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Ancient introgression shapes the evolutionary history of a California Channel Island relictual species, island oak (*Quercus tomentella*)

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ABSTRACT

Hybridization, a common phenomenon among plants, can result in the exchange of neutral or beneficial genetic loci, potentially leading to adaptive introgression. It is often difficult to know whether the genetic composition of contemporary species is the result of recent hybridization or reflects ancient introgression, but examination of a species long separated from a congener provides the opportunity to study ancient introgression. Here, we investigate the rare and endangered island oak *(Quercus tomentella)* that is relictual on the California Channel Islands but was once sympatric with canyon live oak *(Q. chrysolepis)* on the mainland. Recent studies have shown that contemporary populations of island oak include many individuals with essentially 50 % shared co-ancestry between the two species, but very few individuals of non-admixed canyon live oak on any island. The goal of this study is to assess the extent to which the genetic composition of island oak reflects ancient introgression with canyon live oak when they were sympatric on the mainland at least 2.6–7 million years ago. We used evolutionary demographic models that identify the presence and timing of bottleneck events and the extent and timing of ancient introgression between island oak and canyon live oak. Bidirectional gene flow was found throughout their evolutionary history, suggesting that hybridization is not a recent development and may have introduced adaptive alleles into ancient populations that still persist today.

1. Introduction

Interspecific hybridization among plants is relatively common, occurring in at least 25 % of plant species (Mallet, 2005). Hybridization can play a major role in the evolution of species as a cause of speciation events, an instant source of neutral and adaptive genetic variation, a facilitator of range expansion, and even as a driver towards extinction (Rhymer and Simberloff, 1996; Soltis and Soltis, 2009; Abbott et al., 2013; Pfennig et al., 2016; Todesco et al., 2016). The varying consequences of hybridization on participating

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species may be beneficial or detrimental. Adaptations from one species could be passed to another through adaptive introgression, resulting in increased fitness of the parental species in areas of sympatry (Suarez-Gonzalez et al., 2018). Hybrids themselves can develop novel or transgressive traits that allow for the colonization of new environments (Rieseberg et al., 1999), which could then be passed back to the parental species in further backcrosses. However, if hybrids are more fit than their parental species (i.e., heterosis), they could outcompete and replace their parents in a process called genetic swamping (Todesco et al., 2016). On the other hand, if one species is endangered or highly inbred, hybridization could rescue that species from extinction by introducing novel genetic variation, a process known as genetic rescue (Ingvarsson, 2001; Carlson et al., 2014). Studying the presence of ancient introgression can provide

