



# Phylogeny and Introgression of California Scrub White Oaks (*Quercus* section *Quercus*)

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## ABSTRACT

The taxonomy of oaks (*Quercus*) is always a challenge because many species exhibit variable phenotypes that overlap with other species. The scrub White Oaks of California are no exception. In California, *Quercus* section *Quercus* (i.e., White Oaks) includes six species of scrub oaks plus four tree oak species. Field identification utilizes leaf traits and acorns, when available, as well as geographic location, but often botanists – with the exception of specialists – are not confident of their assignments. Complicating our understanding of scrub oaks further is the historical and ongoing introgression among taxa. Fortunately, new research using nuclear microsatellite genetic markers and RADseq-based sequences are clarifying their evolutionary relationships. Based on these genetic markers, we describe the phylogenetic relationships among the California scrub and tree White Oaks. Given the impact of hybridization in oaks, we then present a specific example involving three Southern California oaks – one tree oak (*Q. engelmannii*) and two scrub oaks (*Q. berberidifolia* and *Q. cornelius-mulleri*) – to illustrate how the environment and geography play a role in promoting interspecific gene exchange. This paper provides an overview of a fascinating scrub oak complex in a topographically and climatically diverse region.

**Keywords:** Fagaceae, hybridization, microsatellite, RADseq, species distribution model, taxonomy

## Introduction

Oaks have long challenged taxonomists because of their great degree of intraspecific phenotypic variation, convergent evolution across species and their propensity to hybridize (Hipp 2015; Tucker 1990; Tucker 1974). The taxonomist's task is particularly daunting with the scrub White Oaks in California because multiple species are often sympatric or adjacent in distribution (Ortego et al. 2014; Ortego et al. 2015a; Ortego et al. 2015b; Riordan et al. 2016), thus facilitating introgression and creating hybrid swarms or individuals that appear to be influenced by other species (Roberts 1995). Moreover, these species often converge on a similar leaf morphology of small, thick leaves, faintly lobed margins, and irregular spacing of teeth, requiring consideration of subtle differences among leaves, leaf trichome shape and density, and acorn morphology (Nixon 2002). One could raise the question of whether the California scrub White Oaks are just one big species complex with geographically distributed ecotypes, but Nixon's careful work has shown convincingly that the scrub White Oak species are indeed quite separate even if the evolutionary relationships among them are not well resolved (Ortego et al. 2015b).

It is not surprising that the scrub oak species would diversify in California. California has 20 recognized species of oaks from three major lineages or sections (*Lobatae*, *Protobalanus* and *Quercus*) with the White Oaks (section *Quercus*) being the most diverse (Nixon 2002; Pavlik et al. 1995). The California Floristic Province is considered one of the biodiversity hotspots of the world containing about 4,700 native plant species of which almost half are endemic (Baldwin 2014; Lancaster and Kay 2013; Raven and Axelrod 1978). The considerable topographic complexity in the region creates conditions for divergence among species (Calsbeek et al. 2003). For example, separation by mountain ranges and the Central Valley contribute to the potential for isolation. Moreover, it is highly likely that the emerging Mediterranean climate and dry summers of the middle Miocene (Schierenbeck 2014) would have created favorable conditions for the expansion of scrub oaks. These factors along with low extinction rates (Lancaster and Kay 2013) would have provided ideal conditions for the diversification of scrub White Oaks. While this region may not be as diverse in scrub oaks as parts of Mexico and the Southwestern United States, the species are sufficiently numerous to baffle many field biologists and hamper our ability to understand their evolution.

The first goal of this paper is to present a summary of the current understanding of California scrub White Oaks – their distribution, their phylogeny, and their relationship to the California tree White Oaks. Using the taxonomy of Nixon (Nixon 2002; Nixon and Muller 1994; Nixon and Steele 1981), we report on the following seven Californian endemic scrub White Oaks: *Q. berberidifolia* Liebm, *Q. cornelius-mulleri* Nixon & Steele, *Q. dumosa* Nutt. sensu stricto, *Q. durata* Jeps. var. *durata*, *Q. durata* var. *gabrielensis* Nixon & C.H. Mull., *Q. john-tuckeri* Nixon & C.H. Mull., and *Q. pacifica* Nixon & C.H. Mull. To understand the evolutionary history of these scrub oaks in the broader context, we will include two California endemic tree oaks – *Q. douglasii* Hook. & Arn. and *Q. lobata* Née – and one tree oak found in Mexico and California, *Q. engelmannii* Greene. Nixon categorizes *Q. douglasii*, *Q. lobata*, and *Q. garryana* Douglas ex Hook. var. *garryana*, *Q. garryana* var. *breweri* (Engelm.) Jeps. and *Q. garryana* var. *semota* Jeps. in the same California lobed-leaf White Oak group. We do not include any taxa of the *Q. garryana* complex in our analyses.

