



# Long-distance dispersal drives the genetic variation and historical demography of *Quercus magnoliifolia* and *Quercus resinosa* (Fagaceae) in the Mexican highlands

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## Abstract

While hybridization and introgression can have a strong adaptive importance, it can impede divergence of species. *Quercus magnoliifolia* and *Q. resinosa* are two endemic oak species distributed across the Mexican highlands. These species diverged ecological and morphologically; however, no nuclear genetic differentiation is evident. In this study, we determined the mechanisms that shape patterns of genetic variation and establish the role of migration and hybridization in the evolutionary history of these two oak species. To do this, Bayesian approaches were used for inference on migration rates and directionality and timing of divergence between species using chloroplast microsatellites. We then integrated species distribution models to infer the geographic distribution of *Q. magnoliifolia* and *Q. resinosa* during Last Interglacial, Last Glacial Maximum, and Mid-Holocene time frames. We failed in distinguishing a unique genetic composition for each species. Chloroplast differentiation was more congruent with geography than the taxonomic status of each species. Our study revealed that after the divergence (c. 10 Mya) of these two oak species, high rates of introgression took place at the end of the Pleistocene. Furthermore, past distribution models predicted that *Q. magnoliifolia* and *Q. resinosa* have likely been in sympatry presumable since Last Glacial Maximum and *Q. resinosa* probably expanded geographically towards its current distribution around Mid-Holocene. This expansion was supported by testing migration models, suggesting recent establishment of *Q. resinosa* to the north of Trans-Mexican Volcanic Belt. We hypothesized that after *Q. magnoliifolia* and *Q. resinosa* diverged, colonization events followed by hybridization between oaks and long-distance seed dispersal occurred, explaining the present-day patterns of distribution of chloroplast diversity. We propose that divergence of species remains mainly on loci under natural selection, providing evidence on the “porous” nature of species boundaries among oaks.

**Keywords** Chloroplast microsatellites · Hybridization · Long-distance dispersal · Mexico · *Quercus*

## Introduction

Hybridization has a major role in evolution via the passage of adaptive loci, and catalyzing species radiations (Schley et al. 2022). Regardless of the adaptive importance of hybridization and introgression, differentiation of diverged

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or diverging lineages can be affected by the homogenizing effect of gene flow (Soltis 2013), impeding the creation of new diversity through the production of novel genotypes and phenotypes (Abbott et al. 2013). Within the genus *Quercus* (L.), ancient and recent hybridization has been detected among phylogenetically distinct clades but with overlapping geographic ranges (Zhou et al. 2022). Due to the evolutionary implications, hybridization in oaks has been extensively studied and serves as an important model system for studying speciation considering high levels of gene flow (González-Rodríguez and Oyama 2005; Cavender-Bares et al. 2015; Eaton et al. 2015; Hipp 2015; Sork et al. 2016; Hipp et al. 2018; Kremer and Hipp 2020; and references therein). In addition, studies on population genetics of oak species indicate that geological and climatic changes during the last glacial period have had a significant influence on the current patterns of genetic diversity and structure. European oaks, for example, were restricted to different refugia during the last glaciation, and after the glacial maximum, oak species recolonized the continent following diverse postglacial routes producing populations with reduced genetic diversity but high genetic structure (Petit et al. 1993; Dumolin et al. 1995; Petit et al. 2002; Grivet and Petit 2003; Bagnoli et al. 2016). In contrast, oak species in North America have shown higher genetic diversity and lower genetic differentiation (Grivet and Petit 2003), suggesting that gene movement among their populations has been more stable in response to past climatic and geological events (Magni et al. 2005).

Despite hybridization has been intensively studied as an important mechanism to understand the formation of new species, several authors have reported that hybridization can occur without jeopardizing species integrity (Eaton et al. 2015; Kremer and Hipp 2020). Such findings highlight the role of hybridization, not only as a source of species diversity, but also as one of the most important dispersal mechanisms facilitating colonization of oaks (Potts and Reid 1988; Whittmore and Schaal 1991; Petit et al. 1997; Petit et al. 2004; Pollock et al. 2015; McCauley et al. 2019; Kremer and Hipp 2020). To understand how hybridization may have driven the species evolutionary history as a mechanism of dispersal may seem quite a challenge, mostly because of the difficulties to test macro- and micro-evolutionary hypotheses (Petit et al. 2004).

In Mexico, oak species have shown high genetic diversity and low genetic structure, reflecting historical population processes such as considerable range stability, altitudinal displacements, and dynamic gene flow between populations (González-Rodríguez et al. 2004; Tovar-Sánchez et al. 2008; Rodríguez-Correa et al. 2015; Ramos-Ortiz et al. 2016; Rodríguez-Correa et al. 2017; McCauley et al. 2019; Albarrán-Lara et al. 2019; Peñaloza-Ramírez et al. 2020). However, within the great geological and orographic complexity of Mexico, oak trees might reflect the formation of specific distributional patterns for each biogeographic region. In

particular, the geographic distribution and geological history of oak species in the Mexican highlands may represent interesting models to understand the role of hybridization as a mechanism of species diversity but also as a potential source of long-distance colonization to invade new environments.

The Mexican highlands are a biodiversity hotspot and are part of the transition zone at the northern limit of the tropics (Myers et al. 2000; Morrone 2001; Mastretta-Yanes et al. 2015). Geology and climate have been invoked as the main drivers of the distribution of the biota in Mexican highlands (Mastretta-Yanes et al. 2015; Caballero-Rodríguez et al. 2018). The complexity of the Mexican highlands had a pivotal role in the diversification and hybridization patterns of Mexican oaks (Hipp et al. 2018; Mastretta-Yanes et al. 2018). In Mexico, oaks are particularly numerous because of high rates of lineage diversification into a wide variety of habitats and climates with the most extensive radiations occurring in montane regions (Hipp et al. 2018). However, no consensus about the patterns of genetic diversity have been found in the Neotropics. In some cases, Mexican oak species have experienced more stable climate, and thus, larger population size and relative population stability (González-Rodríguez et al. 2004; Cavender-Bares et al. 2011, 2015; Ramos-Ortiz et al. 2016; Peñaloza-Ramírez et al. 2020), and in other studies, genetic patterns were explained by a combination of geological and climatic changes causing shifts in altitudinal and latitudinal distribution (Rodríguez-Correa et al. 2017; Peñaloza-Ramírez et al. 2020).