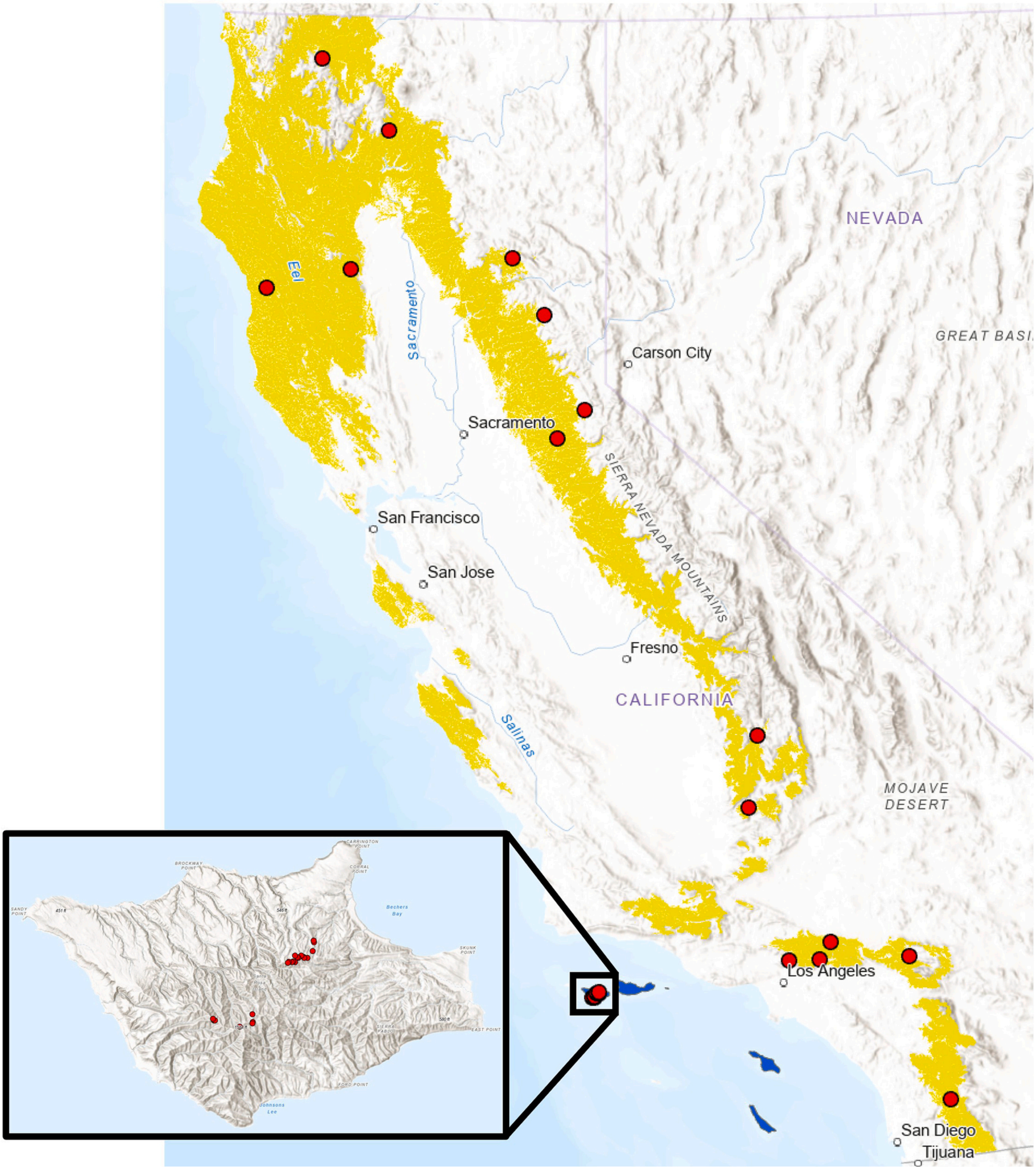

Fig. 1. Distribution maps of *Q. chrysolepis* (yellow) on the mainland and *Q. tomentella* (blue) on the Channel Islands with an enlarged map of Santa Rosa Island overlaid. Sampling points are shown as red dots.

insight into these processes and determine whether conservationists should consider hybridization as a new, potentially human-mediated process or a long-standing, natural one that warrants protection.

Island oak (*Quercus tomentella*), a rare relictual tree existing only on five of the California Channel Islands and on Isla Guadalupe in Mexico (Muller, 1967; Nixon, 2002), provides an interesting case study on the contribution of ancient introgression to contemporary genetic composition. Historically, island oak was widespread throughout mainland California, co-occurring with *Q. chrysolepis* (canyon live oak) during the Miocene and Pliocene 2.6–7 MYA (Axelrod, 1939; 1944; Muller, 1967). The Channel Islands then formed around 5 MYA (Atwater, 1998; Schumann et al., 2012) and were eventually colonized by *Q. tomentella*, but the exact timing is unknown. As the mainland's climate transitioned from a temperate climate (15 MYA) to a Mediterranean climate lacking summer rainfall by 4–7 MYA (Millar, 2012; Rundel et al., 2016), island oak became restricted to the coast and finally just to the islands (Muller, 1967; Axelrod, 1965), while *Q. chrysolepis* remained widespread throughout California, but presumably absent from the Channel Islands. Currently, a few individuals of canyon live oak have been identified on the islands through morphology, but those individuals appear to be F_1 hybrids while non-admixed *Q. chrysolepis* are rare (Mead et al., 2024). Levels of admixture vary across the islands, with some like Catalina and San Clemente containing almost exclusively admixed individuals (at least among sampled trees), Santa Cruz containing some entirely *Q. tomentella* individuals, and Santa Rosa and Anacapa containing no detected *Q. chrysolepis* or admixed individuals (Mead et al., 2024). The lower presence of hybrids on the northern Channel Islands that once comprised a larger island called Santa Rosae (Kennett et al., 2008; Reeder-Myers et al., 2015) and the lack of hybrids on Santa Rosa and Anacapa islands allow for the exploration of colonization and ancient introgression events without the interference of contemporary hybrids.

With whole genome sequences of individuals genetically identified as either exclusively *Q. tomentella* or *Q. chrysolepis* available, it is possible to examine the evolutionary history of the island oak using demographic models (Excoffier and Foll, 2011; Excoffier et al., 2013). We expect to see early bottlenecks in both species with the arrival of the Mediterranean climate, especially in *Q. tomentella* when its distribution was restricted to the coast and then the islands. We will use the same demographic modeling method to test the hypotheses of ancient introgression when the species were sympatric on the mainland. If *Q. chrysolepis* did not colonize the islands along with *Q. tomentella*, then we would see no ancient gene flow between the two species in the last 2.6 MY between when the islands emerged and *Q. tomentella* went extinct on the mainland. Specifically, our goals are to a) determine the timing of *Q. tomentella* island colonization by assessing demographic models that include a bottleneck event, and b) determine the extent to which *Q. chrysolepis* has introgressed with *Q. tomentella* throughout their evolutionary history by examining demographic models with and without ancient gene flow.

