Genomic data reveal cryptic lineage diversification and introgression in Californian golden cup oaks (section *Protobalanus*)

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Summary

• Here we study hybridization, introgression and lineage diversification in the widely distributed canyon live oak (*Quercus chrysolepis*) and the relict island oak (*Q. tomentella*), two Californian golden cup oaks with an intriguing biogeographical history.

• We employed restriction-site-associated DNA sequencing and integrated phylogenomic and population genomic analyses to study hybridization and reconstruct the evolutionary past of these taxa.

• Our analyses revealed the presence of two cryptic lineages within *Q. chrysolepis*. One of these lineages shares its most recent common ancestor with *Q. tomentella*, supporting the paraphyly of *Q. chrysolepis*. The split of these lineages was estimated to take place during the late Pliocene or the early Pleistocene, a time corresponding well with the common presence of *Q. tomentella* in the fossil records of continental California. Analyses also revealed historical hybridization among lineages, high introgression from *Q. tomentella* into *Q. chrysolepis* in their current area of sympatry, and widespread admixture between the two lineages of *Q. chrysolepis* in contact zones.

• Our results support that the two lineages of *Q. chrysolepis* behave as a single functional species phenotypically and ecologically well differentiated from *Q. tomentella*, a situation that can be only accommodated considering hybridization and speciation as a continuum with diffuse limits.

Introduction

The hybridization continuum (*sensu* Hochkirch, 2013) ranges from sporadic interspecific gene flow, with little or no impact on the evolutionary and demographic trajectories of the taxa involved, to the formation of new species reproductively isolated from parental forms (Barton, 2001; Abbott *et al.*, 2013). At one end of the range, hybrids can constitute an ephemeral state through which species are able to colonize new habitats (Bacilieri *et al.*, 1996; Petit *et al.*, 2004) and exchange alleles involved in the adaptation to novel environmental conditions (Lewontin & Birch, 1966; Baskett & Gomulkiewicz, 2011) without compromising the genetic and ecological distinctiveness of parental taxa (i.e. collective evolution; Morjan & Rieseberg, 2004). At the opposite end, hybridization has been recognized to be an important engine of diversification in many organism groups (Dowling & Secor, 1997; Rieseberg, 1997), and involved in the functional extinction of rare species through demographic swamping and genetic assimilation by more abundant species (Levin *et al.*, 1996; Rhymer & Simberloff, 1996). Hybrid speciation mechanisms

include allopolyploid speciation, which generally results in the formation of new hybrid species with strong reproductive barriers that prevent interbreeding between the hybrid and its parents, and homoploid hybrid speciation, which leads to the formation of stable hybrid species that are often reproductively compatible with the parental forms (Rieseberg, 1997; Wood *et al.*, 2009; Abbott *et al.*, 2013). The hybridization/divergence continuum also comprises a broad range of intermediate situations (Hochkirch, 2013; Edwards *et al.*, 2016), including asymmetrical contributions of parental taxa to the genetic composition of hybrid species/lineages (e.g. Sun *et al.*, 2014), low levels of historical introgression followed by reproductive isolation (e.g. Eaton & Ree, 2013; Escudero *et al.*, 2014; Eaton *et al.*, 2015) or strong introgression or resistance to introgression limited to specific genomic regions with important consequences on fitness (Fitzpatrick *et al.*, 2010; Poelstra *et al.*, 2014; Liu *et al.*, 2015).

Disentangling reticulate evolutionary histories of either stable hybrid species or introgressed lineages has been challenging for a long time due to the inherent limitations of phylogenetic tools to deal with nonstrictly bifurcating processes of species

diversification, the poor resolution of small subsets of genetic markers to discern introgression from ancestral polymorphism, and the scarce integration of population genetic approaches into phylogenetic reconstruction (Linder & Rieseberg, 2004; McBreen & Lockhart, 2006; Abbott *et al.*, 2016; Payseur & Rieseberg, 2016; McVay *et al.*, 2017). This task is even more challenging when one of the parental taxa is extinct (e.g. Wang *et al.*, 1990; Currat & Excoffier, 2011) or locally extinct (Melo-Ferreira *et al.*, 2009), when hybridization only involves populations from a portion of the geographical distribution of the focal taxon (e.g. Nettel *et al.*, 2008; Melo-Ferreira *et al.*, 2009; Wall *et al.*, 2013; de Manuel *et al.*, 2016) or if introgression has induced phenotypic assimilation (Rheindt *et al.*, 2014; Huang, 2016).

Here, we employ genomic tools to study lineage diversification, introgression and hybridization between the canyon live oak (*Quercus chrysolepis* Liebmann) and the island oak (*Q. tomentella* Engelmann), two Californian golden cup oaks (section *Protobalanus*) with an intriguing biogeographical history (Muller, 1967; Nixon, 2002; eFloras, 2017). Canyon live oak is a widely distributed tree in California, with relictual populations in Arizona, Nevada, New Mexico, Oregon and northern Baja California (Thornburgh, 1990; eFloras, 2017). Previous microsatellite-based studies have shown that this species presents a deep genetic structure, with two genetic clusters separating populations located north and south of the Transverse ranges (Ortego *et al.*, 2015a; Bemmels *et al.*, 2016). This phylogeographical subdivision contrasts with the shallow patterns of genetic differentiation found among other Californian oak species with similar distribution ranges, including both red oaks (section *Lobatae*; Dodd & Kashani, 2003) and white oaks (section *Quercus*; Ashley *et al.*, 2015; Fitz-Gibbon *et al.*, 2017; Ortego *et al.*, 2017; but see Gugger *et al.*, 2013). Contrasting with the wide distribution of *Q. chrysolepis* across continental California, *Q. tomentella* is currently found in small populations confined to Guadalupe Island (Mexico) and the Channel Islands off the coast of southern California (USA) (Muller, 1967; Nixon, 2002; eFloras, 2017), which has motivated its inclusion in the IUCN Red List of Threatened Species with the status 'endangered' (Beckman & Jerome, 2017). Unlike many other endemic taxa from the Channel Islands that have speciated *in situ* (Thorne, 1969; Backs & Ashley, 2016; Riley & McGlaughlin, 2016), the widespread representation of *Q. tomentella* in late Tertiary fossil floras from continental California supports its origin from a previously more broadly distributed taxon that included the mainland (Axelrod, 1944a,b, 1967; Muller, 1967). Canyon live oak is also known to be present in some of the California Channel Islands, where it occurs as scattered individuals at the highest elevations and often showing strong phenotypic signs of introgression with *Q. tomentella* (Muller, 1967; Thorne, 1969; Nixon, 2002; Ashley *et al.*, 2010; eFloras, 2017).

In this study, we use restriction-site-associated DNA sequencing (ddRAD-seq; Peterson *et al.*, 2012) and a suite of population and phylogenomic analytical approaches to unravel the evolutionary and hybridization history of *Q. chrysolepis* and *Q. tomentella*. In particular, we (1) first use genome-wide single-nucleotide polymorphisms (SNP) data to test for hybridization between the two species in their overlapping distribution at some of the Californian Channel Islands and confirm the presence of interspecific gene flow suggested by previous anecdotal observations and studies (Muller, 1967; Nixon, 2002; Ashley *et al.*, 2010; eFloras, 2017). Second, we employ (2) a coalescent-based simulation framework to infer the timing and directionality of gene flow between *Q. tomentella* and continental populations *Q. chrysolepis*. We hypothesize that interspecific gene flow may have occurred due to increased geographical contact between the two species during the Miocene/Pliocene epochs (23.03–2.58 Myr ago (Ma)), when *Q. tomentella* was widely distributed in continental California (Axelrod, 1944a,b; Muller, 1967; eFloras, 2017), and/or during the Pleistocene glacial periods (2.59–0.01 Ma), when the lower sea levels almost connected the northern Channel Islands (Santa Rosa, Santa Cruz and Anacapa) to the mainland (Johnson, 1978). We (3) also explore whether the deep genetic structure of *Q. chrysolepis* reported in previous studies (Ortego *et al.*, 2015a; Bemmels *et al.*, 2016) represents a phylogeographical break driven by the past geological history of the region and/or hides a cryptic history of hybridization or introgression with *Q. tomentella* (Calsbeek *et al.*, 2003; Chatzimanolis & Caterino, 2007; Vandergast *et al.*, 2008). Finally, we (4) test whether lineages/populations involved in hybrid gene flow interactions show higher levels of genetic diversity than those that have not experienced genetic admixture (Nettel *et al.*, 2008; Streicher *et al.*, 2014).