Glacial cycles have influenced the distribution of trees in mountain communities (Ramírez-Barahona and Eguiarte 2013; Mastretta-Yanes et al. 2015, 2018), providing the opportunity for species to overlap in geographic space and come into secondary contact (Petit et al. 2004; Baena-Díaz et al. 2018). Thus, for species that have the ability to intercross with phylogenetically related species, the knowledge of historical changes of distributional range is essential to understand current geographical patterns of genetic variation (Pettengill and Moeller 2012). In this sense, the integration of phylogeography, species distribution models, and demographic evidence is necessary to gain insights on the evolutionary history of the species (Hewitt 2000; Muir and Schlötterer 2005; Baena-Díaz et al. 2018; McCauley et al. 2019).

*Quercus magnoliifolia* Née and *Q. resinosa* Liebm. are two endemic white oak species distributed across the Mexican highlands, classified in different taxonomic series: *Circinatae* and *Macrophyllae*, respectively. Recent evidence showed morphological and ecological divergence between these two oak species, but low genetic differentiation was recovered at the nuclear level presumably by retention of ancestral polymorphism due to recent divergence (Albarrán-Lara et al. 2019). Notwithstanding, intermediate morphological individuals were recorded between these two species suggesting hybridization (González-Villareal 1986; Albarrán-Lara et al.

2019). These two white oak species offer a particular useful system to investigate the relevance of historical seed dispersal to the biogeography of oaks in the Mexican highlands. Thus, in this study, we integrated phylogeography, historical demography, and species distribution models to determine the mechanisms that shape patterns of historical migration and genetic diversity structure of *Q. magnoliifolia* and *Q. resinosa* based on six chloroplast microsatellite markers.

## Materials and methods

### Study systems

*Quercus magnoliifolia* is distributed from the Sierra Madre Occidental, through the Trans-Mexican Volcanic Belt to the Sierra Madre del Sur (Valencia 2004; Albarrán-Lara et al. 2010, 2019). This species inhabits tropical dry forests and pine-oak forests from 375 to 2,900 m of elevation (Valencia 2004; Albarrán-Lara et al. 2019). *Quercus resinosa* has a restricted geographical distribution, from the west of the Trans-Mexican Volcanic Belt, through southern parts of the Sierra Madre Occidental to the Central Plateau (Albarrán-Lara et al. 2010, 2019) in xeric scrublands and pine-oak forests from 1300 to 2500 m (Valencia 2004). Both species produce ovoid acorns annually, but their size may differ between species: *Q. magnoliifolia* produces solitary acorns (20–30 mm in length; 10–25 mm in diameter), meanwhile *Q. resinosa* produces solitary to grouped (2 to 3) acorns (15–35 mm in length; 15–30 mm in diameter) (González-Villareal 1986). Previous studies have shown that both species co-occur frequently and hybridize within the Trans-Mexican Volcanic Belt and the southern part of the Sierra Madre Occidental (González-Villareal 1986; Albarrán-Lara et al. 2010, 2019).

### Sampling populations

Leaf tissue from 397 trees in 61 populations of *Q. magnoliifolia*, *Q. resinosa*, and intermediate like-forms (hereafter hybrids) was collected across four Mexican biogeographic provinces (Morrone et al. 2017): Sierra Madre Occidental (SMO), Central Mexican Plateau (CP), Trans-Mexican Volcanic Belt (TMVB), and Sierra Madre del Sur (SMS) (Table 1; Fig. 1). We corroborated the taxonomic identity of *Quercus* species and hybrids by examining leaf shape as described in Albarrán-Lara et al. (2019). This procedure resulted in 145 individuals of *Q. magnoliifolia*, 121 hybrids, and 131 of *Q. resinosa*. Hybrid individuals were uniformly distributed in most localities, *Q. resinosa* were identified at the north of TMBV, whereas *Q. magnoliifolia* along TMBV and SMS (see Online Resource 1, Fig. S1). Population names, geographical location, biogeographic region, and morphological assignment for each individual are listed in Table S1

**Table 1** Names, elevation, and geographic position of the localities of *Quercus magnoliifolia*, *Q. resinosa* and their hybrids

A.Pop ID	Name of the locality	N	Elevation (m)	Lat (N)/Long (W)
1	Canelas	10	2561	25. 12/-106. 5
2	Santa Lucía	10	1547	23. 45/-105. 85
3	Cacalután	5	1048	21. 08/-104. 23
4	Compostela	10	1174	21. 22/-104. 8
5	Ocotillo	6	1228	21. 27/-104. 65
6	Mezquitil	10	2067	23. 45/-104. 35
7	Valaparaíso	6	2082	22. 67/-103. 77
8	Mexquitic	8	1881	22. 52/-103. 77
9	Sierra de Bolaños	8	2513	21. 88/-103. 87
10	San Lorenzo	6	1938	21. 97/-103. 2
11	El Plateado	10	1937	21. 92/-103. 03
12	Puertecito	5	2528	21. 68/-103. 17
13	Teul de González	6	1946	21. 4/-103. 52
14	La Congoja	5	2296	22. 18/-102. 52
15	Calvillo	10	2087	21. 92/-102. 58
16	Arroyo Seco	6	1988	21. 72/-102. 63
17	Cerro de los Gallos	5	2139	21. 67/-102. 22
18	Estancia del Cubo	6	2049	21. 38/-101. 12
19	Dolores	6	2144	21. 17/-101. 12
20	Minas	10	1469	21. 68/-100. 05
21	Agua Zarca	6	2174	20. 77/-101. 02
22	Santa Catarina	6	2137	20. 9/-101. 05
23	Guanajuato	7	1983	20. 88/-101. 15
24	Puerto Vallarta	10	473	20. 43/-105. 28
25	Talpa	7	1316	20. 4/-104. 88
26	Cuquio	6	2053	21. 02/-103
27	Avigel	5	2099	20. 87/-102. 8
28	Tepatitlán	5	1932	20. 87/-102. 77
29	Guadalupe	5	1810	19. 87/-103. 46
30	El Llano	8	406	19. 75/-104. 77
31	Casimiro Castillo	5	1366	19. 7/-104. 38
32	Cuzalapa	6	584	19. 45/-104. 52
33	Manantlán	7	1687	19. 6/-104. 22
34	Nogal	5	523	19. 32/-104. 13
35	Coalcomán	6	1643	18. 73/-103. 27
36	Puerto del Gato	5	1905	19. 48/-100. 37
37	Morelia	5	2120	19. 66/-101. 17
38	Tumbiscatio	6	2072	19. 59/-101. 11
39	Guayabos	6	1430	19. 23/-101. 33
40	Benito Juárez	5	1902	19. 35/-100. 4
41	Valle de Bravo	8	1878	19. 25/-100. 13
42	Temascaltepec	5	1724	19. 05/-100. 07
43	Ixcateopan	6	1974	18. 55/-99. 7
44	Chila de las Flores	5	1954	17. 95/-97. 88
45	Platanillos	6	1354	17. 47/-100. 58
46	Filo de Caballo	6	1975	17. 78/-99. 7
47	Magueyal	11	1975	17. 18/-97. 78