2. Materials and methods

2.1. Sample design

We used genotypes from Mead et al. (2024), selecting the 24 individuals from Santa Rosa Island (Fig. 1) genetically identified in their ADMIXTURE analyses as completely *Q. tomentella* with no admixture from *Q. chrysolepis* to minimize the impact of recent hybridization on demographic estimates. Additionally, we included the nine individuals from the mainland genetically identified by Mead et al. (2024) ADMIXTURE analyses as completely *Q. chrysolepis*, adding six more samples from the mainland for a total of 15 *Q. chrysolepis* individuals (Fig. 1). For the additional six samples, approximately 50 mg of leaf tissue from each sample was flash-frozen in liquid nitrogen before bead grinding. DNA was then extracted using a modified version of the Qiagen DNeasy Plant Mini Kit protocol preceded by a prewash step, following Mead et al. (2024) and Li et al. (2007). The pre-wash buffer, consisting of 100uL of Tris, 100uL of EDTA, 200uL of 5 M NaCl, 600uL of molecular grade water, and 0.01 g of PVP, was applied twice to each sample to remove polyphenols. Extracted DNA was then sent to UC Davis DNA Technologies and Expression Analysis Core Laboratory for quality check via Qubit Fluorometer, library preparation using a custom seqWell™ kit, and whole-genome sequencing on a NovaSeq 6000 150 bp paired-end sequencer.

2.2. Filtering and variant calling

Adapter sequences were trimmed from raw reads using Trim Galore (https://github.com/FelixKrueger/TrimGalore), removing reads less than 20 bp in length. Reads were then aligned to the *Q. lobata* reference genome (Sork et al., 2022) rather than the island oak genome (Mead et al., 2024), because it is equally distant to both *Q. tomentella* and *Q. chrysolepis* and is annotated. Alignments were done using BWA-MEM with 'markShorterSplits' and 'readGroupHeaderLine' options enabled (Li, 2013). Duplicate reads were marked and removed using the MarkDuplicates command in GATK (Van der Auwera and O'Connor, 2020). Variants were called using the HaplotypeCaller command in GATK with the 'emit-ref-confidence' option set to 'GVCF'. GVCFs were then imported into GenomicsDB via GATK GenomicsDBImport and genotyped using GenotypeGVCFs. Variants were hard-filtered using the VariantFiltration command in GATK, with SNPs and indels filtered separately. For SNPs, variants with quality by depth (QD) < 2, quality (QUAL) < 30, mapping quality (MQ) < 40, phred-scaled strand bias (FS) > 60, symmetric odds ratio strand bias (SOR) > 3, mapping quality rank sum (MQRankSum) < -12.5, and read position rank sum (ReadPosRankSum) < -8 were removed. Indels with QD < 2, FS > 200, QUAL< 30, and ReadPosRankSum < -20 were removed. Repetitive regions of the genome were removed using vcftools (Danecek et al., 2011) based on the reference genome. From this set of high-quality variants, biallelic SNPs with high coverage across all samples were selected for further analysis. Using vcftools, only biallelic SNPs were selected, individual genotypes with depth < 5 were set to missing, and SNPs with a mean depth across all samples < 5, with a minor allele frequency < 0.01, and with ≥ 10 % missingness across all individuals were removed. The resulting filtered VCF file was converted to BED file format using PLINK (version 1.90b6.26, Chang et al., 2015), and variants were pruned for linkage disequilibrium using a window size of 50 variants, a window shift value of 10, and a strict R^2 threshold of 0.1 to minimize loci under selection (Mead et al., 2024). All downstream analyses were run on this filtered and LD-pruned dataset of 39 individuals and 234,531 SNPs.

2.3. Genetic structure

To ensure the additional samples and full dataset concurred with Mead et al.'s (2024) clustering results and were not admixed, we used the maximum likelihood method ADMIXTURE (Alexander et al., 2009) and examined the genetic structure of *Q. tomentella* samples from Santa Rosa Island and *Q. chrysolepis* samples from the mainland. The number of clusters (K) 1–5 were tested, using the lowest cross-validation value to select the best K. Ancestry coefficients (*Q* values) were visualized using pophelper (Francis, 2017). We also examined genetic structure through an additional method, a Principal Components Analysis (PCA), implemented in the R package ***vegan*** (Oksanen et al., 2013).