Materials and Methods

Population sampling

Between 2010 and 2014, we sampled 12 continental populations of canyon live oak (*Quercus chrysolepis* Liebmann) ($n = 88$ individuals) and three populations of island oak (*Q. tomentella* Engelmann) ($n = 36$ individuals) from Santa Cruz, Santa Catalina and San Clemente Islands (Supporting Information Table S1). We also collected samples from *Q. chrysolepis* from Santa Cruz ($n = 9$) and San Clemente Islands ($n = 1$), most of them tentatively identified as hybrids with *Q. tomentella* based on their morphological appearance (eFloras, 2017). We designed sampling using occurrence records available in the Calflora database (http://www.calflora.org/) and aimed to collect samples representing populations located across the entire distribution of the two species in California (Fig. 1a; Table S1). Samples from Palmer oak (*Q. palmeri* Engelmann) ($n = 5$) and huckleberry oak (*Q. vaccinifolia* Kellogg) ($n = 5$), species also belonging to the section *Protobalanus* (eFloras, 2017), were used in phylogenomic analyses (see below). Spatial coordinates were registered using a Global Positioning System (GPS) unit and leaf samples were stored frozen (–20°C) until needed for genomic analyses (Table S1).

DNA extraction, library preparation and sequencing

We used a mixer mill to grind *c.* 50 mg of frozen leaf tissue in tubes with a tungsten bead and performed DNA extraction and
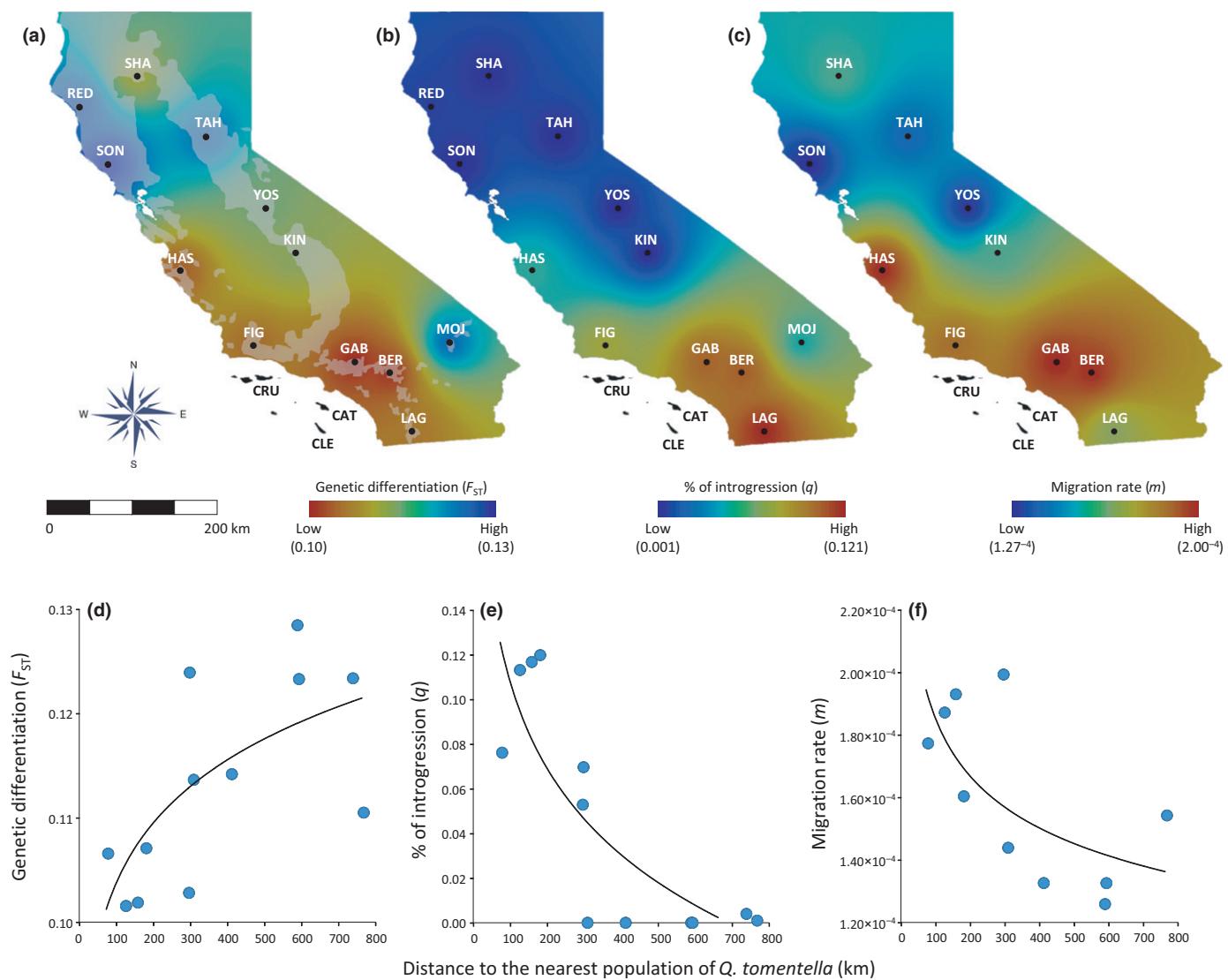
Fig. 1 Maps from California representing the studied populations of canyon live oak (*Quercus chrysolepis*) and island oak (*Q. tomentella*). Color gradients represent spatial interpolations for (a) pairwise genetic differentiation (F_{ST}) between *Q. tomentella* and each continental population of *Q. chrysolepis*, (b) probability of membership (*q*) of each continental population of *Q. chrysolepis* to the *Q. tomentella* genetic cluster as inferred by STRUCTURE analyses (i.e. % of introgression), and (c) pairwise migration rates (*m*) from *Q. tomentella* to each continental population of *Q. chrysolepis* as inferred by FASTSIMCOAL2 analyses. (d, e and f) These panels represent the same genetic parameters in relation to the geographical distance separating each continental population of *Q. chrysolepis* to the nearest population of *Q. tomentella*. Regression lines represent the function yielding the highest fit to observed data (d and f, power; e, logarithmic; see Supporting Information Table S2). Shadowed area in panel (a) shows the distribution of *Q. chrysolepis* in California based on occurrence data for the species obtained from sampling points and herbarium record databases (Ortego *et al.*, 2015a). Only populations with eight sampled individuals (*n* = 10 populations) were considered in analyses of migration rates with FASTSIMCOAL2 and, for this reason, localities MOJ (*n* = 5) and RED (*n* = 3) are not represented in panel (c). Population codes on maps are described in Table S1.

purification with NucleoSpin Plant II kits (Machery-Nagel, Düren, Germany). Genomic DNA was individually barcoded and processed into two libraries using the double-digestion restriction-fragment-based procedure (ddRAD-seq) described in Peterson *et al.* (2012). Briefly, DNA was double-digested using *Eco*RI and *Mse*I restriction enzymes (New England Biolabs, Ipswich, MA, USA), followed by the ligation of Illumina adaptors and unique 7-bp barcodes. Ligation products were pooled, size-selected between 350 and 450 bp using a Pippin Prep (Sage Science, Beverly, MA, USA) machine, and amplified by iProof™ High-Fidelity DNA Polymerase (Bio-Rad) with 12 cycles.

Single-read 150-bp sequencing was performed on an Illumina HiSeq2500 platform at The Centre for Applied Genomics (Toronto, ON, Canada).