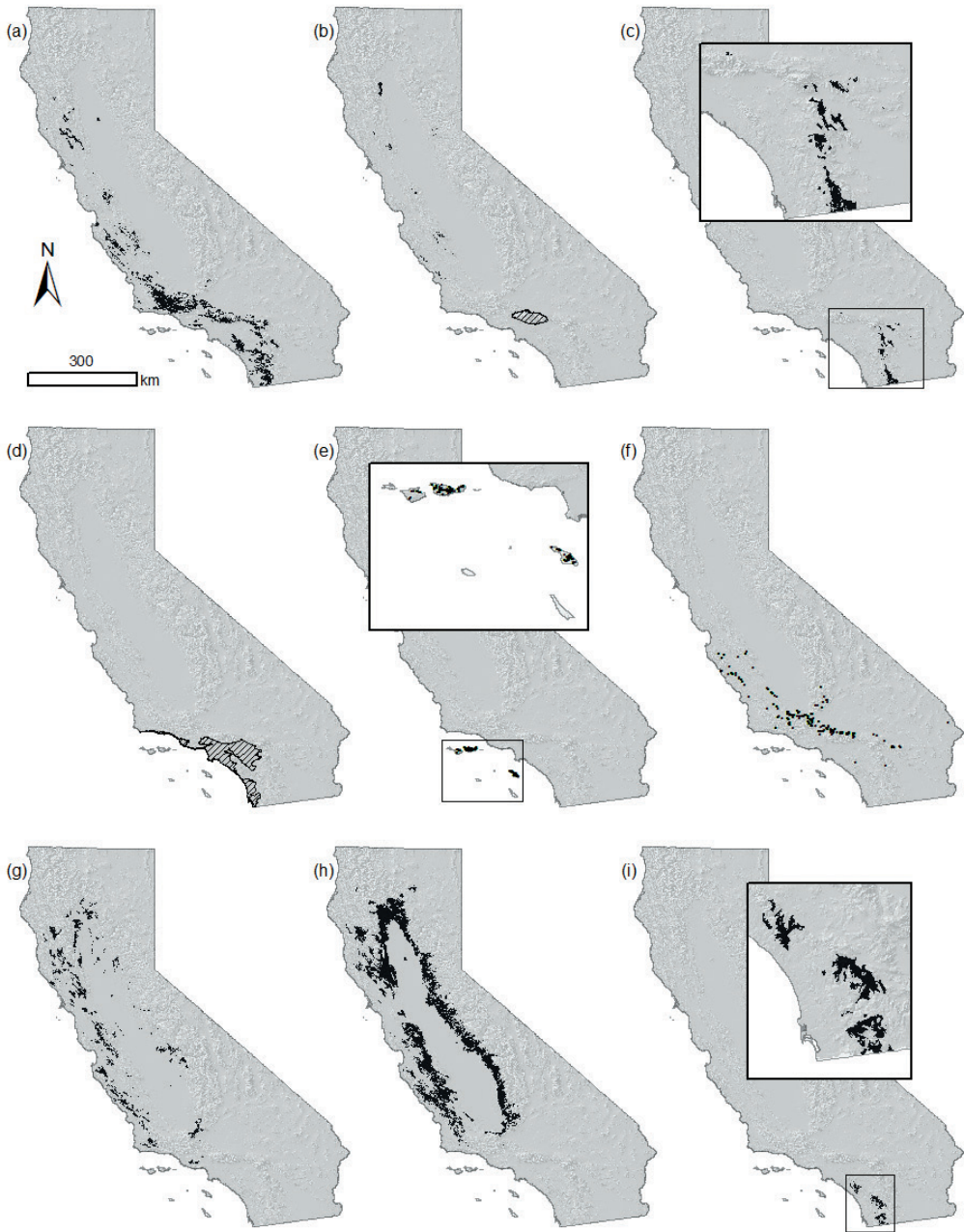
The second goal of this review is to present a special case of introgression of Southern

California scrub oaks. Oaks are considered a challenge to the biological species concept because they maintain their species identity despite interspecific gene flow (Howard et al. 1997; Stebbins and Major 1965; Van Valen 1976). It is often difficult to understand the extent to which introgression has contributed to California scrub oaks because of the extensive phenotypic variation within a species. Environmental factors may promote survival of hybrids that contribute to introgression and enhance phenotypic variation (Anderson 1953; Anderson and Stebbins 1954; Ortego et al. 2014). Here, we show this phenomenon using as an example the introgression between two California endemic scrub White Oaks (*Q. berberidifolia* and *Q. cornelius-mulleri*) and a tree oak, *Quercus engelmannii* (Ortego et al. 2014; Riordan et al. 2016). During our collecting trips through California, though we often found putative hybrid swarms involving scrub oaks, it was much less common to find hybrid swarms between scrub oaks and tree oaks. The Southern California situation is particularly interesting because Engelmann oak is not closely related to the scrub oaks and instead belongs to the *Glaucoidae* subsection of White Oaks, which is found in southern Arizona, New Mexico, and northern Mexico in arid areas that receive most rainfall in the summer months and are some of the driest places that oaks are found in North America (Nixon 2002). Hybrids between this tree species with scrub oaks are common (Ortego et al. 2014; Scott 1990). The leaves and growth form between the tree and scrub oaks are very different making many introgressed individuals relatively easy to find in the field. Thus, this case provides an informative example of the role of introgression in the biology of oaks.