**Table 1** (continued)

A.Pop ID	Name of the locality	N	Elevation (m)	Lat (N)/Long (W)
48	Santa Inés del Monte	6	2072	16. 95/-96. 85
49	San Bernardo	5	1721	16. 85/-96. 92
50	Mitla	7	1910	16. 93/-96. 3
51	Papalutla	6	1761	17. 73/-97. 9
52	Ojo de Agua	5	1167	16. 42/-97. 08
53	Juchitahuaca	10	1987	17. 48/-98. 02
54	Pinos	6	2007	17. 23/-97. 72
55	Cerezal	5	2118	17. 27/-96. 53
56	San Miguel del Río	5	1822	17. 32/-96. 55
57	Sola de Vega	5	1816	16. 58/-96. 93
58	Matatlán	5	1946	16. 83/-96. 35
59	Cerro Metate	5	2131	16. 25/-96. 53
60	Coatlán	6	2104	16. 28/-96. 68
61	Santo Reyes	5	1620	16. 48/-96. 98

### DNA extraction and chloroplast microsatellites genotyping

To isolate DNA, we used cetyltrimethylammonium bromide (CTAB) protocol with an additional phenol-chloroform cleaning step (Lefort and Douglas 1999). The isolated DNA was diluted with deionized water to a final concentration of 20 ng/ $\mu$ L and stored at  $-20^{\circ}\text{C}$ . Six molecular markers derived from chloroplast microsatellites short simple repeats (cpSSR) described in Weising and Gardner (1999) (Ccmp10) and Deguilloux et al. (2003) ( $\mu$ dt1,  $\mu$ d3,  $\mu$ dt4,  $\mu$ cd4, and  $\mu$ cd5) were amplified using multiplex PCR reaction by QIAGEN Multiplex PCR Kit. The thermal cycling program consisted of one cycle at  $95^{\circ}\text{C}$  for 15 min and then 35 cycles, each of  $95^{\circ}\text{C}$  for 30 s, annealing at  $50^{\circ}\text{C}$  for 1:30 min and extension at  $72^{\circ}\text{C}$  for 1 min. A final extension at  $60^{\circ}\text{C}$  for 30 min was included. All amplification reactions were carried out in 5  $\mu$ L volumes including 1X Multiplex PCR Master Mix, 2  $\mu$ M each primer, deionized water, and 20 ng DNA. Multiplex PCR products were diluted 1:1 in deionized water and run in an ABI-PRISM 3100-Avant sequencer with the GeneScan-500 LIZ size standard included (Applied Biosystems, Foster City, California, USA). The software Peak Scanner v1.0 (Applied Biosystems, Foster City, California, USA) was used to determine the size of alleles.

### Genetic diversity and phylogeographic structure

Genetic diversity estimates were assessed per sampled location in terms of number of haplotypes (A), number of private haplotypes ( $P_h$ ), and Nei's index of genetic diversity ( $H_s$ ) estimated without bias (Nei 1973) using Haplotype Analysis

software (Eliades and Eliades 2009). To identified trends in  $H_s$  with respect to latitude, longitude, and elevation, we performed Spearman's rank correlation ( $\rho$ ) in R version 4.1.3 (R core Team 2022). In addition to previous parameters of genetic diversity, the number of shared haplotypes ( $S_h$ ), effective number of haplotypes ( $E_h$ ), and haplotypic richness ( $R_h$ ) were also estimated for both species (*Q. magnoliifolia* and *Q. resinosa*) and their hybrids.