Bioinformatics and data filtering

We used both STACKS v.1.35 (Hohenlohe *et al.*, 2010; Catchen *et al.*, 2011, 2013) and PYRAD v.3.0.66 (Eaton, 2014) to assemble our sequences into *de novo* loci and call genotypes. This allowed us to examine the robustness of our analyses based on single nucleotide polymorphism (SNP) datasets obtained using

two of the most popular programs currently available to assemble RAD-seq data (Catchen *et al.*, 2011; Eaton, 2014). Phylogenetic, demographic and population structure analyses assume that the employed loci are selectively neutral (Luikart *et al.*, 2003; e.g. Guichoux *et al.*, 2013; Benestan *et al.*, 2016). For this reason, we identified loci putatively under selection and created SNP datasets only containing neutral loci (e.g. Brauer *et al.*, 2016) (see details in Methods S1). The choice of different filtering thresholds using either STACKS or PYRAD had little impact on the obtained inferences (see the Results section) (e.g. Eaton *et al.*, 2015). For this reason, all downstream analyses were performed using a SNP dataset obtained with STACKS and including only selectively neutral loci represented in at least five populations and half of the individuals of each population. SNP datasets are available at the Mendeley Data Repository (doi: 10.17632/g49jk9r wk9.2). See Methods S1 for additional details on sequence assembling and data filtering.

Genetic structure and hybrid identification

We identified hybrids and analysed population genetic structure and admixture using the Bayesian Markov chain Monte Carlo (MCMC) clustering method implemented in the program STRUCTURE v.2.3.3 (Pritchard *et al.*, 2000; Falush *et al.*, 2003; Hubisz *et al.*, 2009). We ran STRUCTURE using a random subset of 10 000 SNPs from six different datasets obtained with STACKS and PYRAD and considering different parameters ($P = 5$ and $P = 10$ for STACKS and $c = 0.85$ and $c = 0.90$ for PYRAD; see Methods S1 for further details). For each dataset, we ran STRUCTURE assuming correlated allele frequencies and admixture and without using prior population information (Hubisz *et al.*, 2009). We conducted 15 independent runs for each value of $K = 1–8$ to estimate the 'true' number of clusters with 200 000 MCMC cycles, following a burn-in step of 100 000 iterations. We retained the ten runs having the highest likelihood for each value of K and defined the number of populations best fitting the dataset using log probabilities of $X|K$ (Pritchard *et al.*, 2000) and the ΔK method (Evanno *et al.*, 2005), as implemented in STRUCTURE HARVESTER (Earl & vonHoldt, 2012). We used CLUMPP v.1.1.2 and the Greedy algorithm to align multiple runs of STRUCTURE for the same K value (Jakobsson & Rosenberg, 2007) and DISTRUCT v.1.1 (Rosenberg, 2004) to visualize as bar plots the individual's probabilities of population membership. Complementary to Bayesian clustering analyses, we performed a principal components analysis (PCA) using the R 3.3.2 (R Core Team, 2017) package ADEGENET (Jombart, 2008).

Coalescent analyses and model comparison

We compared different demographic models that considered three populations defined on the basis of STRUCTURE and PCA analyses (e.g. Eaton *et al.*, 2015; Lanier *et al.*, 2015). These analyses (1) revealed the presence of two lineages that separate populations of *Q. chrysolepis* located north and south of the Transverse Ranges and the Mohave Desert (hereafter referred to as northern lineage and southern lineage, respectively) and (2) suggested a

certain degree of introgression (*c.* 7–10%) from *Q. tomentella* into the southern lineage of *Q. chrysolepis* (see the Results section for further details). In total, we tested six models that considered a combination of two migration matrices (total absence of post-divergence gene flow vs a full migration matrix of asymmetric gene flow) and three alternative scenarios of lineage divergence/formation (see Fig. 2).

We estimated the composite likelihood of the observed data given a specified model using the site frequency spectrum (SFS) and the simulation-based approach implemented in FASTSIM-COAL2 (Excoffier & Foll, 2011; Excoffier *et al.*, 2013). For the simulations, we selected 24 individuals from the three localities of *Q. tomentella* (CLE, CRU and CAT), 24 individuals from three populations representing the southern lineage of *Q. chrysolepis* (GAB, LAG and BER) and 24 individuals from three populations representing the northern lineage of *Q. chrysolepis* (SHA, TAH and SON). In the case of *Q. chrysolepis*, we selected for each lineage the three populations showing the highest probability of assignment to their specific genetic cluster (i.e. we excluded highly admixed populations located in contact zones; see the Results section). Note that we found weak evidence for introgression from *Q. vaccinifolia*/*Q. palmeri* into the populations of *Q. chrysolepis*/*Q. tomentella* considered for FASTSIMCOAL2 analyses (see the Results section). Thus, it is unlikely that contemporary or historical hybridization with the two Californian taxa belonging to the section *Protobalanus* and used as outgroups in phylogenomic analyses can bias the inferences obtained from our coalescent-based demographic reconstructions in FASTSIMCOAL2. A folded joint SFS was calculated considering a single SNP per locus to avoid the effects of linkage disequilibrium. Because we did not include invariable sites in the SFS, we fixed the effective population size for one population group (*Q. tomentella*; θ_T) to enable the estimation of other parameters in FASTSIMCOAL2 (e.g. Lanier *et al.*, 2015; Papadopoulou & Knowles, 2015). The effective population size fixed in the model was calculated from the level of nucleotide diversity (π) and estimates of mutation rate per site per generation (μ), because $N_e = (\pi/4\mu)$. Nucleotide diversity (π) for *Q. tomentella* was estimated from polymorphic and nonpolymorphic loci using STACKS ($\pi = 0.0005$; Table S1). The average mutation rate per site per generation (5.92×10^{-8}) was inferred from *Populus* (Tuskan *et al.*, 2006) following Gossmann *et al.* (2012) and considering that the average generation time of *Q. tomentella*/*Q. chrysolepis* is *c.* 50 yr (Bemmels *et al.*, 2016). To remove all missing data for the calculation of the joint SFS and minimize errors with allele frequency estimates, each population group was downsampled to 15 individuals using a custom Python script written by Qixin He and available on Dryad (Papadopoulou & Knowles, 2015). The final SFS contained 5668 variable SNPs.

Each model was run 100 replicated times considering 100 000–250 000 simulations for the calculation of the composite likelihood, 10–40 expectation-conditional maximization (ECM) cycles, and a stopping criterion of 0.001 (Papadopoulou & Knowles, 2015). We used an information-theoretic model selection approach based on the Akaike's information criterion (AIC) to determine the probability of each model given the

observed data (Burnham & Anderson, 1998; e.g. Abascal *et al.*, 2016; Thome & Carstens, 2016). After the maximum likelihood was estimated for each model in every replicate, we calculated the AIC scores as detailed in Thome & Carstens (2016). AIC values for each model were rescaled (ΔAIC) calculating the difference between the AIC value of each model and the minimum AIC obtained among all competing models (i.e. the best model has ΔAIC = 0). Point estimates of the different demographic parameters for the best-supported model were selected from the run with the highest maximum composite likelihood. Finally, we calculated confidence intervals of parameter estimates from 100 parametric bootstrap replicates by simulating SFS from the maximum composite likelihood estimates and re-estimating parameters each time (Excoffier *et al.*, 2013; e.g. Lanier *et al.*, 2015; Papadopoulou & Knowles, 2015). These analyses took *c.* 3 months of run-time using 30 processors on a HP ProLiant XL230a Gen9 with two Intel Haswell E5-2680 processors.

Phylogenomic inference

In order to explore the evolutionary and demographic history of *Q. tomentella* and the two lineages of *Q. chrysolepis* from a phylogenetic perspective, we reconstructed species trees using the multispecies coalescent model implemented in the SNAPP (Bryant *et al.*, 2012) plugin in BEAST v.2.4.1 (Bouckaert *et al.*, 2014). We considered the same genetic groups and populations used for FASTSIMCOAL2 analyses (*Q. tomentella*, and southern and northern lineages of *Q. chrysolepis*) plus five individuals of Palmer oak (*Q. palmeri*) and five individuals of huckleberry oak (*Q. vaccinifolia*). Due to large computational demands of the program, we analyzed five individuals per genetic group and performed independent analyses considering three different subsets of populations to determine the consistency of the obtained inferences (e.g. Kolar *et al.*, 2016). Initially, we ran analyses with different theta priors to allow for different current and ancestral population sizes (alpha = 2, beta = 200; alpha = 2, beta = 2000; alpha = 2, beta = 20 000) and leaving default settings for all other parameters. These analyses yielded the same topology (not shown) and only results for the intermediate prior for theta are presented (alpha = 2, beta = 2000). For each subset of populations, we used different starting seeds to run three independent replicate runs for *c.* 1 million generations sampled every 1000 steps. We used TRACER v.1.4 to examine log files, check stationarity and convergence of the chains, and confirm that effective sampling sizes (ESS) for all parameters were ≫ 200. We removed 10% of trees as burn-in and combined tree and log files for replicated runs using LOGCOMBINER v.2.4.1. We used TREEANNOTATOR v.1.8.3 to obtain maximum credibility trees. The full set of likely species trees was displayed with DENSITREE v.2.2.1 (Bouckaert, 2010), which is expected to show fuzziness in parts of the tree due to gene flow or other causes of phylogenetic conflict.