2.4. Estimating demographic parameters

To explore the demographic history of *Q. tomentella* and determine the influence of *Q. chrysolepis* gene flow, we tested 16 demographic scenarios (Fig. S1) in fastsimcoal2.8 (Excoffier and Foll, 2011; Excoffier et al., 2013). The various scenarios tested included models with and without bottlenecks and all possible gene flow scenarios in between demographic events, including no gene flow, episodic, and continuous. Due to the presence of missing data (total missingness in the filtered dataset was 5 %), we used easySFS (https://github.com/isaacovercast/easySFS) to downsample our dataset to 12 individuals of *Q. chrysolepis* with 194,295 SNPs and 21 of *Q. tomentella* with 201,031 SNPs (total missingness was now 0 %) and generate a folded 2-dimensional site frequency spectrum (SFS). Each demographic model was replicated 250 times using 40 expectation–conditional maximization (ECM) cycles, a limit of five unsuccessful cycles before parameter reset, a log precision of 18, and 250,000 simulations to calculate the likelihood. A mutation rate of 1.01×10^{-8} per site per generation was implemented (Sork et al., 2022). To convert output parameter estimates, a generation time of 20 years was assumed (e.g., 100 generations = 2000 yr ago). We bounded divergence time of the two species to 500,000 generations to roughly align with Hipp et al.'s (2020) estimate. We also bounded effective population sizes between 10 and 1,000,000 on a log uniform distribution and migration rates between 1×10^{-3} and 100 on a log uniform distribution. We used Akaike's information criterion (AIC) to find the most probable model given the observed data. Confidence intervals on parameter estimates for the best-supported model were then generated using parametric bootstrapping. We first simulated 100 replicate datasets from the best fitting model, then ran these 100 new SFS in *fsc*2.8 50 independent times each, using the same parameters and conditions as the original runs with the point estimates from the best-supported model used as starting values. The estimates from the highest likelihood

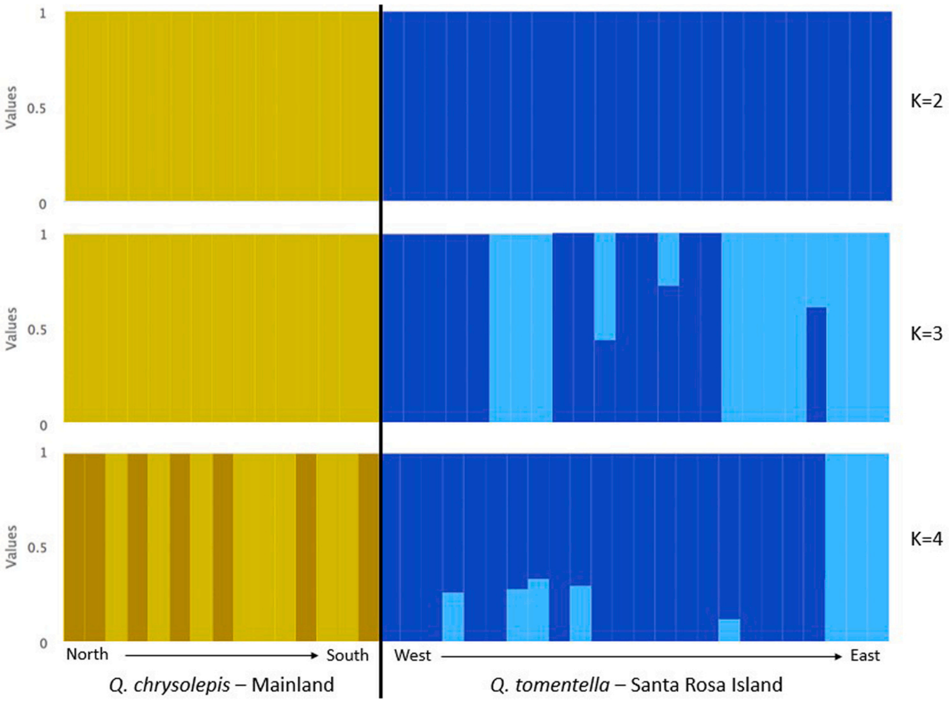

Fig. 2. ADMIXTURE (Alexander et al., 2009) results of K= 2–4 visualized in pophelper (Francis, 2017). The best model was K= 1 with no separation by species (not pictured). K= 2 shows clear separation between the mainland *Q. chrysolepis* (yellow) and Santa Rosa Island *Q. tomentella* (blue) samples. *Quercus chrysolepis* samples are arranged North to South and *Q. tomentella* West to East.

of the 50 replicates for each 100 SFS bootstrap runs were then used to compute confidence intervals. This work used computational and storage services associated with the Hoffman2 Cluster, which is operated by the UCLA Office of Advanced Research Computing's Research Technology Group.

