus engelmannii*	Daley Ranch	33.165724	-117.044648	375	0
50--4	*Quercus engelmannii*	Daley Ranch	33.166256	-117.049365	376	0
51--6	*Quercus engelmannii*	Pasadena	34.147693	-118.052012	181	1
51--7	*Quercus engelmannii*	Pasadena	34.139128	-118.057162	170	1
51--12	*Quercus engelmannii*	Pasadena	34.139128	-118.057162	170	1
51--13	*Quercus engelmannii*	Pasadena	34.139128	-118.057162	170	1
51--14	*Quercus engelmannii*	Pasadena	34.139128	-118.057162	170	1
51--16	*Quercus engelmannii*	Pasadena	34.139128	-118.057162	170	1
51--18	*Quercus engelmannii*	Pasadena	34.139128	-118.057162	170	1
51--19	*Quercus engelmannii*	Pasadena	34.139128	-118.057162	170	1
52--1	*Quercus engelmannii*	Pasadena	34.134150	-118.118803	223	1
52--2	*Quercus engelmannii*	Pasadena	34.129225	-118.120617	213	1
52--3	*Quercus engelmannii*	Pasadena	34.131655	-118.121470	221	1
52--5	*Quercus engelmannii*	Pasadena	34.130833	-118.120256	212	1
52--7	*Quercus engelmannii*	Pasadena	34.132678	-118.117842	219	1
52--8	*Quercus engelmannii*	Pasadena	34.130789	-118.119753	212	1
52--10	*Quercus engelmannii*	Pasadena	34.137130	-118.125649	230	1
52--11	*Quercus engelmannii*	Pasadena	34.137084	-118.122379	229	1

Bio4	Bio15	Bio18	Bio19	AET	CWD	Tmn	Tmx
380.1364	97.3892	10.1223	198.8824	266.9767	1095.6433	5.6746	27.1754
380.1364	97.3892	10.1223	198.8824	266.9767	1095.6433	5.6746	27.1754
370.2700	98.4751	10.3097	227.8383	271.5767	1097.4301	6.5644	27.1258
369.2776	97.5917	10.2504	223.1429	268.8400	1091.0967	6.2719	26.9641
370.0009	97.5239	10.2224	220.4200	339.5033	1017.2700	6.3659	27.0147
370.0009	97.5239	10.2224	220.4200	339.5033	1017.2700	6.3659	27.0147
373.9874	97.5115	10.2564	206.5997	333.7500	1030.5634	6.2270	27.1378
373.9874	97.5115	10.2564	206.5997	333.7500	1030.5634	6.2270	27.1378
373.9874	97.5115	10.2564	206.5997	333.7500	1030.5634	6.2270	27.1378
374.0985	97.4593	10.2830	214.7017	333.2400	1033.0000	6.2141	27.2172
374.0985	97.4593	10.2830	214.7017	333.2400	1033.0000	6.2141	27.2172
374.0985	97.4593	10.2830	214.7017	333.2400	1033.0000	6.2141	27.2172
378.2494	97.3497	10.1684	202.8957	333.2467	1028.6033	5.9076	27.2664
378.2494	97.3497	10.1684	202.8957	333.2467	1028.6033	5.9076	27.2664
438.8159	92.1400	13.1310	220.2800	371.5300	1008.7067	5.2637	30.1226
439.5643	92.3695	13.2423	221.7277	334.6100	1040.4733	5.3694	30.2230
477.3221	92.7517	15.8276	261.3906	411.2567	978.3800	5.8033	30.8449
467.0341	92.9702	15.0943	257.8180	324.9567	1067.7600	5.7570	30.9136
470.2392	92.7860	15.2823	258.0377	406.7367	979.9167	5.6803	30.8587
470.2392	92.7860	15.2823	258.0377	406.7367	979.9167	5.6803	30.8587
459.1645	93.0333	14.6077	254.6253	375.2333	1017.2367	5.6799	30.9626
459.1645	93.0333	14.6077	254.6253	375.2333	1017.2367	5.6799	30.9626
459.1645	93.0333	14.6077	254.6253	375.2333	1017.2367	5.6799	30.9626
458.8594	93.0007	14.5886	254.4893	304.9567	1081.5634	5.6598	30.9502