Genetic introgression and geographical distance

We calculated different estimates of introgression/gene flow from *Q. tomentella* into continental populations of *Q. chrysolepis* and
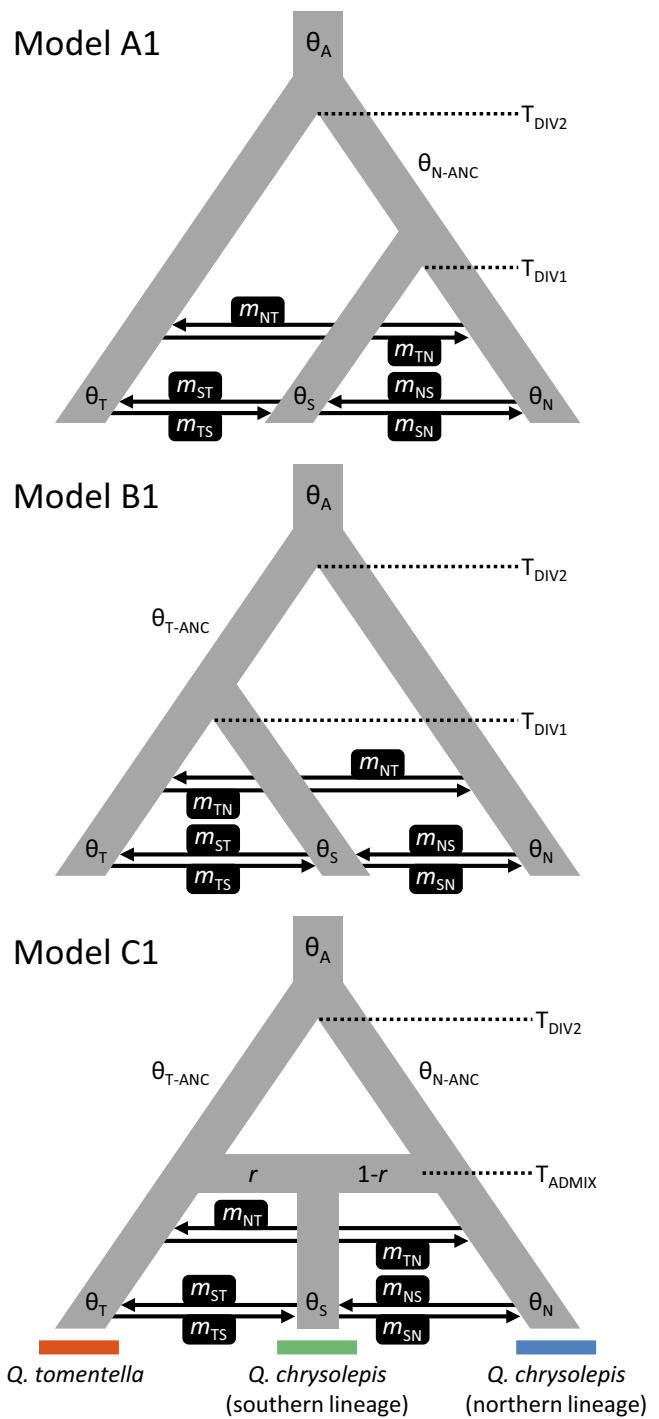
Fig. 2 Alternative demographic models tested using FASTSIMCOAL2. The three models consider different origins of the southern lineage of canyon live oak (*Quercus chrysolepis*) with respect to the island oak (*Q. tomentella*) and the northern lineage of canyon live oak. Parameter abbreviations include mutation-scaled effective population sizes (θ), migration rates per generation (m), timing of population divergence (T_{DIV}) and, in the case of the admixture model (Model C1), timing of admixture (T_{ADMIX}) and proportion of lineages transferred (r) from source to sink populations. Identical models not considering gene flow were also tested (A2, B2 and C2).

analyzed their association with the geographical distance separating each population of *Q. chrysolepis* from the nearest population of *Q. tomentella*. In particular, we analysed: (1) pairwise genetic

differentiation (F_{ST}) between *Q. tomentella* and each continental population of *Q. chrysolepis*; (2) the probability of membership (*q*) of each continental population of *Q. chrysolepis* to the *Q. tomentella* genetic cluster as inferred by STRUCTURE analyses (i.e. % of introgression); and (3) migration rates (*m*) from *Q. tomentella* to each continental population of *Q. chrysolepis*. We pooled all individuals of *Q. tomentella* and calculated their degree of genetic differentiation (F_{ST}) with each population of *Q. chrysolepis* using STACKS. Estimates of F_{ST} obtained with STACKS and ARLEQUIN v.3.5 (Excoffier & Lischer, 2010) were highly correlated ($r = 0.97$) and provided analogous results (data not shown). Pairwise migration rates (point estimates ± 95% CI) between *Q. tomentella* ($n = 24$ individuals from CRU, CAT and CLE) and each continental population of *Q. chrysolepis* were inferred with FASTSIMCOAL2 as described above (for a similar approach, see Barley *et al.*, 2015; Papadopoulou & Knowles, 2015). Only continental populations of *Q. chrysolepis* with eight genotyped individuals ($n = 10$ populations) were considered for these analyses (Table S1). The SFS was calculated downsampling to 15 and five individuals for *Q. tomentella* and each population of *Q. chrysolepis*, respectively. We tested four different gene flow models considering all possible migration matrices, including total absence of post-divergence gene flow. A full migration model considering asymmetrical gene flow was the most supported in all pairwise comparisons ($\Delta AIC > 2$ in all cases) (not shown) and subsequent analyses were based on estimates of migration rates per generation obtained using this model. The relationship between the different estimates of introgression/gene flow and the distance to the nearest population of *Q. tomentella* was analysed using linear and nonlinear (logarithmic, inverse, power and exponential) regressions in SPSS v.23. We considered nonlinear functions because these may potentially explain spatial patterns of introgression/gene flow better than a standard linear regression (e.g. if gene flow is mediated by long-distance pollen dispersal; Pluess *et al.*, 2009).

Results

Genomic data

A total of 151 285 222 (mean ± SD = 1719 150 ± 271 257 reads per individual) and 57 818 009 (mean ± SD = 1 606 055 ± 251 996 reads per individual) reads were obtained for 88 and 36 individuals of *Q. chrysolepis* and *Q. tomentella*, respectively. The number of reads retained after data processing and assembly averaged 86% per individual (Fig. S1). The datasets obtained with STACKS and parameters $P = 5$ and $P = 10$ contained 30 022 and 17 947 SNPs, respectively. The datasets obtained with PYRAD and parameters $c = 0.85$ and $c = 0.90$ contained 12 971 and 16 009 SNPs, respectively. See Methods S1 for further details.

Genetic structure and hybrid identification

STRUCTURE analyses and the statistic ΔK indicated an 'optimal' value of $K = 2$ (Fig. S2), splitting populations of *Q. chrysolepis*

and *Q. tomentella* into two distinct genetic clusters (Figs 3, S3). STRUCTURE analyses for $K = 3$ divided populations of *Q. chrysolepis* located north and south of the Transverse Ranges and the Mohave Desert, with some genetic admixture in contact zones (FIG, HAS and KIN; Figs 3, S3). Bayesian clustering analyses confirmed that individuals of *Q. chrysolepis* collected from Santa Cruz and San Clemente Islands are hybrids with *Q. tomentella* and all of them showed a high degree of admixed ancestry (*c.* 50%) typical of first generation (F_1) hybrids or back-crosses between them (Figs 3, S3). Finally, STRUCTURE analyses revealed that southern populations of *Q. chrysolepis* (MOJ, LAG, BER, GAB and FIG) present some degree of introgression (*c.* 10%) from *Q. tomentella*, a pattern that was particularly clear for $K = 2$ (Figs 3, S3). Results obtained with STRUCTURE were supported by PCAs: PC1 separated populations of *Q. tomentella* and *Q. chrysolepis*, and PC2 split populations of *Q. chrysolepis* located north and south of the Transverse Ranges and the Mohave Desert (Fig. 4). Hybrid individuals from Santa Cruz and San Clemente Islands presented intermediate values along PC1 and continental populations of *Q. chrysolepis* from contact zones (FIG, HAS and KIN) had intermediate scores along PC2 (Fig. 4).