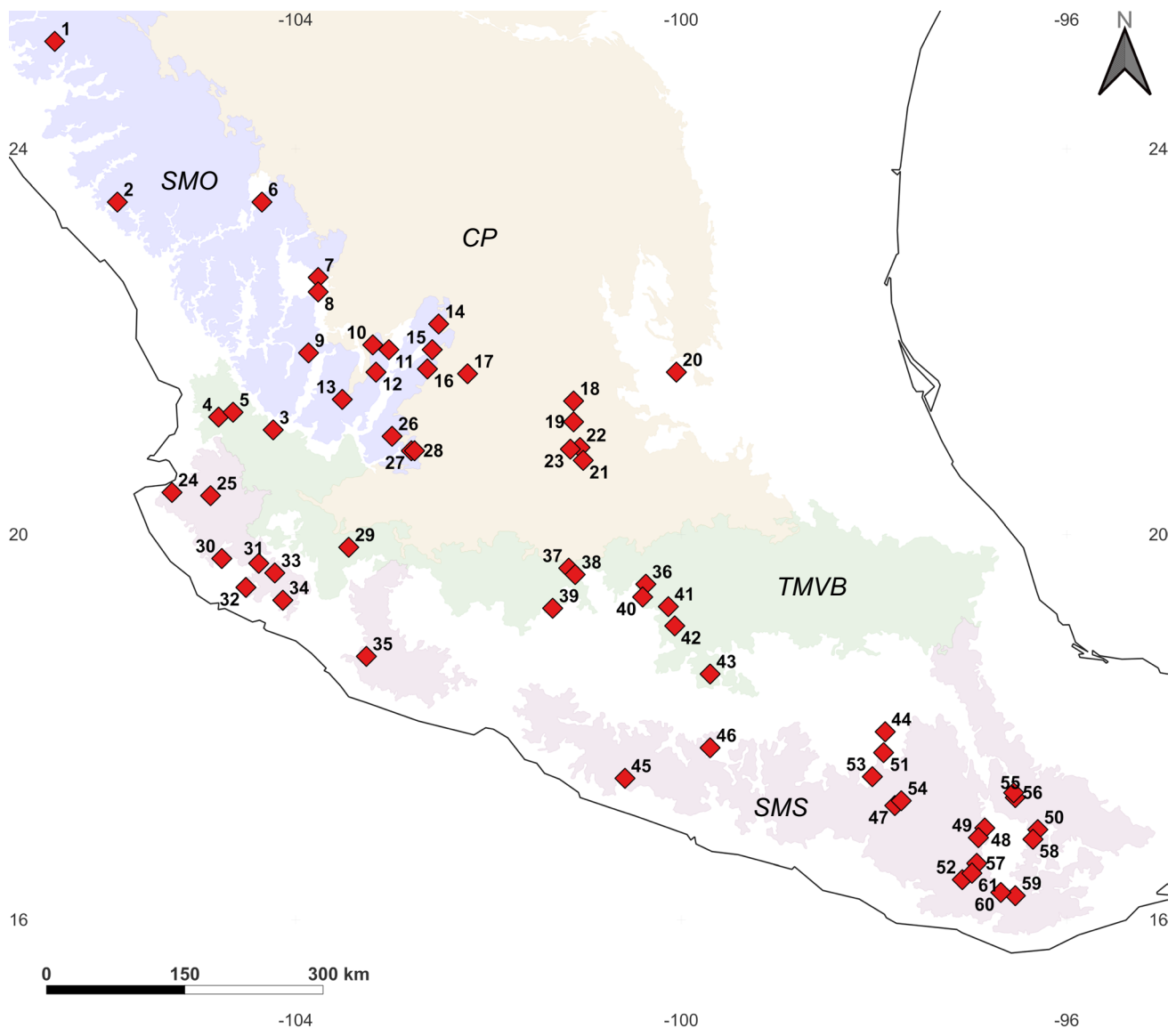
To assess the genetic differentiation, we first computed  $F_{ST}$  among species (and hybrid forms) and among sampling collection using Haplotype Analysis software. We also evaluated the effect of geographic distance on genetic structure among populations across the entire range covered by the two oak species by performing a Mantel test with 9999 permutations. We measured genetic distance as  $F_{ST} / (1 - F_{ST})$  and calculated geographic distances (km) between sampling collection using the R package "fossil" (Vavrek 2011). Then, AMOVA was run to determine the proportion of genetic variance explained by 1) grouping by species and hybrids, 2) grouping by biogeographic provinces (SMO, CP, TMVB, and SMS), and 3) grouping localities of *Q. resinosa* at the north of TMVB and grouping *Q. magnoliifolia* localities along TMBV and SMS (with no distinction of hybrids). AMOVA ran with 10,000 permutations to compute p-values using Arlequin version 3.5 (Excoffier and Lischer 2010).

The genealogical relationship between haplotypes was inferred by Haplotype network based on minimum spanning network with 1000 permutations using the R package "pegas" (Paradis 2010). Finally, we inferred genetic partition using tess3r (Caye et al. 2016) by estimates of ancestry proportions and ancestral allele frequencies. We performed 10 independent runs for each  $K$  value, which ranged from 1 to 15, and retained repetitions of  $K$  with the lowest root mean squared errors. To determine the optimum value of  $K$ , we employed a cross-validation method to identify when the curve exhibits a plateau or starts increasing again (Caye et al. 2016).

### Approximate Bayesian Computation (ABC)

To test for different hypothesis of historical demography between *Q. magnoliifolia* and *Q. resinosa*, we contrasted two evolutionary scenarios using DIYABC version 2.1.0 (Cornuet et al. 2014). Evolutionary scenario A modeled a relative ancient divergence from a common ancestor (with an effective population size  $N1+N2$ ) of *Q. magnoliifolia* and *Q. resinosa* at a time  $t2$  followed by recent unidirectional introgression from *Q. magnoliifolia* ( $N2$ ) to *Q. resinosa* ( $N1$ ) at a time  $t1$ . Evolutionary scenario B described a simple species divergence at a time  $t2$ . As starting point, we considered  $t2$  and  $t1$  as the time of divergence of the two species ( $\sim 8$  Mya) proposed by Hipp et al. (2018) and the timing for the last glaciation event ( $\sim 29,000 - 19,000$  years), respectively, both translated into generational time. The later was considered as





**Fig. 1** Sample collection localities of *Quercus magnoliifolia*, *Quercus resinosa*, and their hybrids. The geographical position of the 61 sampling points is represented by diamonds. Populations were collected across four Mexican biogeographic provinces: SMO, Sierra Madre

Occidental; SMS, Sierra Madre del Sur; TMVB, Trans-Mexican Volcanic Belt; CP, Central Mexican Plateau. The numbers correspond to PopID in Table 1

the first event of flowering and seed production, which occur between 15 and 25 years for most oak species (Johnson et al. 2002). After fine-tuning, prior distributions of demographic parameters were set as follow: Normal distribution for  $N1$  and  $N2$  (min = 10, max = 500, mean = 100, sd = 50; min = 100, max = 1000, mean = 200, sd = 50, respectively). Uniform for  $t1$  with min = 1000, max = 3500;  $t2$ , min = 300,000, max = 500,000; and the unidirectional introgression rate ( $r2$ ) with min = 0.01, max = 0.7. We assumed a stepwise mutation model with a mean mutation rate of  $1 \cdot 10^{-5} - 3 \cdot 10^{-3}$ . The summary statistics of each simulation included the mean number of alleles, mean genetic diversity,

mean size variance, and  $F_{ST}$ . We computed 1,000,000 simulations for each evolutionary model and selected the 1% of the simulated data closest to the observed data to assess the posterior probabilities of scenarios based on logistic regression and direct method (Cornuet et al. 2014).