3. Results

3.1. Genetic clustering

We used ADMIXTURE (Alexander et al., 2009) and PCA to confirm the genetic identity of *Q. tomentella* samples from Santa Rosa Island and *Q. chrysolepis* from the mainland. The best K was 1, as it was in Mead et al. (2024), but K= 2 appropriately separated the individuals corresponding to species designations (Fig. 2, Table S1). Similarly, the individuals separated into distinct groups matching species identities in our PCA, with PCA axis 1 representing 10.9 % of genetic variation and PCA axis 2 representing 5.6 % (Fig. S2). None of the *Q. tomentella* samples from Santa Rosa Island included evidence of hybridization with *Q. chrysolepis*, and all *Q. chrysolepis* individuals from the mainland showed no genetic evidence of recent hybridization with *Q. tomentella*, matching the results from Mead et al. (2024).

3.2. Demographic modeling

To determine the timing of *Q. tomentella* island colonization and the history of *Q. chrysolepis* introgression, we used the whole genome sequences to compare sixteen demographic models including bottleneck events with and without gene flow (Fig. S1). The colonization of the Channel Islands would have likely resulted in a large reduction in population size due to founder effects (Nei et al., 1975; James et al., 2016) and California's shift to a Mediterranean climate would have likely resulted in the same. As the ranges of *Q. chrysolepis* and *Q. tomentella* rapidly shifted, they likely came in and out of contact, resulting in episodic gene flow with periods of sustained introgression followed by periods of isolation. To discover the true evolutionary history of these two species, we tested models that included bottlenecks and those that did not, as well as models with varying episodes of gene flow and models without.

The model that best explained our data (Fig. 3) revealed two bottleneck events, one in each species, with *Q. tomentella* having a more recent bottleneck estimated to end an average of 214,000 years ago (10,700 generations ago), which was during a warm interglacial period. The *Q. chrysolepis* bottleneck event ended an average of 7.3 MYA. This model included ancient introgression from the time of species divergence to the first bottleneck event, no migration during either bottleneck events, and then migration continued until present, with more gene flow from *Q. chrysolepis* into *Q. tomentella* (Table 1). Gene flow was bidirectional but asymmetrical, with more average migrants per generation coming from *Q. chrysolepis* into *Q. tomentella* after divergence and *Q. chrysolepis*'s bottleneck, but *Q. tomentella* having more migrants into *Q. chrysolepis* more recently. When taking confidence intervals into consideration, gene flow remains bidirectional but the asymmetry becomes questionable with the minimum and maximum estimated number of migrants per year overlapping within each gene flow event. Effective population sizes fluctuated throughout the species' evolutionary histories, with *Q. chrysolepis* estimated to currently have a larger population size on average (73,242 individuals) than *Q. tomentella* (41,253 indiv.), yet *Q. tomentella* had a larger average population size in all other time periods.

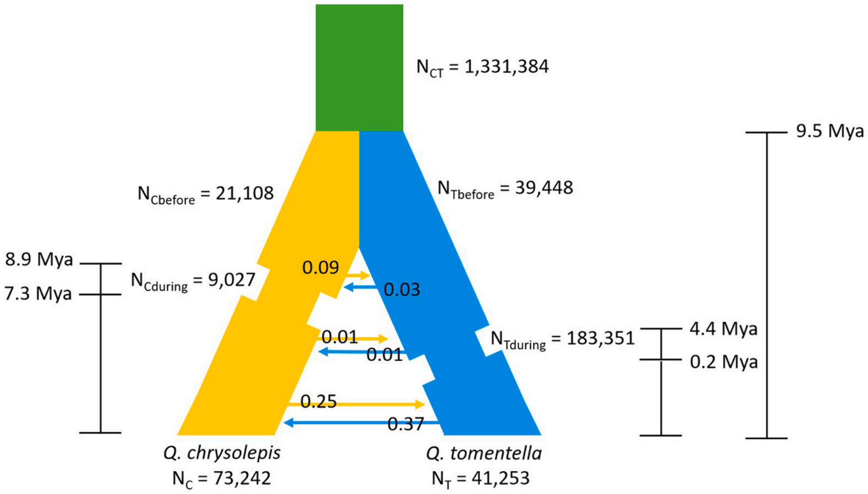

Fig. 3. Best demographic model tested in fastsimcoal2 (Excoffier and Foll, 2011; Excoffier et al., 2013) showing ancient admixture (gene flow events represented by arrows, with numbers indicating migrants per year) and two bottleneck events (represented by the narrow rectangles), one in each species, with *Q. tomentella* having a more recent bottleneck. Colors indicate separate lineages (green = ancestral before divergence (CT), yellow = *Q. chrysolepis* (C), and blue = *Q. tomentella* (T)), "N"s represent effective population sizes, and vertical lines represent times of demographic events. All parameters shown are averages of estimated confidence intervals, for full intervals see Table 1.