Coalescent analyses and model comparison

Results of FASTSIMCOAL2 showed that the most supported scenario (Model C1) was the one considering an admixed ancestry for the southern lineage of *Q. chrysolepis* (Table 1; Fig. 2). Parameter estimates obtained under this model indicate that this lineage shares a higher proportion of ancestry with *Q. tomentella* (*c.* 93%) than with the northern lineage of *Q. chrysolepis* (*c.* 7%) (Table 2). In fact, this model was statistically equivalent ($\Delta AIC = 2.3$; Burnham & Anderson, 1998) to Model B1, which considered that the southern lineage of *Q. chrysolepis* and *Q. tomentella* share their most recent common ancestor (Table 1; Fig. 2). Due to the similarity in parameters estimated by these two models, our inferences are based on model-averaged parameter values (e.g. Thome & Carstens, 2016; Table 2). Assuming an average generation time of 50 yr for these species (e.g. Bemmels *et al.*, 2016), the split between the northern lineage of *Q. chrysolepis* and the two other lineages (T_{DIV2}) was estimated to happen during the Pliocene (*c.* 3.7 Ma). The event leading to the split of *Q. tomentella* and the southern lineage of *Q. chrysolepis* (T_{ADMIX} in model C1 and T_{DIV1} in model B1) was estimated to take place during the early Pleistocene or the late Pliocene (*c.* 1.8–1.0 Ma) (Table 2). Note, however, that our estimates of divergence time must be interpreted with extreme caution due to the wide confidence intervals around our point estimates and considerable uncertainty in mutation rates and generation time for long-lived tree species (Table 2) (see Ortego *et al.*, 2015b; Tsuda *et al.*, 2015). Migration rates per generation (*m*) were estimated to be significantly higher (i.e. 95% CI do not overlap) from *Q. tomentella* to the two lineages of *Q. chrysolepis* than in the opposite direction (Table 2). Also, the estimate of migration rate from *Q. tomentella* to the southern lineage of *Q. chrysolepis* was significantly higher than that inferred from *Q. tomentella* to the northern lineage of *Q. chrysolepis* (Table 2). Pilot runs for more complex models
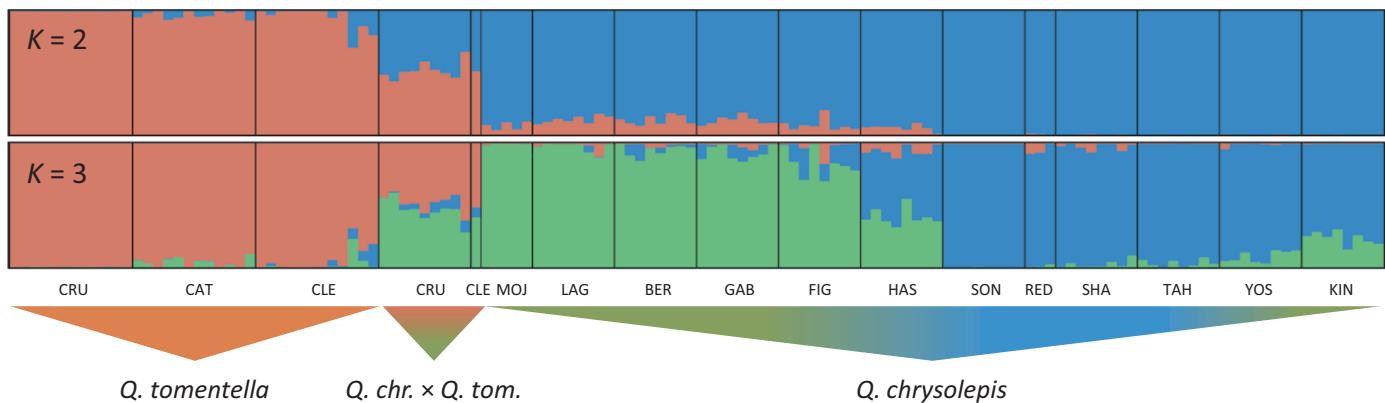
Fig. 3 Results of genetic assignments for canyon live oak (*Quercus chrysolepis*), island oak (*Q. tomentella*) and their hybrids (*Q. chrysolepis* × *Q. tomentella*) based on the Bayesian method implemented in the program STRUCTURE (*K* = 2 and *K* = 3). Analyses are based on a random subset of 10 000 SNPs data. Each individual is represented by a vertical bar, which is partitioned into *K* colored segments showing the individual's probability of belonging to the cluster with that color. Thin vertical black lines separate individuals from different sampling localities/species. Population codes are described in Supporting Information Table S1.

considering different sets of incomplete migration matrices (e.g. lack of migration between *Q. tomentella* and the northern lineage of *Q. chrysolepis*), gene flow after the first genetic split (T_{DIV2}) and/or migration limited to a certain period of time consistently provided a lower model support (e.g. see Fig. 2 in Filatov *et al.*, 2016) (data not shown).

Phylogenomic inference

Analyses with SNAPP considering three different combinations of populations showed that *Q. tomentella* and the southern lineage of *Q. chrysolepis* share their most recent common ancestor (Fig. 5), supporting the results obtained with FASTSIMCOAL2. Phylogenetic analyses also suggested the presence of gene flow between *Q. vaccinifolia* and the northern lineage of *Q. chrysolepis* (Fig. 5). Accordingly, STRUCTURE analyses performed considering the same three subsets of populations and individuals used for SNAPP analyses (i.e. balanced in terms of sample size for all taxa/lineages) revealed asymmetric hybridization from *Q. chrysolepis* into *Q. vaccinifolia* (Figs S4, S5). Three out of the five genotyped individuals of *Q. vaccinifolia* showed a high degree (*c.* 50%) of admixed ancestry (Fig. S5). In agreement with SNAPP analyses, we found no signature of hybridization or introgression between *Q. palmeri* and the other taxa/lineages (Fig. S5).

Genetic introgression and geographical distance

All estimates of introgression/gene flow from *Q. tomentella* to continental populations of *Q. chrysolepis* were significantly associated with the geographical distance to the nearest population of *Q. tomentella* (Table S2; Fig. 1). Genetic differentiation (F_{ST}) was positively associated with geographical distance following a power function (Table S2). The proportion of genetic introgression (*q*) estimated with STRUCTURE and pairwise migration rates per generation (*m*) inferred with FASTSIMCOAL2 (Table S3) were negatively associated with geographical distance following a

logarithmic and a power function, respectively (Table S2; Fig. 1). Note, however, that simpler linear functions provided similar fits to the data than nonlinear functions for all estimates of introgression/gene flow (Table S2).

Genetic diversity and effective population sizes

The southern lineage of *Q. chrysolepis* presented higher estimates of genetic diversity and effective population sizes (N_e) than *Q. tomentella* or the northern lineage of *Q. chrysolepis* (Fig. 6; Table S1; see also Table S4 for genetic drift). Also, the southern lineage of *Q. chrysolepis* presented higher estimates of N_e than *Q. vaccinifolia* and *Q. palmeri*, the two other Californian golden cup oaks (Fig. 6). Estimates of genetic diversity and N_e were remarkably low for all populations of *Q. tomentella*, suggesting that they have experienced strong genetic drift due to their small size and geographical isolation (Fig. 6). Accordingly, STRUCTURE analyses showed that genetic drift after divergence (*F*-value) for the cluster of *Q. tomentella* was double the estimates obtained for the two lineages of *Q. chrysolepis* (Table S4).