434.2958	92.0631	12.8876	217.1597	332.0667	1046.1899	5.2913	30.0104
434.2958	92.0631	12.8876	217.1597	332.0667	1046.1899	5.2913	30.0104
438.8159	92.1400	13.1310	220.2800	371.5300	1008.7067	5.2637	30.1226
438.8159	92.1400	13.1310	220.2800	371.5300	1008.7067	5.2637	30.1226
576.2894	91.0272	22.7684	277.1040	373.1167	983.2700	3.0804	32.5149
629.1365	85.5563	34.2197	309.8180	472.1333	886.1467	2.1594	31.0288
629.1365	85.5563	34.2197	309.8180	472.1333	886.1467	2.1594	31.0288
629.1365	85.5563	34.2197	309.8180	472.1333	886.1467	2.1594	31.0288
629.1365	85.5563	34.2197	309.8180	472.1333	886.1467	2.1594	31.0288
628.5595	85.1225	35.3570	312.2357	374.7100	984.4933	2.1316	30.9558
591.1665	87.9083	29.1979	293.1047	441.9267	901.0100	1.5434	33.3664
591.0498	88.2075	28.6613	291.4730	437.1867	897.1600	1.5357	33.5461
591.0498	88.2075	28.6613	291.4730	437.1867	897.1600	1.5357	33.5461
590.6892	88.3595	28.3473	290.0426	336.3200	1008.8133	1.6612	33.3259
590.6892	88.3595	28.3473	290.0426	336.3200	1008.8133	1.6612	33.3259
595.0372	72.5893	55.0823	221.0423	293.9633	944.3300	-0.6444	31.6790
595.0372	72.5893	55.0823	221.0423	293.9633	944.3300	-0.6444	31.6790
595.0372	72.5893	55.0823	221.0423	293.9633	944.3300	-0.6444	31.6790
595.7227	72.3635	55.0151	218.7166	291.0067	940.1100	-0.8712	31.8237
595.7227	72.3635	55.0151	218.7166	291.0067	940.1100	-0.8712	31.8237
595.7227	72.3635	55.0151	218.7166	291.0067	940.1100	-0.8712	31.8237
595.7227	72.3635	55.0151	218.7166	291.0067	940.1100	-0.8712	31.8237
595.1228	72.4333	55.6597	223.3609	296.9967	943.4967	-0.6829	31.5688
595.3404	72.3422	56.1543	226.0340	300.6600	944.5967	-0.5432	31.4323
424.1799	89.2308	10.8634	182.0436	290.5133	1072.4733	5.4009	28.9638
424.1799	89.2308	10.8634	182.0436	290.5133	1072.4733	5.4009	28.9638
424.1799	89.2308	10.8634	182.0436	290.5133	1072.4733	5.4009	28.9638
486.7906	86.5695	14.4440	208.8703	309.8333	1047.7333	3.2761	31.8762
486.7906	86.5695	14.4440	208.8703	309.8333	1047.7333	3.2761	31.8762
484.0013	86.7524	14.1674	207.8947	343.1233	1012.3867	3.1508	32.0899
484.0013	86.7524	14.1674	207.8947	343.1233	1012.3867	3.1508	32.0899

484.0013	86.7524	14.1674	207.8947	343.1233	1012.3867	3.1508	32.0899
484.6028	86.4464	14.6947	208.2640	311.5967	1031.0900	3.2532	31.8492
486.7600	86.3605	14.8267	209.3064	314.6900	1035.2933	3.3448	31.7353
578.5043	83.1494	30.3453	279.1177	334.8667	967.8067	2.1519	31.6718
576.0093	82.4472	32.8696	294.9427	399.7233	859.7233	1.5962	31.3068
576.0093	82.4472	32.8696	294.9427	399.7233	859.7233	1.5962	31.3068
576.0093	82.4472	32.8696	294.9427	399.7233	859.7233	1.5962	31.3068
576.0093	82.4472	32.8696	294.9427	399.7233	859.7233	1.5962	31.3068
576.0093	82.4472	32.8696	294.9427	399.7233	859.7233	1.5962	31.3068
576.0093	82.4472	32.8696	294.9427	399.7233	859.7233	1.5962	31.3068
576.0093	82.4472	32.8696	294.9427	399.7233	859.7233	1.5962	31.3068