Table 1
Estimated parameters of the best model inferred from fastsimcoal2 (Excoffier and Foll, 2011; Excoffier et al., 2013) with upper and lower bounds of the 90 % confidence intervals (CI). Parameters are defined as N = effective population size, t = time of event, and m = migration rates. C represents parameters for *Q. chrysolepis* and T for *Q. tomentella*. A generation time of 20 years was assumed to convert the per generation parameters into per year shown in Fig. 3.

Parameter	Model average	Lower bound CI	Upper bound CI
N_C	73,242 individuals	14,782	404,248
N_T	41,253 indiv.	7668	285,690
N_{ancestor}	1,331,384 indiv.	542	14,530,959
$N_{\text{C-bot}}$	9027 indiv.	55	98,064
$N_{\text{C-before}}$	21,108 indiv.	69	112,856
$N_{\text{T-bottleneck}}$	183,351 indiv.	159	397,876
$N_{\text{T-before}}$	39,448 indiv.	724	327,643
$t_{\text{T-bottleneck}}$	10,715 generations	2383	70,426
$t_{\text{T-end}}$	222,044 gen.	28,313	453,168
$t_{\text{C-bottleneck}}$	336,074 gen.	149,466	480,688
$t_{\text{C-end}}$	449,664 gen.	149,466	480,688
$t_{\text{coalescence}}$	474,171 gen.	373,691	497,939
1m01	7.44 migrants/gen	4.50	16.14
1m10	5.05 migrants/gen	4.09	7.34
2m01	0.12migrants/gen	5.20×10^{-3}	0.72
2m10	0.14 migrants/gen	1.85×10^{-4}	2.41
3m01	0.61 migrants/gen	4.36×10^{-4}	12.03
3m10	1.88 migrants/gen	5.46×10^{-4}	30.99

4. Discussion

As predicted, our findings reveal genetic bottlenecks after the two species diverged from their common ancestor that coincide with the transition to a Mediterranean climate starting at most 15 MYA (Rundel et al., 2016) and completing 4 – 7 MYA (Millar, 2012) for *Q. chrysolepis* and the restriction of *Q. tomentella* to the coast and the Channel Islands in the Pliocene 2.6 – 5.3 MYA (Muller, 1967; Axelrod, 1965). Demographic modeling suggests ancient introgression occurred several times throughout their evolutionary history, pausing only during bottleneck events. With the large confidence intervals (Table 1), we interpret these findings cautiously and point out that the highest levels of gene exchange occurred more recently after both bottlenecks when the two species would have likely been allopatric. During the early period after divergence and also after the first bottleneck, migration was asymmetric from canyon live oak into island oak, which would have taken place when both species were on the mainland. After the *Q. tomentella* bottleneck began, about 4.4 MYA, that species presumably became restricted to the Channel Islands so it is puzzling why we observe gene flow at all, and why it is asymmetric from *Q. tomentella* into *Q. chrysolepis*, especially when these individuals were collected from the mainland where the last fossil record of *Q. tomentella* was 2.6–5.3 MYA. We discuss these findings in more detail below.

4.1. Recent bottlenecks may indicate island colonization and Mediterranean shift

Two bottleneck events were detected, one in each species, with *Q. tomentella* having a more recent bottleneck. As island colonization can cause a drastic reduction in population size (Nei et al., 1975; James et al., 2016), this event is likely *Q. tomentella*'s colonization of the Channel Islands. The exact timing of the demographic events varies with the generation time chosen and similarly with the estimated mutation rates (Takahata and Nei, 1985), but the real times are likely on the lower end of these estimates given Hipp et al. (2020) estimated time of divergence to be ~7 MYA; however fossil evidence of its ancestor *Q. declinata* date up to 24 MYA (Kindsvater, 2006). The bottleneck event was estimated to begin around 4.4 MYA on the lower end, about the time the islands formed ~5 MYA (Atwater, 1998; Schumann et al., 2012) and California was shifting to a mediterranean climate (Axelrod, 1939, 1944; Muller, 1967).