### ***Distribution of scrub and tree oaks***

The distributions of the scrub and tree White Oaks range from patchy to continuous distributions and locally restricted to widespread (Figure 1). The most broadly distributed scrub oak species is *Q. berberidifolia* (Figure 1a), which is found in the western regions from northern Baja California through Northern California. *Quercus durata* is comprised of two subspecies (Nixon 2002): *Q. durata* var. *durata* and *Q. durata* var. *gabrielensis*. *Quercus durata* var. *durata*, which is mostly found on serpentine outcrops, occurs in patches within the Northern California region where *Q. berberidifolia* is found (Figure 1b) and has similar climate requirements as *Q. berberidifolia* (Ortego et al. 2015). The other variety, *Q. durata* var. *gabrielensis*, is restricted to the lower elevations of the San Gabriel Mountains of Los Angeles County (Roberts 1995) (Figure 1b), though its distribution within that region is patchy and interspersed with *Q. berberidifolia*. It is not clear whether *Q. durata* var. *gabrielensis* is restricted to a particular soil type (Nixon 2002). *Quercus cornelius-mulleri*, the desert scrub oak, occurs in the desert regions of Southern California and northern Baja California (Figure 1c).

Two Southern Californian species with very local distributions are *Q. dumosa* sensu stricto and *Q. pacifica*. It is very difficult to identify the exact distribution of *Q. dumosa* because the herbarium records are dominated by misidentifications due to the previous use of the name, *Q. dumosa*, for the widespread California scrub oak now called *Q. berberidifolia* and the frequent mislabeling of specimens as *Q. berberidifolia* and vice versa. Our map (Figure 1d) indicates the general region where it can be found, but within that region it occurs in very small patches along the coast, most notably in Santa Barbara Co. and San Diego Co., and there is also an inland population near Perris, California (Ortego et al. 2015b). The range of *Q. dumosa* partially overlaps that of *Q. berberidifolia*,



**Figure 1/** Distribution of nine White Oak species in California: (a) *Quercus berberidifolia*; (b) *Q. durata* var. *durata* and *Q. durata* var. *gabrielensis* (shown as single hatching in the San Gabriel Mountains); (c) *Q. cornelius-mulleri*; (d) *Q. dumosa* (due to identification issues and taxonomic changes in *Q. dumosa*, the ecoregion where the species occurs is shown as a single hatching); (e) *Q. pacifica*; (f) *Q. john-tuckeri*; (g) *Q. lobata*; (h) *Q. douglasii*; (i) *Q. engelmannii*. Distribution data was obtained from the California Gap Analysis Project (Davis et al. 1998) except in the cases of *Q. dumosa*, *Q. pacifica*, and *Q. john-tuckeri* which were not well represented in the database. Distributional data for *Q. pacifica* and *Q. john-tuckeri* (e, f) are based on herbarium records collected since 1950 and obtained from the Consortium of California Herbaria (CCH; <http://ucjeps.berkeley.edu/consortium/>).

and the two species are sometimes sympatric, which also creates confusion in the herbarium records if collectors identify a specimen based on locality. *Quercus pacifica* is restricted to the Channel Islands – Santa Catalina, Santa Cruz, and Santa Rosa (Figure 1e). The last of the scrub oak species is *Q. john-tuckeri*, formerly called *Q. turbinella* (Nixon 2002; Tucker 1953), with a range that is north and disjunct from *Q. cornelius-mulleri* (Figure 1f).

Throughout California, it is extremely common that at least one of the California endemic tree White Oaks is located within close proximity of one or more of the scrub White Oaks creating potential for interspecific gene flow. *Quercus lobata* Née (valley oak) is found along the eastern foothills of the Coastal Ranges, western foothills of the Sierra Ranges and Transverse Ranges, forming a ring around the Central Valley (Figure 1g). This species is usually found in valley floors in savanna oak habitat preferring sandy loam soil but it also occurs within riparian forest (Pavlik et al. 1995), and is now found in vineyards and other human-created landscapes. The current distribution of valley oak has been relatively stable for at least the last 150,000 years (Gugger et al. 2013), potentially shifting up and down in elevation. The current distribution of chloroplast haplotypes provides evidence that current populations have remained localized (Grivet et al. 2006; Gugger et al. 2013). However, the hypothesized presence of a hybrid between *Q. lobata* and *Q. cornelius-mulleri* in Joshua Tree National Park, San Diego County, California (Tucker 1968) would suggest that its southern range may have gone much further south during cooler glacial periods. *Quercus douglasii* (blue oak, Figure 1h) is a species of great abundance in California. Its distribution seems very similar to that of valley oak, but the highly dense stands tend to be along slopes and occur at higher elevation. Hybrids between these two species can be found, but they are not common (personal observation; Craft et al. 2002). Another tree White Oak found in southern California is *Q. engelmannii*, which is found in savanna-like densities from northern Baja California northward to the southern part of Los Angeles County (Figure 1i). Currently, it is not sympatric with any of the other White Oak tree species. Our research has shown that environmental conditions shape the distribution of the genetic and phenotypic variation of Engelmann oak populations (Ortego et al. 2012; Riordan et al. 2016) that often form mixed stands with *Q. berberidifolia* and *Q. cornelius-mulleri*, when all three species are present. When co-occurring, the scrub oaks tend to segregate into the more xeric microhabitats and Engelmann oak into the more mesic microhabitat. Hybrid swarms are frequently found between the scrub and tree species (Ortego et al. 2014; Riordan et al. 2016).