### Past changes in species distribution

To gain insights about the more recent evolutionary history of the two oak species, we reconstructed species distribution models during the Mid-Holocene (MH; ~ 6,000 years BP), Last Glacial Maximum (LGM; ~ 21,000 years BP), and

Last Interglacial (LIG; ~ 120,000 years BP). To do this, a database of 917 and 390 occurrence records was compiled from herbarium collections (MEXU, IEB, XAL) and GBIF data to *Q. magnoliifolia* and *Q. resinosa*, respectively. To diminish the spatial autocorrelation effects of aggregation in the modeling procedure (e.g., Zorrilla-Azcué et al. 2021), all records except one within 10 km<sup>2</sup> were deleted, leaving a database with 450 and 220 occurrence records for *Q. magnoliifolia* and *Q. resinosa*, respectively, that was used in further analysis. Nineteen bioclimatic variables for the locations of each sampled population were obtained from the WorldClim Global v1.0 database (Hijmans et al. 2005) with a 0.8° resolution. Bioclimatic variables with high correlations (> 0.8) were eliminated to avoid collinearity, resulting in nine variables that were used in the subsequent analysis: annual mean temperature, mean diurnal range of temperature, temperature seasonality, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation seasonality, precipitation in the wettest quarter, and precipitation in the driest quarter.

To model the ecological niche, we used a random partition method to split the available data into training and test sets. Fifteen randomized subsets containing 60% of the records (270 occurrence records for *Q. magnoliifolia* and 130 for *Q. resinosa*) were run as independent analyses using MaxEnt 3.3.3 (Phillips et al. 2006; Phillips and Dudik 2008). We obtained a model for each subset (considered replicates) using a default convergence threshold with a maximum number of 1000 iterations. Then, the obtained models were binarized using the probabilities at which 90% of the input occurrence points were included in each prediction as a threshold (Zhu et al. 2016). Model validation was performed using the kappa index (Cohen 1960). We selected three models with the highest kappa index (> 0.86 for *Q. magnoliifolia* and > 0.82 for *Q. resinosa*) as the best subset of models that were subsequently used to project the distribution to past climate scenarios. The overlapping area of the three best models was considered the current distribution.

The best subsets of current niche models were projected into the reconstructed climatic conditions during the Mid-Holocene, Last Glacial Maximum, and Last Interglacial periods. For the Mid-Holocene and Last Glacial Maximum periods, we used three general circulation models: the Community Climate System Model (CCSM), Model for Interdisciplinary Research on Climate (MIROC), and Max Planck Institute for Meteorology Earth System Model (MPI-ESM) (Cooper et al. 2016; Zhu et al. 2016); and for the Last Interglacial period, only the CCSM was used (Otto-Bliesner et al. 2008). Before projection into the past, we identified whether non-analogous climatic conditions were present between the past scenarios with respect to our current model (climate anomaly analysis proposed by Silva et al. (2020)); temperature seasonality and precipitation in the driest quarter

variables were identified to have anomalous behavior in the Last Interglacial period, and both variables were therefore excluded in this projection. The intersection area of the replicates with the highest kappa index was considered the distribution range of the species in each time horizon. The maps of each period of each species were intersected to determine a probable area of sympatry between both species. The number of pixels (0.08°) was counted for each horizon for each species, for MH and LGM only the area where the three models coincide was quantified.

## Migration models

Along with the species distribution modelling, we tested migration models that describe different hypotheses of ancient populations' connectivity. We implemented the Bayesian inference strategy from Migrate-n version 3.7.2 (Beerli and Felsenstein 2001; Beerli 2006; Beerli and Palczewski 2010) to estimate historical population size ( $\Theta = N_e\mu$ ) and migration rates ( $Nm = \Theta M/1$ ). This method can be used to compare marginal likelihoods and Bayes Factor (BF) to test the best fit of the data. Here, we compared three migration models: The full migration model (model 1) considering all populations exchange migrants at individual rates (Fig. S2); model 2 described the areas of *Q. magnoliifolia* based on distribution models during the LGM, including the prediction of recent colonization of *Q. resinosa* towards the north (pop 2), and *Q. magnoliifolia* to the east of TMVB (pop 3) (Fig. S2); and model 3 describing a similar migration model suggested by *Q. castanea* Née in Mexico (Peñaloza-Ramírez et al. 2020), in which pop 3 was historically connected with southern populations (SMS; pop 4) and only received migrants recently from the west of TMVB (pop 1; Fig. S2). We first ran migrate-n using the complete dataset; however, migration parameters did not converge after one million steps and using a variety of running schemes, probably because many private haplotypes prevented chain convergence. Thus, we constructed a data subset including only haplotypes present in three or more localities. In this way, we conserved putative ancestral haplotypes that could have had enough time to disperse. This data subset left us with 229 individuals, and 36 sampling localities (available at <https://doi.org/10.5281/zenodo.7641499>).

Based on this subset, we ran migrate-n again and fitted prior distributions using the full migration model. Uniform prior distribution was as follow:  $\Theta_{\min} = 0$ ;  $\Theta_{\max} = 5$ ;  $\delta = 0.05$ ; and  $M_{\min} = 0$ ;  $M_{\max} = 60$ ;  $\delta = 6$ . Each model implemented the Brownian motion model with initial values computed using  $F_{ST}$ . We performed three replicates with a static heading scheme using four short chains and a single long chain. We recorded 1,000,000 steps with sample increment of 10; sampling 30,000,000 of parameter values and discarding 100,000 trees per chain. We evaluated chain convergence examining the posterior distribution of histograms of each

parameter looking for a smooth curve with a single peak. Finally, to determine the best fit model, we used the marginal likelihoods by thermodynamic integration with Bezier approximation to calculate BF and posterior probabilities (Beerli and Palczewski 2010).