Quercus chrysolepis's bottleneck event took place approximately 7.3–8.9 MYA, almost coinciding with California's shift to a drier Mediterranean climate, which likely resulted in large range contractions before less temperate adaptations became more prevalent. The lack of hybridization during bottleneck events may suggest that the species were not in contact during these periods of severe population size reduction. This hypothesis would align with a severe reduction in range of either *Q. tomentella*, *Q. chrysolepis*, or both during the end of the Miocene when California became less temperate, and with the isolation during island colonization by *Q. tomentella*.

4.2. Ancient introgression prevalent between Q. tomentella and Q. chrysolepis

The presence, direction, and magnitude of gene flow between *Q. tomentella* and *Q. chrysolepis* were tested in several demographic models, with high levels of ancient introgression detected between the two species. We point out the broad confidence intervals around parameter estimates, but the models with ancient gene flow were more likely than models without, and the four models tested without gene flow were the four worst models (Table S2). Thus, the evidence for ancient introgression is convincing. The best model indicated that gene flow occurred between species divergence and *Q. chrysolepis*'s bottleneck event, ceasing during the bottleneck, then continuing until *Q. tomentella*'s bottleneck event, stopping again during that bottleneck, and finally continuing through the present. These few million-year breaks in gene flow were likely due to lack of contact during range contraction (in the case of *Q. chrysolepis*) or island colonization (*Q. tomentella*). Similar patterns of episodic hybridization events were observed in sympatric white oaks (Kim et al., 2018). This recurring bidirectional gene flow implies a lack of reproductive isolating mechanisms present in the two species. Perhaps selection against their hybrids is not strong enough or not enough time has passed since species divergence for reproductive isolating mechanisms to form (Mallet, 2005).

The level of gene flow varied throughout their evolutionary history, but was mostly from *Q. chrysolepis* into *Q. tomentella*, with the exception of the period after *Q. tomentella*'s bottleneck to present day. It is strange that more contemporary gene flow would be higher from *Q. tomentella* into *Q. chrysolepis*, especially considering *Q. tomentella* is restricted to the islands and the *Q. chrysolepis* samples were collected from the mainland; however it is important to note the overlapping confidence intervals found and that levels of gene flow might differ among islands. We propose three hypotheses to explain this phenomenon; however further studies must be done to determine their validity: 1) island oak did not go extinct on the mainland until ~2 MYA and continued to exchange genes, 2) genes from *Q. tomentella* were traveling back to the mainland from the isolated Channel Islands, or 3) these signals are a result of incomplete lineage sorting (ILS).

Hypothesis 1. For the first hypothesis, *Q. tomentella* could have continued existing on the mainland in small diminishing populations, allowing introgression into *Q. chrysolepis* until a more recent extinction than previously thought (2.6–7 MYA). No individuals of *Q. tomentella* currently occur on the mainland and fossils for *Q. tomentella* have been found on the mainland from the Plieocene (2.6–7 MYA), but not more recently (Axelrod, 1939; 1944; Muller, 1967). That does not rule out its existence on the mainland beyond that time; however, fossils of *Q. chrysolepis* have been found more recently (up to 2 MYA), without the co-occurrence of *Q. tomentella* (Mensing, 2005).

Hypothesis 2. For the second hypothesis, the distance from the islands to the mainland is currently too far for wind-mediated pollen dispersal (Sork et al., 2002; Buschbom et al., 2011); however, during the Pleistocene, lower sea levels resulted in the islands being only 5 miles from the mainland at their closest point (National Parks Service). This smaller distance resulted in the island colonization of many species (Johnson, 1978) and could have resulted in the dispersal of pollen by the northwesterly winds or seed by corvid or even human dispersers (Johnson, 2002; Rick et al., 2019). Further, the Pleistocene lasted 2.6 MYA to 11,000 years ago, which matches the estimated start of gene flow from *Q. tomentella* in our model (Fig. 3).

Hypothesis 3. Finally, these signals of ancient gene flow could instead be a result of incomplete lineage sorting (Yu et al., 2011). While testing demographic models with and without gene flow can usually tease apart ancient introgression and ILS, fastsimcoal2 does not have methods to explicitly test for signals of ILS, which can become muddied especially if levels of gene flow are high right after divergence (Meyer et al., 2017). The relatively recent divergence of these two lineages, combined with their high population sizes could result in signals of ILS (Maddison and Knowles, 2006). Support for this lack of complete divergence can be seen in higher support for being one genetic cluster instead of two (Table S1; Mead et al., 2024).