The scrub oaks tend to segregate geographically with separations by mountain ranges, suggesting that the topographical and environmental heterogeneity has contributed to divergence among species (Ortego et al. 2015). However, hybrids of all of the mainland scrub oaks with the widely distributed *Q. berberidifolia* can be found throughout the state (Ortego and Sork, personal observations; Roberts 1995). It is less common to find hybrids between the scrub oaks and the California endemic tree White Oaks, but as stated above and discussed below, hybrid swarms between Engelmann oak and its two sympatric scrub oaks are frequent. Overall, it appears that geographic and ecological isolation has contributed to speciation in California scrub White Oaks and despite the presence of introgression these oaks are maintaining their species identity (Ortego et al. 2016).

## Phylogeny of California scrub oaks

The phylogeny of oaks has been elusive because ongoing and historical hybridization events hamper the construction of phylogenetic trees. However, with sufficient genetic markers and sampling it is possible to clarify the evolutionary relationships between taxa (Hipp et al. 2013; Hipp et al. 2014). Recently, we pursued two strategies to understand the phylogeny of scrub White Oaks. The first approach samples many individuals of each species across California and genotypes leaf samples with nuclear microsatellites (Ortego et al. 2015b). The second and complementary approach uses a reduced-representation library sequencing approach through RADseq, which generates thousands of loci with single nucleotide polymorphisms (SNPs) for each individual sampled (Eaton and Ree 2013; Hipp et al. 2013; Hipp et al. 2014). This approach provides improved genetic resolution to develop a phylogeny, even with some degree of historical introgression (Eaton and Ree 2013).

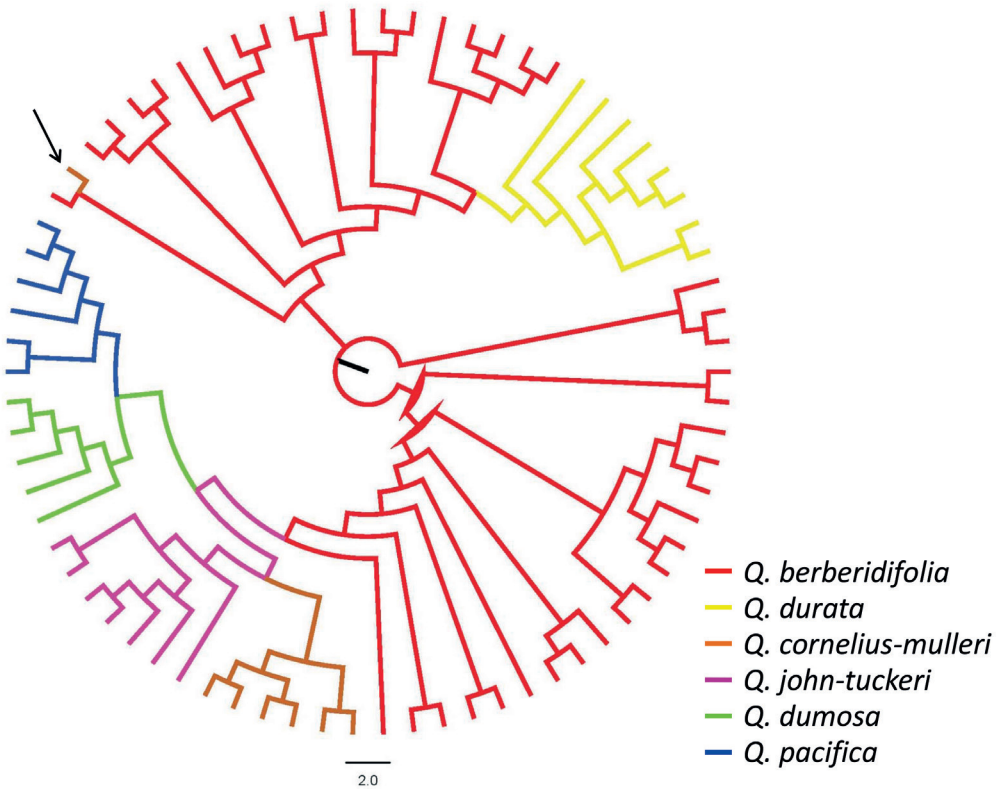


Figure 2/ Unrooted neighbor-joining tree of six California scrub oak species based on 812 samples from 87 localities sampled throughout California using Cavalli-Sforza's distance metric of allele frequencies based on 16 nuclear microsatellite loci. (See Ortego et al. 2015b for details of sampling and statistical methods.) Arrow indicates samples of *Quercus cornelius-mulleri* that may be in hybrid swarm with *Q. berberidifolia* (Modified from data reported in Ortego et al. 2015b).