Discussion

Our analyses showed that *Quercus tomentella* and *Q. chrysolepis* comprise three lineages, one corresponding with *Q. tomentella* and two separating populations of *Q. chrysolepis* located north and south of the Transverse Ranges and the Mohave Desert (Figs 3–5). These lineages present levels of genetic differentiation (F_{ST} *c.* 0.12) similar to that typically reported for other sister or closely related oak taxa (e.g. Muir & Schlotterer, 2005; Ortego *et al.*, 2015b, 2017). Both phylogenomic and population genomic coalescent-based analyses supported that the southern lineage of *Q. chrysolepis* shares its most recent common ancestor with *Q. tomentella* rather than with the northern lineage *Q. chrysolepis*. The northern lineage of *Q. chrysolepis* was estimated to have originated during the Pliocene, whereas the split between *Q. tomentella* and the southern lineage of *Q. chrysolepis*
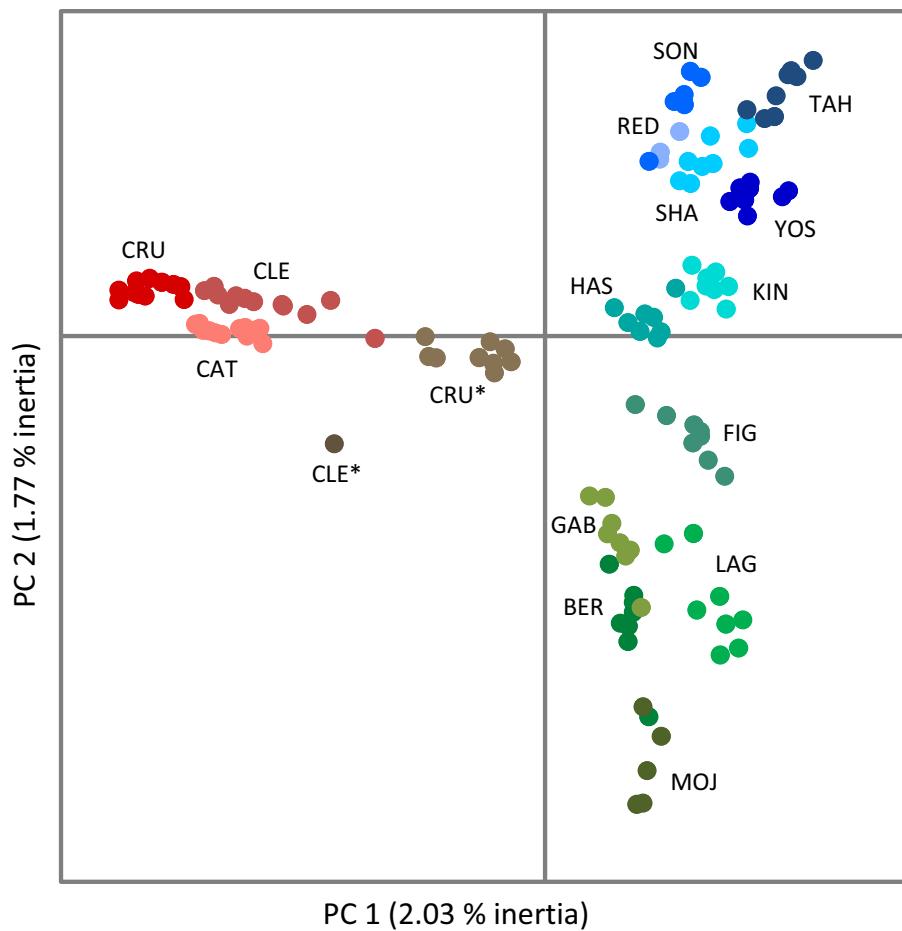
Fig. 4 Principal component analysis (PCA) of genetic variation (29 811 single nucleotide polymorphisms) for canyon live oak (*Quercus chrysolepis*) and island oak (*Q. tomentella*). Asterisks denote interspecific hybrids from Santa Cruz and San Clemente Islands. Population codes are described in Supporting Information Table S1.

Table 1 Comparison of demographic models analyzed with FASTSIMCOAL2 for the island oak (*Quercus tomentella*) and the two lineages of canyon live oak (*Quercus chrysolepis*)

Model	$\log_{10}L$	k	AIC	ΔAIC	ω_i
A1	−11 579.74	12	23 183.49	36.48	0.00
A2	−17 391.03	6	34 794.06	11 647.06	0.00
B1	**−11 562.81**	**12**	**23 149.62**	**2.62**	**0.21**
B2	−11 824.79	6	23 661.58	514.57	0.00
C1	**−11 559.50**	**14**	**23 147.01**	**0.00**	**0.79**
C2	−11 811.82	8	23 639.64	492.63	0.00

Best supported models are indicated in bold. Model description is detailed in Fig. 2. $\log_{10}L$, maximum likelihood estimate of the model; k, number of parameters in the model; AIC, Akaike's information criterion value; ΔAIC, difference in AIC value from that of the strongest model; ω_i, AIC weight.

probably occurred during the late Pliocene or the early Pleistocene. Although our estimated dates for lineage formation must be interpreted with extreme caution, they correspond well with the common presence of *Q. chrysolepis* and *Q. tomentella* (or their extinct forms, *Q. hannibali* and *Q. declinata*, respectively) in the Miocene and Pliocene fossil records of continental California (Hannibal, 1911; Axelrod, 1944a,b; see also Axelrod, 1938, 1958). Our analyses also revealed signatures of historical introgression from *Q. tomentella* into the continental populations of the southern lineage of *Q. chrysolepis*. Thus, the past coexistence

of these two taxa or their extinct ancestors in the continent probably offered an ideal scenario for hybridization until the progressively drier and cooler climate during the Miocene and Pliocene pushed *Q. tomentella* and many other temperate species toward a shrinking belt of mild climate restricted to the California coastal strip and the Channel Islands (Hannibal, 1911; Axelrod, 1958, 1967, 1983; Muller, 1967).

A complex evolutionary history

Our coalescent analyses showed that the southern lineage of *Q. chrysolepis* shares a higher proportion of ancestry with *Q. tomentella* (*c.* 93%) than with its conspecific northern lineage, supporting the paraphyly of *Q. chrysolepis* (Fig. 5). In contrast with other oak complexes including taxa with very similar phenotypes (e.g. the Californian scrub white oak species complex; Roberts, 1995; Nixon, 2002; Ortego *et al.*, 2015b), *Q. tomentella* can be easily distinguished from *Q. chrysolepis* by its larger and thicker leaves with more prominent regular teeth and a characteristic corrugated leaf blade (Nixon, 2002; see also Manos, 1993 for differences in foliar trichome variation). In fact, *Q. chrysolepis* shows a higher phenotypic affinity with *Q. vaccinifolia* and *Q. palmeri*, the most divergent taxa within the section (Fig. 5), than with *Q. tomentella* (Tucker, 1980; Axelrod, 1983; see also Manos, 1993). Thus, the most

Table 2 Parameters inferred from coalescent simulations with FASTSIMCOAL2 under the two most supported demographic models for the island oak (*Quercus tomentella*) and the two lineages of canyon live oak (*Q. chrysolepis*)

Parameter	Model B1	Model C1	Model average	Lower bound	Upper bound
θ_A	105 451	84 741	89 090	26 879	167 286
θ_S	726 282	515 891	560 073	353 715	1 118 399
θ_N	249 080	175 747	191 147	106 267	415 700
$\theta_{N\text{-}ANC}$	308 920	136 204	172 474	74 596	374 292
$\theta_{T\text{-}ANC}$		314 952	248 812	95 586	430 452
T_{DIV2}	97 732	67 405	73 774	45 861	313 678
T_{DIV1}	36 392		36 392	17 060	108 348
T_{ADMIX}		19 792	19 792	7285	106 647
r		0.93	0.93	0.63	0.97
m_{TS}	2.18×10^{-04}	1.98×10^{-04}	2.02×10^{-04}	1.68×10^{-04}	2.33×10^{-04}
m_{TN}	9.77×10^{-05}	1.16×10^{-04}	1.12×10^{-04}	8.54×10^{-05}	1.40×10^{-04}
m_{ST}	3.95×10^{-07}	1.56×10^{-09}	8.43×10^{-08}	3.95×10^{-11}	4.00×10^{-06}
m_{SN}	8.92×10^{-06}	9.58×10^{-06}	9.44×10^{-06}	8.61×10^{-07}	1.08×10^{-05}
m_{NT}	3.03×10^{-07}	4.56×10^{-09}	6.73×10^{-08}	2.78×10^{-11}	6.11×10^{-06}
m_{NS}	1.34×10^{-05}	2.48×10^{-05}	2.24×10^{-05}	7.63×10^{-06}	5.10×10^{-05}