576.0093	82.4472	32.8696	294.9427	399.7233	859.7233	1.5962	31.3068
576.0093	82.4472	32.8696	294.9427	399.7233	859.7233	1.5962	31.3068
574.8914	82.6703	32.4713	290.9890	404.4267	868.5867	1.6461	31.5582
574.8914	82.6703	32.4713	290.9890	404.4267	868.5867	1.6461	31.5582
580.4568	81.9983	33.7061	298.7904	360.3067	910.8267	1.6970	31.1319
589.7266	79.2732	38.4704	331.9111	508.8900	757.4333	1.7506	29.6564
569.9323	81.8352	41.6803	335.2399	362.6367	890.4633	1.1870	31.7301
569.9323	81.8352	41.6803	335.2399	362.6367	890.4633	1.1870	31.7301
579.5109	81.4345	42.4523	332.5860	373.6500	907.7633	1.6139	31.6443
579.5109	81.4345	42.4523	332.5860	373.6500	907.7633	1.6139	31.6443
579.5109	81.4345	42.4523	332.5860	373.6500	907.7633	1.6139	31.6443
569.9323	81.8352	41.6803	335.2399	362.6367	890.4633	1.1870	31.7301
582.6415	80.2860	37.4563	274.5073	332.5967	945.8233	1.0448	32.9506
600.2476	79.0623	35.7639	246.3356	315.6967	991.2300	0.8502	33.1650
610.8379	77.6105	34.0413	216.9031	371.1867	922.8167	0.5490	33.7404
610.8379	77.6105	34.0413	216.9031	371.1867	922.8167	0.5490	33.7404
610.8379	77.6105	34.0413	216.9031	371.1867	922.8167	0.5490	33.7404
621.8040	75.7177	32.7863	192.6657	282.9533	1035.0333	0.6176	34.3213
618.9254	75.6537	33.1863	193.4190	343.4700	968.2400	0.6704	34.2583
618.9254	75.6537	33.1863	193.4190	343.4700	968.2400	0.6704	34.2583
618.9254	75.6537	33.1863	193.4190	343.4700	968.2400	0.6704	34.2583
612.3323	77.8606	51.5206	367.9579	378.3333	689.9600	-1.9514	27.5531
613.6111	78.5271	49.8343	371.2664	408.1967	668.3600	-1.7757	27.6808
607.0230	81.3031	39.6603	359.1536	338.8867	808.3267	-0.9068	28.0386
607.0230	81.3031	39.6603	359.1536	338.8867	808.3267	-0.9068	28.0386
607.0169	81.3256	39.2463	357.4363	330.9467	817.4100	-0.8869	28.0281
555.0564	79.3772	30.1353	230.8517	306.1100	937.0567	0.2806	31.6334
554.6608	79.4054	30.2267	231.1196	302.6867	941.5067	0.3666	31.5946
554.6608	79.4054	30.2267	231.1196	302.6867	941.5067	0.3666	31.5946
554.6608	79.4054	30.2267	231.1196	302.6867	941.5067	0.3666	31.5946
554.6608	79.4054	30.2267	231.1196	302.6867	941.5067	0.3666	31.5946
554.6608	79.4054	30.2267	231.1196	302.6867	941.5067	0.3666	31.5946
554.6608	79.4054	30.2267	231.1196	302.6867	941.5067	0.3666	31.5946
555.0564	79.3772	30.1353	230.8517	306.1100	937.0567	0.2806	31.6334
555.0564	79.3772	30.1353	230.8517	306.1100	937.0567	0.2806	31.6334
555.0564	79.3772	30.1353	230.8517	306.1100	937.0567	0.2806	31.6334
553.6221	75.3658	33.2117	163.1417	263.9033	1026.1567	0.9832	31.4209
555.3928	75.3475	33.1590	162.8717	263.6100	1026.7700	0.9557	31.4562

555.3928	75.3475	33.1590	162.8717	263.6100	1026.7700	0.9557	31.4562
555.3928	75.3475	33.1590	162.8717	263.6100	1026.7700	0.9557	31.4562
555.3928	75.3475	33.1590	162.8717	263.6100	1026.7700	0.9557	31.4562
555.3928	75.3475	33.1590	162.8717	263.6100	1026.7700	0.9557	31.4562