### Evidence based on nuclear DNA microsatellite patterns

In a larger study of the evolutionary and demographic history of the Californian scrub White Oak species complex (Ortego et al. 2015b), we sampled 812 scrub White Oaks from a total of 87 localities in California and genotyped leaf samples with 16 nuclear

(nuSSR). Using a Bayesian structure analysis (Falush et al. 2003; Pritchard et al. 2000), we assigned all individuals to one of six scrub oak species (excluding *Q. durata* var. *gabrielensis*) if 90% or more of their genetic composition could be assigned to one species. To visualize the phylogenetic relationships between all taxa and populations, we reconstructed a population-based neighbor-joining (NJ) tree (Fig. 2) (for details see Ortego et al. 2015b).

Results from the NJ tree suggest that *Q. berberidifolia* and *Q. durata* are closely related and more distant from the rest of the species (Figure 3). This tree also suggests that the pairs of species *Q. cornelius-mulleri*/*Q. john-tuckeri* and *Q. dumosa*/*Q. pacifica* are more closely related with each other than with either of the two other species within the clade. We concluded from this tree in conjunction with species distribution models and niche differentiation analyses that geography and climate have shaped the process of divergence among the scrub oaks.

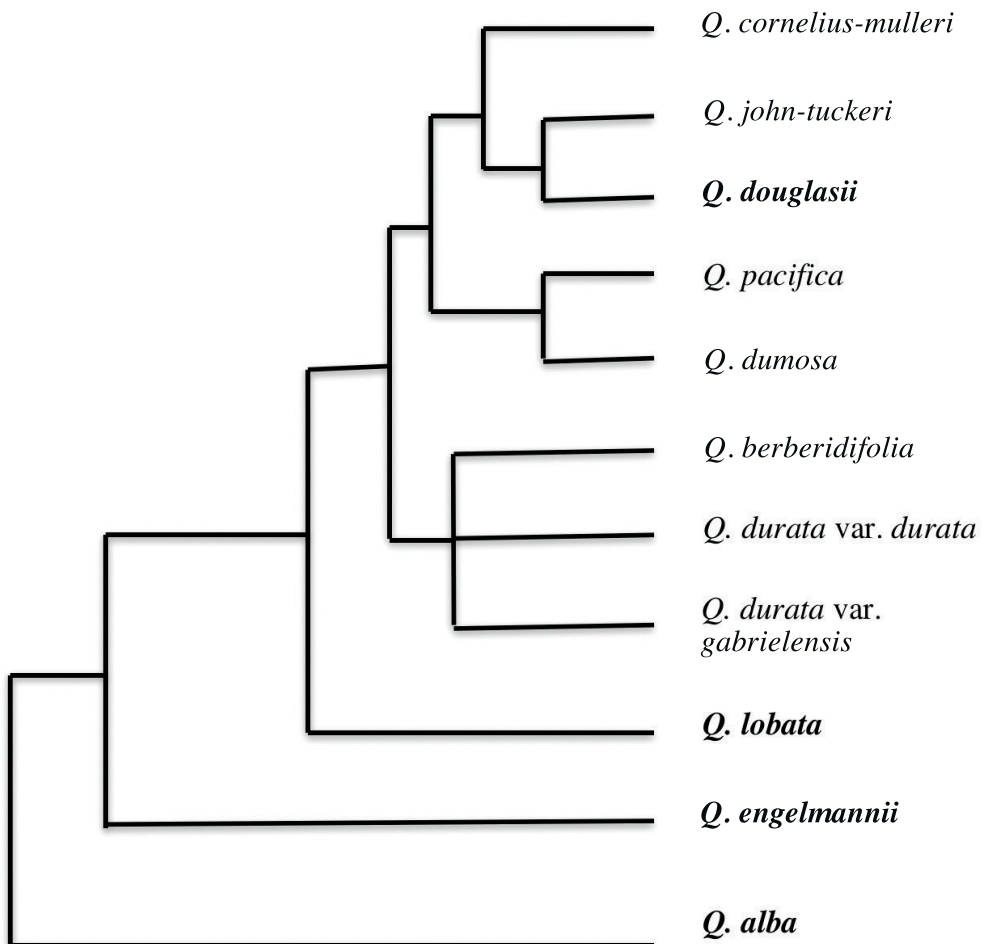


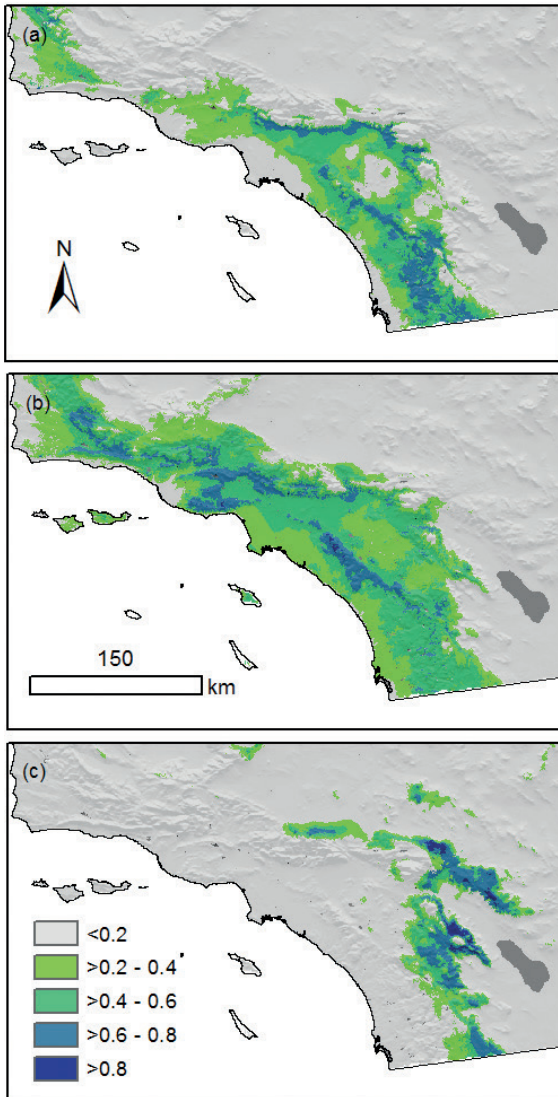
Figure 3/ Idealized phylogenetic tree of seven California white scrub oak species or subspecies, three California tree oaks, and *Quercus alba* from eastern North America as the outgroup. Tree oaks are indicated in bold. Phylogeny is based on RADseq-generated SNPs and RAxML – generated tree using methods of Hipp et al. (2014). (Tree is based on findings of Wei, Ortego, Bernard, Fitz-Gibbon, Gugger, Lohmueller, and Sork, MS in prep.)

### Evidence based on phylogenomic tree

In a separate study of the phylogeny of California White Oaks and analysis of historical introgression based on *D*-statistics (Wei et al., in preparation), we created a phylogenetic tree that included the seven scrub oak taxa, three tree oak species (*Q. douglasii*, *Q. lobata*, and *Q. engelmannii*) and *Q. alba* L., an Eastern North American oak, as an outgroup. The samples were obtained from field collections for the Ortego et al. (2015) study