## Results

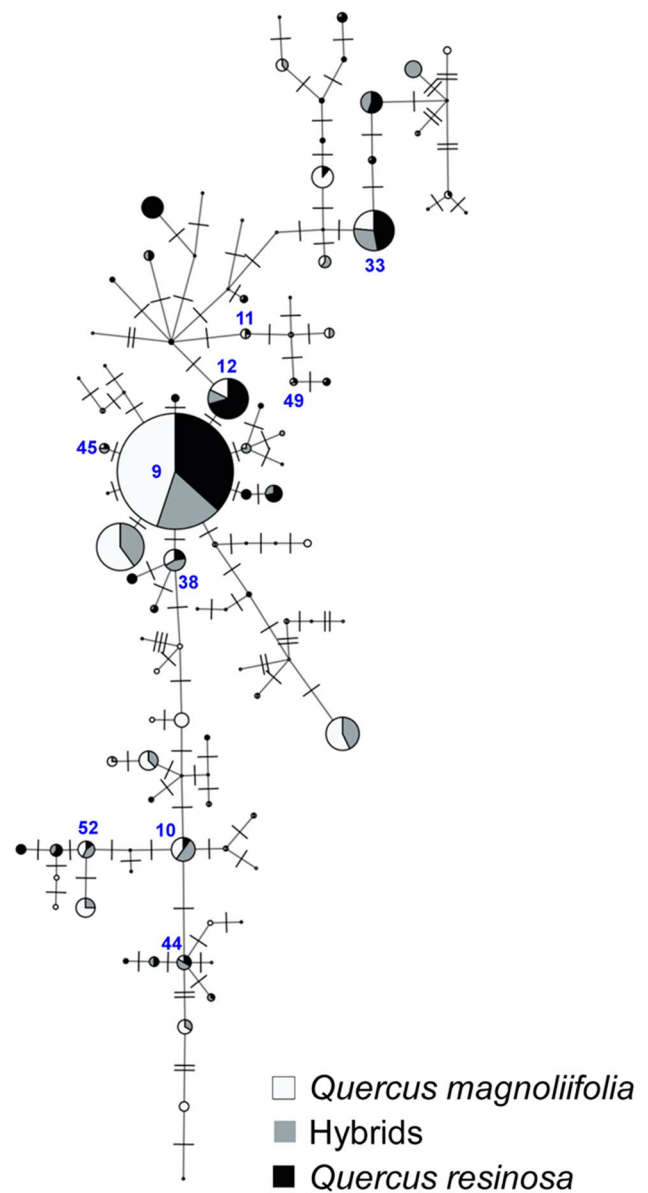
### Genetic diversity

We obtained a total of 103 haplotypes (A) with a large fraction of private ones (Table S2), which accounted for 71 % ( $P_h = 73$ ) of the total number of haplotypes identified through 61 localities; 12 of them in high frequencies ( $\geq 0.5$ ). Private haplotypes were distributed in 38 localities, 15 at the north of TMVB, and 23 along the TMVB and SMS (Fig. S3). We also observed nine sampling localities completely composed of private haplotypes (Table S2; Fig. S3). The rest of the haplotypes were restricted to two or three localities. Notwithstanding, we identified nine haplotypes with a wider geographical distribution (hap-7, hap-9, hap-10, hap-12, hap-18, hap-38, hap-75, hap-56, hap-44; Fig. S3). For instance, hap-9 occurred in most of the geographic distribution of both species, whereas hap-12 was restricted to the current distributional range of *Q. resinosa*.

Genetic diversity ( $H_s$ ) was different among all populations (Table S3), ranging from no genetic diversity ( $H_s = 0$ ) to very high ( $H_s = 0.9$ ), with no particular geographic trend in latitude, longitude or elevation ( $\rho = -0.1, p = 0.4$ ;  $\rho = 0, p = 0.9$ ;  $\rho = -0.07, p = 0.5$ , respectively); even when we tested trends based only on localities that resembled a linear distribution on vertical ( $\rho = 0.16, p = 0.5$ ) and horizontal axis ( $\rho = 0.06, p = 0.8$ ). *Quercus magnoliifolia*, hybrid individuals, and *Q. resinosa* shared ten haplotypes with a similar contribution among them (Fig. 2). Hybrids resulted with higher values of genetic diversity except for the number of private haplotypes (Table 2).

### Genetic and phylogeographic structure

Genetic differentiation between species and hybrids, and among populations revealed low values of  $F_{ST}$  which ranged from 0.002 (*Q. magnoliifolia* vs. hybrids) to 0.004 (*Q. magnoliifolia* vs. *Q. resinosa*), and from 0 to 0.012 among populations. We did not detect that geographic distance had an influence on genetic structure ( $r = 0.05, p = 0.14$ ). The AMOVA results showed no genetic differentiation when grouping by species and hybrids ( $F_{CT} = 0.013, p = 0.098$ ) or following biogeographic provinces ( $F_{CT} = 0.032, p = 0.077$ ) (Table 3). However, when we took into account the geographic distribution of *Q. resinosa* at the north and *Q. magnoliifolia* along the TMVB and SMS, AMOVA suggested low but significant genetic differentiation ( $F_{CT} = 0.04; p = 0.03$ ) (Table 3).



**Fig. 2** Minimum spanning network inferred between *Quercus magnoliifolia*, *Quercus resinosa* and their hybrids. Circle sizes proportional to the haplotype frequencies; the area within circles proportional to the number of observed individuals of *Q. magnoliifolia* (white), hybrids (gray), and *Q. resinosa* (black). Mutational steps are symbolized by dashes. Numbers represent the haplotype IDs shared among all taxa

The distribution of haplotype frequencies confirmed the extensive haplotype sharing between *Q. magnoliifolia* or *Q. resinosa* and putative hybrids (Fig. 2). In most cases, haplotypes were separated by one mutational step. The haplotype network revealed a single ancestral haplotype (hap-9) from which all others derived. Interestingly, this ancestral and widely distributed haplotype (Fig. 2), was closely related with hap-12. Note that in several hap-12 derived haplotypes, the proportion of *Q. resinosa* individuals increased (Fig. 2),

**Table 2** Genetic diversity estimates for *Quercus magnoliifolia*, *Q. resinosa* and their putative hybrids in Mexico

Species name	N	A	Ph	Eh	Rh	Hs
<i>Quercus magnoliifolia</i>	145	49	18	20.19693	44.22878	0.957088
Hybrids	121	59	19	33.3508	58	0.978099
<i>Quercus resinosa</i>	131	47	24	20.75091	44.60613	0.959131
Mean		51.6666667	20.33333	24.76621	48.94497	0.964773