549.1346	81.7484	24.8850	192.7637	286.5600	1046.0267	1.5194	32.0478
549.7033	81.8236	24.8687	193.3321	286.6967	1042.0367	1.6104	31.9716
547.4017	82.0205	24.6663	193.5746	288.1733	1047.4667	1.5930	31.9602
547.4017	82.0205	24.6663	193.5746	288.1733	1047.4667	1.5930	31.9602
547.4017	82.0205	24.6663	193.5746	288.1733	1047.4667	1.5930	31.9602
547.5016	82.0355	24.4060	194.1287	290.9000	1056.6567	1.5941	31.9649
435.7986	86.6003	11.9040	179.1353	300.6567	1019.9367	4.7250	29.7848
435.7986	86.6003	11.9040	179.1353	300.6567	1019.9367	4.7250	29.7848
435.7986	86.6003	11.9040	179.1353	300.6567	1019.9367	4.7250	29.7848
486.7124	85.3683	16.5353	218.3247	312.0533	1010.4200	4.2133	31.1232
486.7124	85.3683	16.5353	218.3247	312.0533	1010.4200	4.2133	31.1232
486.7124	85.3683	16.5353	218.3247	312.0533	1010.4200	4.2133	31.1232
486.7124	85.3683	16.5353	218.3247	312.0533	1010.4200	4.2133	31.1232
496.0538	85.2838	17.0480	221.5853	315.4300	999.9600	3.8827	31.1367
500.4679	85.2451	17.1100	221.8370	313.8700	1005.5467	3.7170	31.0994
500.4679	85.2451	17.1100	221.8370	313.8700	1005.5467	3.7170	31.0994
500.4679	85.2451	17.1100	221.8370	313.8700	1005.5467	3.7170	31.0994
500.4679	85.2451	17.1100	221.8370	313.8700	1005.5467	3.7170	31.0994
500.4679	85.2451	17.1100	221.8370	313.8700	1005.5467	3.7170	31.0994
500.4679	85.2451	17.1100	221.8370	313.8700	1005.5467	3.7170	31.0994
491.8141	85.1956	16.9910	219.9160	315.8967	1002.9933	3.9869	31.0233
481.8214	85.5794	16.1957	218.4880	368.2833	947.0667	4.2812	31.2217
489.6395	85.3523	16.7690	220.0287	311.1233	1000.8067	4.0246	31.0702
489.6395	85.3523	16.7690	220.0287	311.1233	1000.8067	4.0246	31.0702
488.7370	84.0830	16.6531	206.4296	392.9833	969.0733	4.6167	31.5930
488.7370	84.0830	16.6531	206.4296	392.9833	969.0733	4.6167	31.5930
490.6395	83.9263	16.8110	206.4753	369.7200	997.7100	4.8198	31.5370
491.9266	83.9593	17.0303	207.5510	351.6300	1011.1933	4.7639	31.5282
491.9266	83.9593	17.0303	207.5510	351.6300	1011.1933	4.7639	31.5282
492.8613	84.0850	17.2221	210.3427	366.4400	992.2433	4.5687	31.5124
492.8613	84.0850	17.2221	210.3427	366.4400	992.2433	4.5687	31.5124
455.8214	87.3179	13.9237	193.2837	309.8200	1058.9667	4.6767	31.0046
455.8214	87.3179	13.9237	193.2837	309.8200	1058.9667	4.6767	31.0046
455.8214	87.3179	13.9237	193.2837	309.8200	1058.9667	4.6767	31.0046
455.8214	87.3179	13.9237	193.2837	309.8200	1058.9667	4.6767	31.0046
589.3147	84.6608	22.8960	222.6654	322.8533	1111.7800	3.8684	33.6287

589.3147	84.6608	22.8960	222.6654	322.8533	1111.7800	3.8684	33.6287
589.3147	84.6608	22.8960	222.6654	322.8533	1111.7800	3.8684	33.6287
589.3147	84.6608	22.8960	222.6654	322.8533	1111.7800	3.8684	33.6287
589.3147	84.6608	22.8960	222.6654	322.8533	1111.7800	3.8684	33.6287
559.7331	83.6388	19.9613	172.8073	298.2600	1103.7667	3.7692	33.8581
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