augmented by collecting trips to obtain *Q. durata* var. *gabrielensis*, and previously collected samples for the tree White Oaks. We extracted DNA and used the same RADseq procedures and the same core facility described by Hipp et al. (2014). A. Hipp provided the sequence data for the outgroup, *Q. alba*. Unlike Hipp et al. (2014), we aligned our DNA sequences to a valley oak reference genome (version 0.5, available at <http://valleyoak.ucla.edu> or NCBI accession LRBV00000000) and used the Genome Analysis Tool Kit to identify variants (McKenna et al. 2010). Based on criteria of 90% complete data across samples, we identified approximately 90,000 SNPs and constructed a phylogeny based on RAxML (Stamatakis 2014), using the approach of Eaton and Ree (2006). Similar to our microsatellite study, we attempted to use individuals that can be classified as putatively pure individuals either through their microsatellite analysis described above or through principle component analysis of the full SNP dataset (Wei et al., manuscript in prep.).

The phylogenetic analysis yields a tree consistent with the NJ tree but with new information about the evolutionary relationships between the scrub oaks (Figure 4). Based on extensive phylogenomic analyses (Wei et al. in prep.), we have developed an idealized tree that indicates that the seven scrub oak taxa divide into two main



**Figure 4/** Regional species distribution models of (a) *Quercus engelmannii*, (b) *Q. berberidifolia*, and (c) *Q. cornelius-mulleri* based on climate variables (modified from Riordan et al. 2016). Models were made using the algorithm Maxent (Phillips 2006) and occurrence data from herbarium specimens and field surveys. Maps show climatically suitable habitat for each species: areas with greatest climatic suitability shown in dark blue, lowest in green.



clades with 100% bootstrap support (Figure 4). *Q. berberidifolia* and *Q. durata* clustered together but with weak bootstrap support for their differences. The second clade included *Q. dumosa*, *Q. pacifica*, *Q. cornelius-mulleri*, and *Q. john-tuckeri*, along with the tree oak, *Q. douglasii*, which appears to be closely related to *Q. john-tuckeri*. This result was a bit surprising because Nixon (2002) categorized it with the lobed White Oak group; however, this relationship is also emerging in the phylogeny of the North American oaks (A. Hipp and P. Manos, personal communication). At this point we cannot rule out the possibility that their relationship is complicated by prior introgression between *Q. douglasii* and *Q. john-tuckeri*. For example, Benson et al. (1967) describe a hybrid swarm between the two species at the Tejon Pass of the Transverse Ranges in California. Nonetheless, two phylogenomic analyses with different samples both yield phylogenetic trees that indicate that *Q. douglasii* shares a common ancestor that was a scrub oak with the other scrub White Oaks in its clade.