Table shows point estimates under models B1 and C1 (illustrated in Fig. 2), model averaged estimates, and lower and upper 95% confidence intervals. Note that the effective population size of *Quercus tomentella* (θ_T) is not presented in this table because it was fixed in FASTSIMCOAL2 analyses to enable the estimation of other parameters (see the Materials and Methods section for further details). θ, mutation-scaled effective population sizes; T, timing of population divergence or admixture (given in number of generations); *r*, proportion of lineages transferred from source to sink populations; *m*, migration rates per generation. Each specific parameter is illustrated in Fig. 2.
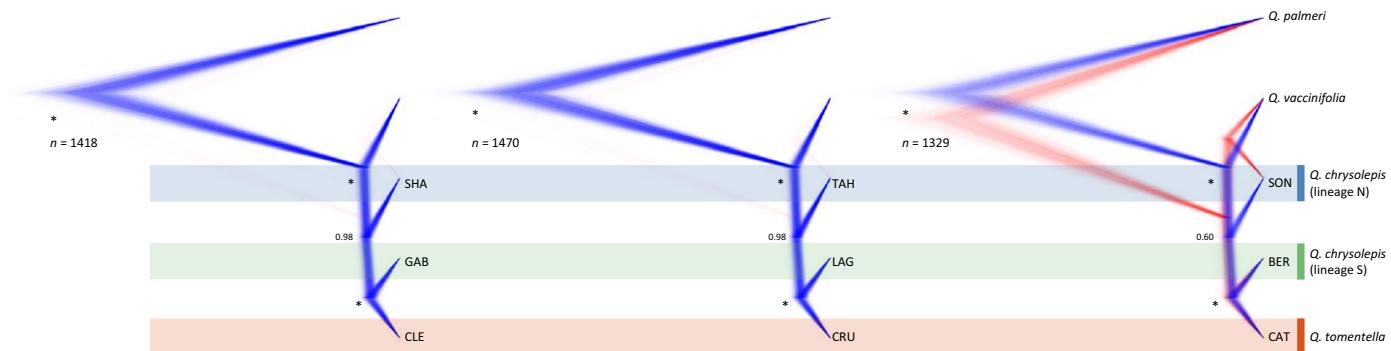
Fig. 5 SNAPP trees reconstructed considering different subsets of populations from the three genetic clusters inferred by STRUCTURE and principal component analysis (PCA) analyses for canyon live oak (*Quercus chrysolepis*) and island oak (*Q. tomentella*). Huckleberry oak (*Q. vaccinifolia*) and Palmer oak (*Q. palmeri*), species also belonging to the section *Protobalanus*, were also included. The first (blue) and second (red) most supported topologies are shown. The number of loci (*n*) shared across all clades and retained for SNAPP analyses are presented with each tree and posterior probabilities for the most supported topology are indicated on the nodes (* = 1). Population codes are described in Supporting Information Table S1.

parsimonious explanation for the morphological and ecological integrity of *Q. chrysolepis* across its entire distribution range is that this species represents the ancestral phenotypic state and that *Q. tomentella* has phenotypically and ecologically diverged as a separate species after it split from the southern lineage of *Q. chrysolepis*. Fossil records indicate that *Q. tomentella* gradually evolved larger leaves in response to milder oceanic climate when it migrated coastward, supporting a phenotypic transition in this taxon that has not been documented in the fossil record of *Q. chrysolepis* (Axelrod, 1941, 1944b, 1958).

An alternative explanation for the phenotypic and ecological integrity of *Q. chrysolepis* across its entire distribution range is that the two lineages of this taxon have converged in response to similar environmental conditions. Accordingly, previous studies have shown that oaks present considerable evolutionary lability in important physiological and morphological traits and

communities composed by phylogenetically distant species tend to converge to similar phenotypes (Cavender-Bares *et al.*, 2004; Hipp *et al.*, 2018). Another possibility to explain the phenotypic integrity of *Q. chrysolepis* may be related with processes of phenotypic assimilation (Rheindt *et al.*, 2014; Huang, 2016) resulted from gene flow between its two lineages (Fig. 3) and introgression at a few genomic islands or specific genes involved in ecological adaptation and trait expression (Poelstra *et al.*, 2014; Yeaman *et al.*, 2016). Previous studies on oaks and other organisms have shown that convergence toward one parental phenotype may occur even when the genetic background of the other parental species is high (Hercus & Hoffmann, 1999; Masta *et al.*, 2002; Ortego & Bonal, 2010). Anecdotal evidence supporting this hypothesis in our system comes from the single individual *Q. chrysolepis* collected on San Clemente Island. This individual, the only one found on the island, did not present phenotypic
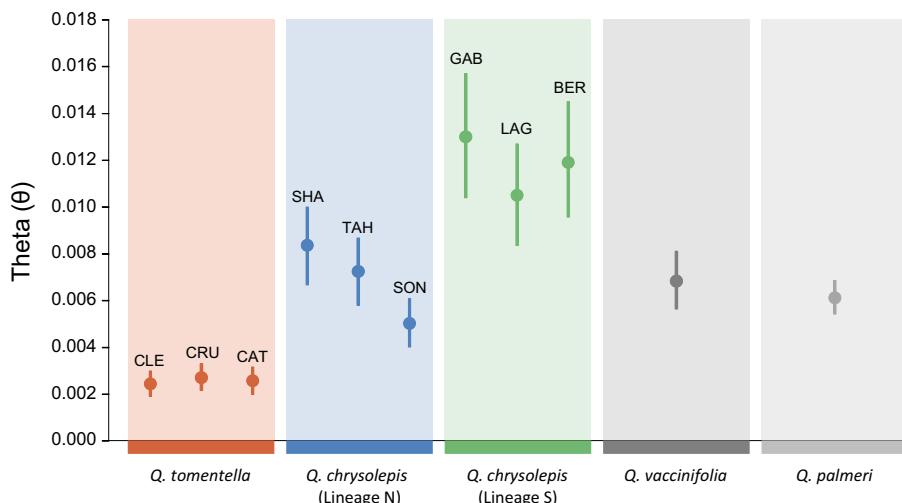
Fig. 6 Estimates of theta (θ) (mean ± 95% CIs) inferred by Snapp for different populations of canyon live oak (*Quercus chrysolepis*), island oak (*Q. tomentella*), Palmer oak (*Q. palmeri*) and huckleberry oak (*Q. vaccinifolia*). Estimates are presented for those populations used in the three subsets of Snapp analyses presented in Fig. 5. Population codes are described in Supporting Information Table S1.

signs of hybridization in spite of having a high degree of admixed ancestry with *Q. tomentella* (*c.* 54%; Figs 3, 4).

Historical vs contemporary introgression

Estimated migration rates per generation inferred with Fast-simcoal2 indicate higher rates of gene flow from *Q. tomentella* to continental populations of *Q. chrysolepis* than in the opposite direction (Table 2). In agreement with the results of Bayesian clustering analyses, the migration rate from *Q. tomentella* to the southern lineage of *Q. chrysolepis* was estimated to be significantly higher than that inferred from *Q. tomentella* to the northern lineage of *Q. chrysolepis* (Table 2; Fig. 3). Accordingly, different estimates of genetic introgression were negatively associated with the distance from each continental population of *Q. chrysolepis* to the nearest population of *Q. tomentella*, which suggests a pattern of isolation-by-distance probably resulted from a diffusion cline of neutral gene flow (Rieux *et al.*, 2013). Wind currents around the California Channel Islands have been largely stable for the past 10 000 years and are dominated by northwesterly winds and the periodic Santa Ana easterly winds (Riley & McGlaughlin, 2016 and references therein). Thus, although oaks have a high potential for long-distance pollen dispersal (Buschbom *et al.*, 2011; Hampe *et al.*, 2013), it is expected that the amount of pollen from *Q. tomentella* reaching nowadays continental populations from *Q. chrysolepis* is very limited to explain observed patterns of introgression. Structure analyses also showed that introgressed individuals of *Q. chrysolepis* from the continent present a small and homogeneous background of genetic admixture characteristic of populations at equilibrium, which indicates that observed patterns of introgression have not resulted from contemporary gene flow but reflect a past history of hybridization (Barton & Gale, 1993; Brelsford & Irwin, 2009). These lines of evidence, together with the high admixture between the two lineages of *Q. chrysolepis*, support that past hybridization between *Q. tomentella* and *Q. chrysolepis* in southern California and subsequent gene flow

among continental populations of the latter is the most likely explanation for the observed correlation between genetic introgression and the distance to the nearest stand populations of *Q. tomentella*.