558.9682	83.7526	19.8040	173.3357	304.3700	1091.4933	3.8380	33.7920
562.9213	84.0854	18.9474	172.3863	296.5000	1101.7367	3.5990	34.1368
562.9213	84.0854	18.9474	172.3863	296.5000	1101.7367	3.5990	34.1368
562.9213	84.0854	18.9474	172.3863	296.5000	1101.7367	3.5990	34.1368
562.9213	84.0854	18.9474	172.3863	296.5000	1101.7367	3.5990	34.1368
562.9213	84.0854	18.9474	172.3863	296.5000	1101.7367	3.5990	34.1368
562.9213	84.0854	18.9474	172.3863	296.5000	1101.7367	3.5990	34.1368
562.9213	84.0854	18.9474	172.3863	296.5000	1101.7367	3.5990	34.1368
562.9213	84.0854	18.9474	172.3863	296.5000	1101.7367	3.5990	34.1368
461.8186	100.2285	16.9077	234.0354	304.8167	1122.8533	7.0244	29.9824
461.8186	100.2285	16.9077	234.0354	304.8167	1122.8533	7.0244	29.9824
445.9816	101.0420	16.1323	234.2706	323.5000	1099.9933	7.1517	29.6490
461.8186	100.2285	16.9077	234.0354	304.8167	1122.8533	7.0244	29.9824
476.2762	98.2270	18.1660	222.6603	317.7167	1095.9700	7.0254	29.6659
475.0566	98.2820	18.1700	221.9803	316.8400	1098.0967	7.0284	29.4826
475.0566	98.2820	18.1700	221.9803	316.8400	1098.0967	7.0284	29.4826
475.0566	98.2820	18.1700	221.9803	316.8400	1098.0967	7.0284	29.4826
476.2762	98.2270	18.1660	222.6603	317.7167	1095.9700	7.0254	29.6659
476.2762	98.2270	18.1660	222.6603	317.7167	1095.9700	7.0254	29.6659
476.2762	98.2270	18.1660	222.6603	317.7167	1095.9700	7.0254	29.6659
476.2762	98.2270	18.1660	222.6603	317.7167	1095.9700	7.0254	29.6659
476.2762	98.2270	18.1660	222.6603	317.7167	1095.9700	7.0254	29.6659
476.2762	98.2270	18.1660	222.6603	317.7167	1095.9700	7.0254	29.6659
476.2762	98.2270	18.1660	222.6603	317.7167	1095.9700	7.0254	29.6659
476.2762	98.2270	18.1660	222.6603	317.7167	1095.9700	7.0254	29.6659
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287

500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
500.5787	94.6115	13.8806	214.5976	325.5267	1084.9200	3.7753	32.4287
497.3231	87.2053	14.5283	203.1863	352.8233	996.3733	3.4950	31.9582
497.3231	87.2053	14.5283	203.1863	352.8233	996.3733	3.4950	31.9582
497.3231	87.2053	14.5283	203.1863	352.8233	996.3733	3.4950	31.9582
497.3231	87.2053	14.5283	203.1863	352.8233	996.3733	3.4950	31.9582
497.3231	87.2053	14.5283	203.1863	352.8233	996.3733	3.4950	31.9582
523.7929	86.9059	12.7527	188.8943	332.8833	1012.8700	3.8596	32.9324
523.7929	86.9059	12.7527	188.8943	332.8833	1012.8700	3.8596	32.9324
523.7929	86.9059	12.7527	188.8943	332.8833	1012.8700	3.8596	32.9324
533.9698	92.7985	19.1821	266.3623	355.2133	982.9300	3.6253	32.3518
533.9698	92.7985	19.1821	266.3623	355.2133	982.9300	3.6253	32.3518
533.9698	92.7985	19.1821	266.3623	355.2133	982.9300	3.6253	32.3518
533.9698	92.7985	19.1821	266.3623	355.2133	982.9300	3.6253	32.3518
533.9698	92.7985	19.1821	266.3623	355.2133	982.9300	3.6253	32.3518
533.9698	92.7985	19.1821	266.3623	355.2133	982.9300	3.6253	32.3518