When we look at the distribution of most of the scrub oaks, except *Q. berberidifolia*, it is clear that the species in the other clade most likely diverged because of their geographic isolation from each other and probably due to selection by the contrasting environments (Ortego et al. 2015b). The divergence of *Q. durata* var. *durata* may be driven by its association with serpentine outcrops (Forde and Faris 1962; Kruckeberg 1984; Moyle et al. 2012; Whittaker 1954); however, its genetic divergence is weak in the phylogenomic tree (Wei et al., in prep). The divergence of *Q. pacifica* on the Channel Islands with the mainland scrub White Oaks is expected due to its geographic isolation, but its relationship to *Q. dumosa* is very close. The separation between *Q. douglasii* and *Q. john-tuckeri* has good bootstrap support (Wei et al., in prep.), so it may be that the change in growth form also contributed to speciation. The general trend of weak bootstrap support for most of the scrub oak species might be due to their recent divergence or it could be due to introgression. It may be that a focus on genes that underlie species-distinguishing differences (e.g., trichomes and acorn and cup morphology) may be more informative in a phylogenetic tree of the species. It is also possible that better phylogenetic models will be developed that can overcome the impact of introgression. Nonetheless, our combined analysis provides genetic support for these scrub oak species assignments and particularly strong support for membership of *Q. douglasii* within the California scrub White Oak clade, suggesting that scrub White Oaks are not monophyletic.

### ***Case study of Southern California oaks: introgression and geographic variation***

Numerous studies of California oaks or scrub oaks illustrate that both geography and climate shape their distribution, genetic variation, and frequency of hybridization (Benson et al. 1967; Dodd and Afzal-Rafii 2004; Forde and Faris 1962; Grivet et al. 2008; Gugger et al. 2013; Nason et al. 1992; Ortego et al. 2014; Ortego et al. 2015a; Ortego et al. 2012; Riordan et al. 2016; Sork et al. 2010). It is clear that climate variation favors different leaf morphology and ecophysiological traits (Abrams 1989), but it is not well understood how much of that variation is enhanced by introgression of favorable alleles from other species. Yet, it has long been recognized that the ability of oaks to hybridize has allowed these species to occupy habitats that are intermediate to those occupied by the parental species (Anderson 1953; Anderson and Stebbins 1954). Thus, hybridization in oaks is probably not just a consequence of sympatric distributions but a process that is enhanced by environmental conditions.

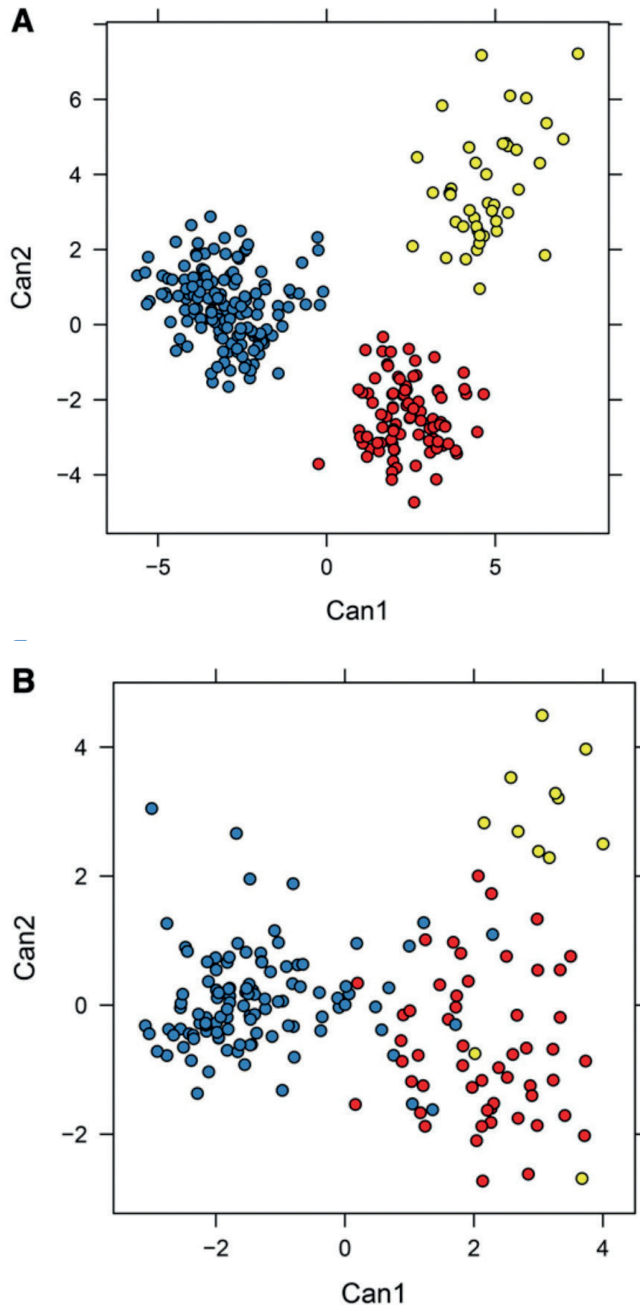


Figure 5/ Comparison of genetic (A) and phenotypic (B) variation in three southern California oaks: *Quercus engelmannii*, *Q. berberidifolia*, and *Q. cornelius-mulleri* for individuals sampled across individuals in the southern California region. Only species with at least 90% genetic assignment to one species are included (for details, see Riordan et al. 2016). Genetic variation is based on canonical discriminant analysis of nine nuclear microsatellite loci for 157 *Q. engelmannii*, 91 *Q. berberidifolia*, and 43 *Q. cornelius-mulleri* individuals. Phenotypic variation is based on eight leaf traits for 109 *Q. engelmannii*, 53 *Q. berberidifolia*, and 12 *Q. cornelius-mulleri* individuals. (From Riordan et al. 2016)