Regardless of the cause, introgression between *Q. chrysolepis* and *Q. tomentella* could have helped island establishment by introducing novel traits and genetic variation, or hindered by homogenizing divergent genotypes (Caujapé-Castells et al., 2017; Buck and Flores-Rentería, 2022). If *Q. tomentella* colonized the Channel Islands in isolation, then restarted gene flow with *Q. chrysolepis* at a later point as our model suggests, the adaptive introgression of island-adapted genes into *Q. chrysolepis* from *Q. tomentella* could have allowed for the more recent colonization of the islands by *Q. chrysolepis*. The lack of non-admixed *Q. chrysolepis* genotypes on the island may support this claim by suggesting that there is either selection against *Q. chrysolepis* genotypes that do not hybridize or selection for admixed individuals.

4.3. Implications for island oak management and restoration

Extensive contemporary hybridization was detected by Ortego et al. (2018) and Mead et al. (2024) during their conservation research on *Q. tomentella*. Island oak is a species of conservation concern (Ashley et al., 2018; Woolsey et al., 2018; Mead et al., 2024) due to its IUCN Endangered classification (Beckman and Jerome, 2017; Jerome et al., 2017), loss of dispersers (Delaney et al., 2008), reduction in historic range (Kindsvater, 2006), and vulnerability to climate change (Mead et al., 2024). Land managers are actively deciding if transferring seeds within and among islands is a viable and sensible option for restoration, however the presence of *Q. tomentella* × *Q. chrysolepis* hybrids complicates their decision. It appears that gene flow has been ongoing and a natural part of their shared evolutionary history, but the consequences of recent hybridization should still be examined. The introduction of maladapted foreign genotypes into already endangered populations could put them at further risk of extinction (Todesco et al., 2016). On the other hand, because hybridization has been ongoing, admixed genotypes could introduce beneficial adaptations through adaptive introgression that could save *Q. tomentella,* a process called genetic rescue (Ingvarsson, 2001; Carlson et al., 2014; Suarez-Gonzalez et al., 2018; Buck and Flores-Rentería, 2022). Further, hybridization could result in the masking of deleterious recessive alleles through the creation of heterozygotes, resulting in increased fitness (Whaley, 1944).

Restoration projects should still be cognizant of their use of non-admixed island oak or canyon live oak hybridized individuals, but the two species are so closely related, outbreeding depression is unlikely. If land managers are seeking to preserve only "pure" *Q. tomentella* genotypes, then they may want to avoid admixed individuals when seed sourcing; however most sampled individuals outside of Santa Rosa and Anacapa Islands were admixed to some degree (Mead et al., 2024). This lack of non-admixed genotypes may be a result of genetic swamping, where hybrids have a selective advantage and have replaced the parental genotypes (Todesco et al., 2016). Less likely, those admixed genotypes possibly could be signals of incomplete lineage sorting rather than hybridization; however, analyses differentiating the two evolutionary processes need to be done to assess that hypothesis. Heterosis or even novel traits may have arisen within the admixed individuals, allowing for their increased survival or reproduction, yet this same increased fitness could be beneficial to *Q. tomentella*'s survival if used in restoration (Rieseberg et al., 1999; Barton, 2001; Hamilton, Miller, 2016; Pfennig et al., 2016). Fitness tests between the hybrids and their parental species should be performed to determine if the hybrids would be more or less fit, especially under future climate regimes, and thus better options for restoration.

5. Conclusion

Hybridization has played a major role in many species' evolutionary histories, partly by introducing novel traits and variants. Recently, hybridization was detected between the rare endemic island oak and the closely related canyon live oak but its role in their shared evolutionary history was unknown. Demographic modeling suggests introgression between the two species has taken place consistently throughout their evolutionary history, demonstrating that gene flow has been ongoing and is not just a recent development. With conservation projects underway for island oak, land managers would benefit from information about the genetic makeup of their populations. A key question is whether the presence of current admixed individuals could benefit or harm the restoration of this endangered island oak now facing warmer temperatures.

CRediT authorship contribution statement

Ryan Buck: Writing – original draft, Formal analysis, Writing – review & editing, Methodology, Visualization. **Sorel Fitz-Gibbon:** Methodology, Writing – review & editing, Data curation. **Alayna Mead:** Data curation, Writing – review & editing. **Victoria L. Sork:** Resources, Investigation, Conceptualization, Writing – original draft, Supervision, Writing – review & editing, Funding acquisition. **John Knapp:** Conceptualization, Writing – review & editing, Funding acquisition.

Ethics

Not applicable: This manuscript does not include human or animal research.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03706.

Data availability

Sequencing data are available at NCBI BioProject accession PRJNA808370.

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