N: sample size in each population; A: number of haplotypes; Ph: number of private haplotypes; Eh: effective number of haplotypes; Rh: haplotypic richness; and Hs: genetic diversity

**Table 3** Analysis of molecular variance (AMOVA) testing three population clustering hypotheses among *Quercus magnoliifolia*, *Q. resinosa* and their putative hybrids

Source of variation	d.f.	Percentage of variation	Fixation indices	p-value
<i>Between species and hybrids</i>				
Among groups	2	1.33	FCT=0.013	0.098
Among populations within groups	7	6.63	FSC=0.07	0
Within populations	784	92.04	FST=0.08	0
<i>Among biogeographic provinces</i>				
Among groups	3	3.23	FCT=0.032	0.077
Among populations within groups	57	63.18	FSC=0.65	0
Within populations	733	33.59	FST=0.66	0
<i>Between north and south</i>				
Among groups	1	4.41	FCT=0.044	0.032
Among populations within groups	56	62.95	FSC=0.66	0
Within populations	690	32.63	FST=0.67	0

Grouping hypotheses: H1: grouping by species and hybrids; H2: following biogeographic provinces: SMO (Sierra Madre Occidental), CP (Central Mexican Plateau), TMVB (Trans-Mexican Volcanic Belt), and SMS (Sierra Madre del Sur); and H3: grouping localities at the north following *Q. resinosa* and *Q. magnoliifolia* distribution (Fig. S1)

suggesting some chloroplast differentiation between *Q. magnoliifolia* and *Q. resinosa* (irrespective of hybrids). In addition, geographic distribution of hap-12 and its position within the haplotype network (Fig. 2) suggested colonization events that could take place to the north.

Regarding TESS analysis, cross-validation suggested an optimum genetic partition at  $K = 8$ ; however, the error increased from  $K = 4$  to  $K = 8$  (Fig. 3A). Thus, we found  $K = 3$  as a reasonable number of genetic subdivisions (Fig. 3B, C). The pattern of genetic differentiation obtained from  $K = 3$  yielded similar results as from AMOVA and the haplotype network: high genetic admixture between species and hybrids, but with an apparent differentiation between the geographic distribution of *Q. resinosa* and *Q. magnoliifolia* (Fig. 3B, C).

### Approximate Bayesian computation

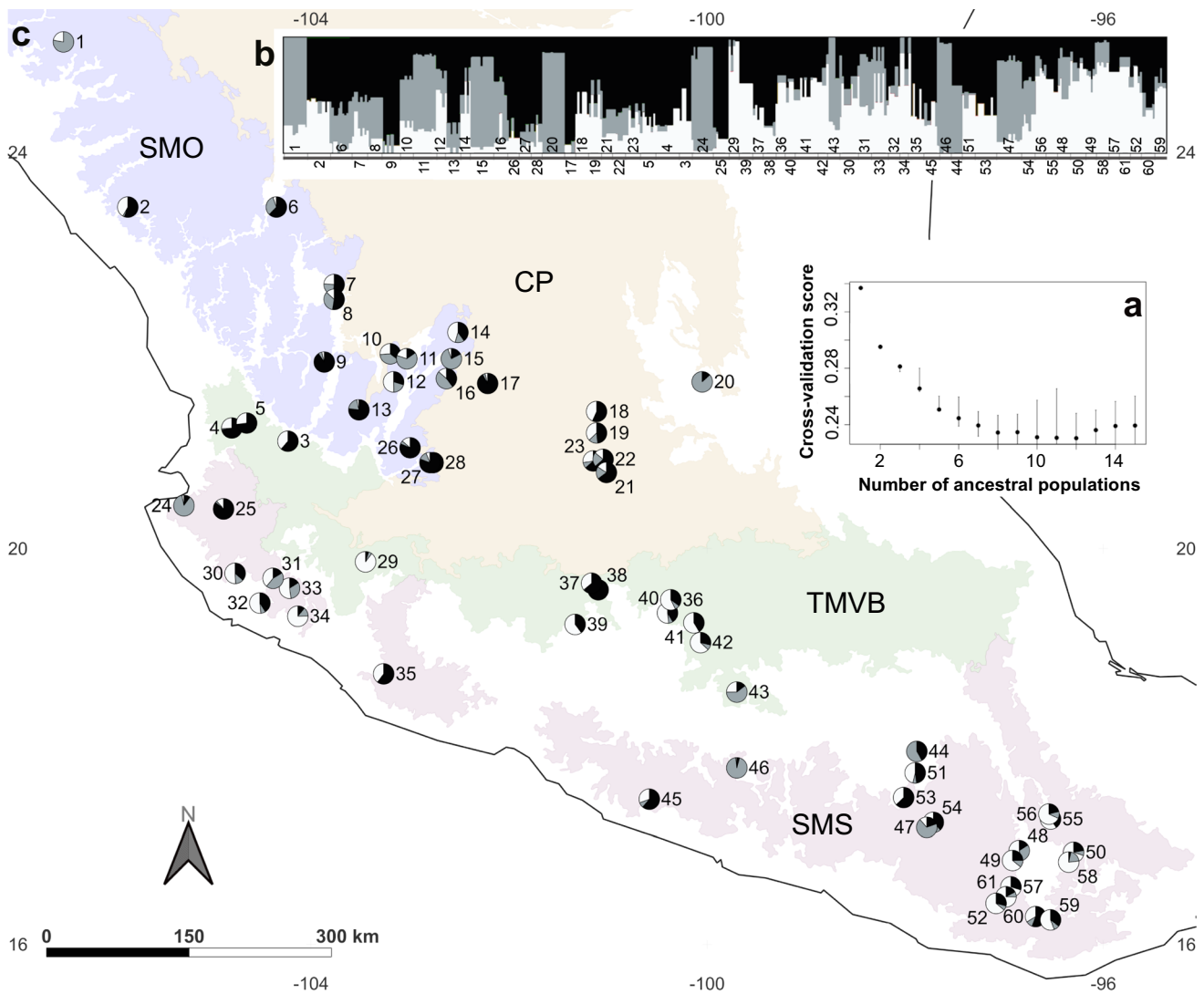
Evolutionary scenarios tested in DIYABC (Fig. 4) showed a clear statistical support for evolutionary scenario A, which modeled recent introgression and ancient divergence from a common ancestor. Data from the prior distribution and

the observed data set were within the posterior predictive distribution, suggesting that scenario A explained better the observed data (Fig. S4). Assuming a generational time of 25 years (Johnson et al. 2002), ABC analysis suggested that *Q. resinosa* and *Q. magnoliifolia* diverged back to c. 10 Mya followed by recent introgression with a mean rate of 0.67 at c. 35,000 years ago (Table 4).