A key hypothesis explaining the high frequency of hybridization in oaks is that introgression through hybridization facilitates the migration of beneficial alleles for survival in environmental habitats novel to the two parental species. This tendency would enhance both genetic and phenotypic variation in new habitats as well as the parental habitats. If true, hybrid swarms should occur in different niches than parental niches. Ortego et al. (2014) tested whether climatic suitability explains patterns of hybridization beyond spatial overlap in distributions of the geographically restricted Engelmann oak (*Q. engelmannii*) and the widespread scrub oak species complex consisting of both *Q. berberidifolia* and *Q. cornelius-mulleri*. Using 343 Engelmann and scrub oaks sampled across 31 localities, we genotyped individuals based on nine microsatellite loci and assigned them to tree oak, scrub oak, or hybrid. We used species distribution models (SDMs) to describe the climate niche for each of the parental species and the hybrids. We found that the hybrids were always near Engelmann oak populations but occupying a climatic niche that was significantly different from parental niches. Thus, these results support the early work of Anderson (1948) and Benson et al. (1967) suggesting that hybridization in oaks provides an opportunity for oaks to broaden their niches by taking advantage of beneficial alleles from other species. Yet, despite the occurrence of hybrid individuals, the frequency is low with few F1 hybrids, suggesting that interspecific gene flow is not “swamping” out the species pools (Ortego et al. 2014).

To what extent does geography versus climate explain patterns of variation in scrub oaks? Riordan et al. (2016) used Maxent to model the geographic distributions of *Q. engelmannii*, *Q. berberidifolia*, and *Q. cornelius-mulleri* separately (Figure 4). Our goal was to better understand regional patterns of climatic suitability, as well as climatic influences on genetic and phenotypic variation, for each species. Despite a high degree of overlap in spatial distribution, all three species showed distinct differences in predicted climatic suitability, even *Q. engelmannii* and *Q. berberidifolia* which had the greatest degree of geographic overlap. *Quercus berberidifolia* is the most widespread species with a distribution closest to the coast, while *Q. cornelius-mulleri* has the most restricted and most eastern distribution. These three species also showed significant genetic differentiation between each other when we compared multilocus genotypes based on microsatellite markers with a canonical discriminant model (Figure 5A). In contrast, phenotypic variation in leaf morphology was much more variable within species than genetic variation, illustrating how variable each species can be in appearance. At the same time, some individuals that were assigned to one species based on nuclear microsatellite markers possessed morphological variation clearly within the distribution of a different species (Figure 5B). In fact, we have other unpublished data showing that individuals that are assigned to one species based on a set of neutral markers will look entirely like a different species. One dramatic example is a scrub oak with multiple stems and small leaves that might show 95% genetic assignment to Engelmann oak (Sork, personal observation). Such examples illustrate that functional genes are likely to introgress differently than neutral genes. In sum, whether incongruences between genotype and phenotype reflect the introgression of genes underlying phenotypic traits or variability within a species is an open question and a challenge for future studies on scrub oak taxonomy.

## Conclusion

The scrub White Oaks provide an informative case of oak species with extensive hybridization that still retain their species identity. Certainly geographic and ecological separation of the majority of the scrub White Oaks promotes their divergence. However, given how recently it seems that these species diverged (as indicated by our phylogenetic tree), it is difficult to be sure whether the phenotypic similarities among taxa are due to a common ancestor, ancient introgression, more recent hybridization events, or phenotypic plasticity. Nonetheless, given the sympatric-parapatric distribution of *Q. berberidifolia* with almost all other scrub oaks (except the Channel Islands scrub oak) and the frequent observations of hybrids involving *Q. berberidifolia* (Benson et al. 1967; Ortego et al. 2014; Pavlik et al. 1995; Riordan et al. 2016; Roberts 1995; Tucker 1990), it is likely that introgression contributes to the scrub oak taxonomic confusion. One wonders how these species manage to retain their species identity, but our recent analyses of the climate differences in their distribution models suggests that ecological factors may maintain their divergence. Thus, oaks may benefit from interspecific flow of favorable alleles but selection will also act against alleles from other species that interfere with local adaptation.

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**Photographers.** Title page: Béatrice Chassé (*Quercus john-tuckeri*). Page 74: Béatrice Chassé (*Quercus cornelius-mulleri*).

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*Quercus cornelius-mulleri* (Joshua Tree National Monument).