533.9698	92.7985	19.1821	266.3623	355.2133	982.9300	3.6253	32.3518
533.9698	92.7985	19.1821	266.3623	355.2133	982.9300	3.6253	32.3518
533.9698	92.7985	19.1821	266.3623	355.2133	982.9300	3.6253	32.3518
533.9698	92.7985	19.1821	266.3623	355.2133	982.9300	3.6253	32.3518
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097

662.6185	66.9198	48.8130	160.1556	302.0800	1077.4000	2.2377	31.4097
627.3567	74.4334	38.4769	194.9559	297.8800	1055.0601	2.0179	30.3397
627.3567	74.4334	38.4769	194.9559	297.8800	1055.0601	2.0179	30.3397
627.3567	74.4334	38.4769	194.9559	297.8800	1055.0601	2.0179	30.3397
627.3567	74.4334	38.4769	194.9559	297.8800	1055.0601	2.0179	30.3397
627.3567	74.4334	38.4769	194.9559	297.8800	1055.0601	2.0179	30.3397
623.1758	73.7847	35.4147	166.7344	274.5900	1109.7900	2.7034	32.1259
575.9579	85.1717	23.0976	303.4927	475.1933	826.0367	1.8777	31.8282
575.9579	85.1717	23.0976	303.4927	475.1933	826.0367	1.8777	31.8282
575.9579	85.1717	23.0976	303.4927	475.1933	826.0367	1.8777	31.8282
705.4928	69.5020	53.9587	115.0303	192.0000	1097.8033	-0.2228	32.1726
705.4928	69.5020	53.9587	115.0303	192.0000	1097.8033	-0.2228	32.1726
705.4928	69.5020	53.9587	115.0303	192.0000	1097.8033	-0.2228	32.1726
705.4928	69.5020	53.9587	115.0303	192.0000	1097.8033	-0.2228	32.1726
538.7769	86.5944	16.3506	179.4683	311.4133	1144.5200	4.3690	33.3533
587.3458	77.0261	38.9309	278.8337	473.6233	910.0833	2.7858	30.2922
589.2693	81.1778	29.4617	261.1390	352.3933	1035.2500	3.4763	31.7341
449.9070	96.4526	15.5174	334.4863	403.1400	1018.5733	6.6146	30.1487
447.3210	96.1826	16.2613	323.3467	383.4367	1062.7867	5.8034	30.5354
432.1971	92.6876	11.6744	219.9007	305.7767	1064.3000	4.3389	29.8892
430.6538	92.4782	11.7403	219.0403	305.9767	1065.4067	4.3653	29.8372
430.9745	97.9927	12.0467	270.3863	338.0067	1097.3733	6.2701	30.8770
430.5948	98.5373	11.6650	260.9733	329.3333	1100.6899	6.1744	30.8812
430.5948	98.5373	11.6650	260.9733	329.3333	1100.6899	6.1744	30.8812
430.5948	98.5373	11.6650	260.9733	329.3333	1100.6899	6.1744	30.8812
430.5948	98.5373	11.6650	260.9733	329.3333	1100.6899	6.1744	30.8812
430.5948	98.5373	11.6650	260.9733	329.3333	1100.6899	6.1744	30.8812
430.5948	98.5373	11.6650	260.9733	329.3333	1100.6899	6.1744	30.8812
430.5948	98.5373	11.6650	260.9733	329.3333	1100.6899	6.1744	30.8812
424.2923	100.0189	11.7950	279.1964	337.6567	1084.6533	6.0121	30.3599
423.1475	100.3171	11.6763	276.7510	335.9633	1088.8433	5.9866	30.3800
424.1457	100.0716	11.7693	278.6053	337.4300	1086.2032	6.0043	30.3660
424.1457	100.0716	11.7693	278.6053	337.4300	1086.2032	6.0043	30.3660
424.9162	100.0536	11.8170	277.8597	337.0300	1085.9667	5.9673	30.3781
424.1457	100.0716	11.7693	278.6053	337.4300	1086.2032	6.0043	30.3660
423.4190	100.0772	11.8169	279.7927	337.8367	1084.6467	6.0554	30.3339
423.7306	100.0175	11.7910	279.7327	337.6800	1083.7032	6.0277	30.3367