Exclusively focusing on the populations from the Channel Islands, Structure analyses revealed that the rate of introgression from *Q. tomentella* into *Q. chrysolepis* (*c.* 54%) is much higher than in the opposite direction (*c.* 3%; Fig. 3). The fact that all individuals of *Q. chrysolepis* from San Clemente and Santa Cruz Islands have a high degree of admixed ancestry (typical of F1 hybrids or backcrosses between them) suggests that nowadays they constitute a hybrid swarm and confirms previous descriptive studies noticing that the two species have a strong history of hybridization on the Channel Islands (Muller, 1967; Thorne, 1969; Nixon, 2002; Ashley *et al.*, 2010; eFloras, 2017). Although *Q. tomentella* sustain higher census numbers than *Q. chrysolepis* on the Channel Islands, the populations of the former are also generally limited to small groves (e.g. Santa Cruz or Santa Catalina Islands) or scattered individuals (e.g. San Clemente Island) (Junak *et al.*, 1995; McCune, 2005; Ashley *et al.*, 2010). Thus, the highly asymmetrical introgression of *Q. chrysolepis* by *Q. tomentella* at different temporal scales suggests that the latter may present stronger pre- or post-zygotic barriers to interspecific gene flow, show a higher invasive capacity (e.g. Bacilieri *et al.*, 1996; Ortego *et al.*, 2017) and/or experience processes of parental genotype reconstruction (*sensu* Cannon & Scher, 2017; see also Petit *et al.*, 2004). Our analyses also revealed asymmetric introgression from the northern lineage of *Q. chrysolepis* into *Q. vaccinifolia* (Fig. 5 and Fig. S5), which is in agreement with previous studies describing hybridization between these two taxa (Myatt, 1980; Tucker, 1980; Hickman, 1993; Nixon, 2002; eFloras, 2017). However, we found no signature of introgression between *Q. palmeri* and the other taxa/lineages (Fig. S5). This supports previous studies suggesting that *Q. palmeri* hybridizes with relictual populations of *Q. chrysolepis* in Arizona (Tucker, 1980; Nixon, 2002), whereas ecological isolation prevents interspecific gene flow between these two taxa in California (Tucker, 1980).

Genetic diversity of parental and admixed lineages

Estimates of genetic variation and effective population sizes (N_e) are consistent with the inferred history of hybridization (Nettel *et al.*, 2008; Streicher *et al.*, 2014). The introgressed lineage of *Q. chrysolepis* from southern California presented the highest levels of genetic diversity and N_e (Fig. 6; Table S1). This supports the notion that hybridization can boost levels of genetic diversity of natural populations (Nettel *et al.*, 2008; Ortego *et al.*, 2014; Streicher *et al.*, 2014), particularly when the resulting hybrid population/lineages are not reproductively isolated from parental taxa and have not passed through severe demographic bottlenecks during the speciation/divergence process (Templeton, 1981; Rieseberg, 1997). Estimates of genetic diversity and N_e were remarkably low for *Q. tomentella*, suggesting that their small-size and isolated populations have experienced strong bottlenecks (Beckman & Jerome, 2017; Ashley *et al.*, 2010). This is also supported by Structure analyses, which showed that genetic drift after divergence (*F*-value) for the cluster of *Q. tomentella* was twice as high as the estimates obtained for the two lineages of *Q. chrysolepis* (Table S4; e.g. Papadopoulou & Knowles, 2015). Such considerable genetic drift can also explain why the two lineages of *Q. chrysolepis* clustered together for $K = 2$ when both demographic and phylogenomic analyses strongly support that the southern lineage shares its most recent common ancestor with *Q. tomentella* (Fig. 3).

Conclusions

Overall, this study highlights the importance of integrating demographic and phylogenomic analyses to understand lineage diversification in taxa with complex biogeographic histories. Our results support that the two lineages of *Q. chrysolepis* can be considered as part of a single paraphyletic taxon ecologically and phenotypically well differentiated from *Q. tomentella* (Thornburgh, 1990; Fralish & Franklin, 2002; Nixon, 2002). Populations resulted from admixture between the two lineages *Q. chrysolepis* are not restricted to narrow contact zones and extend across large geographical areas (Fig. 3; see also Ortego *et al.*, 2015a; Bemmels *et al.*, 2016). This represents a very different situation to that frequently described for most hybridizing oak species that, although can occasionally form hybrid swarms, maintain their genetic and phenotypic distinctiveness across overlapping portions of their respective distribution ranges and when they co-occur in mixed stands (Ortego *et al.*, 2014). Collectively, these results broaden the debate about species definition toward more complicated circumstances that can be probably only accommodated considering hybridization and speciation processes as a continuum with diffuse limits (Abbott *et al.*, 2013; Hochkirch, 2013; Edwards *et al.*, 2016). Future studies considering detailed phenotypic information and genome scans to detect potential loci under selection implicated in phenotypic trait expression and ecological adaptation would be of great help to get a better understanding of the processes underlying the evolutionary history of this and other intriguing species complexes (Hohenlohe *et al.*, 2013; Stolting *et al.*, 2013; Poelstra *et al.*, 2014; Suarez-Gonzalez *et al.*, 2016).

Author contributions

J.O. conceived and designed the study, analysed the data and wrote the manuscript; J.O. and P.F.G. collected the samples; and J.O., P.F.G. and V.L.S. interpreted and discussed the results and edited the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Number of reads per individual before and after different quality filtering steps by STACKS.

Fig. S2 Mean ($\pm$ SD) log probability of the data (Ln Pr($X|K$)) for each value of K and the magnitude of ΔK over 10 runs of STRUCTURE for canyon live oak (*Quercus chrysolepis*) and island oak (*Q. tomentella*).

Fig. S3 Results of genetic assignments for canyon live oak (*Quercus chrysolepis*) and island oak (*Q. tomentella*) based on the Bayesian method implemented in the program STRUCTURE.

Fig. S4 Mean ($\pm$ SD) log probability of the data (Ln Pr($X|K$)) for each value of K and the magnitude of ΔK over 10 runs of STRUCTURE for huckleberry oak (*Quercus vaccinifolia*), Palmer oak (*Q. palmeri*), canyon live oak (*Q. chrysolepis*) and island oak (*Q. tomentella*).

Fig. S5 Results of genetic assignments for huckleberry oak (*Quercus vaccinifolia*), Palmer oak (*Q. palmeri*), canyon live oak (*Q. chrysolepis*) and island oak (*Q. tomentella*) based on the Bayesian method implemented in the program STRUCTURE.

Table S1 Geographical location and genetic statistics (P, H_O, H_E and π) for the studied populations of canyon live oak (*Quercus chrysolepis*) and island oak (*Q. tomentella*)

Table S2 Linear and nonlinear regressions analyzing the relationship between different genetic parameters (F_{ST}, q and m) and the geographical distance from each continental population of canyon live oak (*Quercus chrysolepis*) to the nearest population of island oak (*Q. tomentella*)

Table S3 Pairwise estimates of migration rates per generation (m) between island oak (*Quercus tomentella*) and continental populations of canyon live oak (*Q. chrysolepis*) inferred from coalescent simulations with FASTSIMCOAL2

Table S4 Amount of genetic drift after divergence (F-values) estimated by STRUCTURE for each inferred genetic cluster

Methods S1 Supplemental methods.

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