### Past changes in species distribution

The kappa values of the three best replicates for *Q. magnoliifolia* ranged between 0.86 and 0.89, while for *Q. resinosa* ranged between 0.82 and 0.87, indicating agreement for the three models contrasting the current distribution of both species. The most important climatic variables were the seasonality of temperature and precipitation for *Q. magnoliifolia*, while for *Q. resinosa* were seasonality of temperature and mean temperature in warmest quarter. Past distribution models for *Q. resinosa* suggested a more patchy and restricted geographical distribution than observed today (Fig. 5); whereas for *Q. magnoliifolia*, models predicted a more stable geographic distribution over time. During the LIG, *Q.*





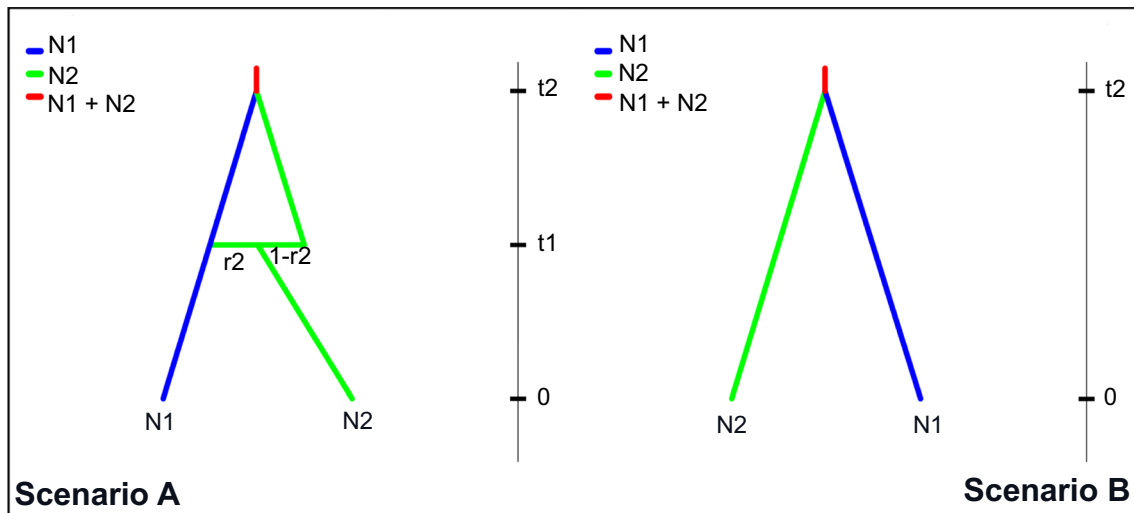
**Fig. 3** Clustering results for 397 individual trees from 61 localities. **a**) Cross-validation score from TESS3 plotted against the number of ancestral populations ( $K$ ). **b**) Bar plot of the probability of assignment to  $K = 3$  for each individual (vertical bars). Probability is proportional to the color length. **c**) Represents the geographical distribu-

tion for the same three genetic clusters ( $K = 3$ ) suggested by TESS3. The proportion of colors in each pie charts reflects the proportion of ancestry to each genetic cluster. Biogeographic provinces: SMO, Sierra Madre Occidental; SMS, Sierra Madre del Sur; TMVB, Trans-Mexican Volcanic Belt; CP, Central Mexican Plateau

*magnoliifolia* and *Q. resinosa* were likely in sympatry; however, the predicted area of contact becomes more extensive during LGM, in which a large fraction of the distribution range of *Q. resinosa* lied within that of *Q. magnoliifolia*. Towards the Mid-Holocene relevant changes in geographic distribution were predicted for *Q. resinosa*, which migrated northward to reach its current distribution. This occurred parallel with the expansion of sympatric areas from LGM to Mid-Holocene (Fig. 5). Regarding *Q. magnoliifolia*, past distribution models suggested that this species had a wider geographic distribution since LIG; and likely experienced shorter geographic expansion eastward since LGM to Mid-Holocene (Fig. 5).

**Migration models**

The comparison of migration models showed strong support for model 2 (posterior probability = 0.9999; Table 5). The best-fitting model described the recent establishment of *Q. resinosa* at the north of the TMVB and to the east of some *Q. magnoliifolia* populations (Fig. S2). Those populations were likely linked by unidirectional gene flow from the west of TMVB. Estimated average  $Nm$  values ranged between 1.67 and 22.9 individuals per generation with the highest gene flow occurring northward for *Q. resinosa* populations (Fig. S2).



**Fig. 4** Approximate Bayesian Computation (ABC) analysis. Schematic representation of models tested. Scenario A (left) represents species divergence followed by unidirectional introgression ( $r_2$ ) from *Q. mag-*

*noliifolia* (N2) to *Q. resinosa* (N1). Scenario B (right) represents divergence between *Quercus* species from a common ancestor with population size  $N_1 + N_2$

**Table 4** Posterior distribution of parameters using DIYABC for the best supported model

Parameter	Mean	Median	Mode	q250	q750	q950
N1	172	172	160	147	195	231
N2	234	232	234	206	259	301
$r_1$	3.50E+04	3.00E+04	2.50E+04	2.68E+04	3.80E+04	6.45E+04
$r_2$	1.04E+07	1.06E+07	1.22E+07	9.25E+06	1.17E+07	1.23E+07
$r_2$	0.67	0.688	0.7	0.671	0.696	0.7
u	2.70 E-003	2.75 E-003	3 E-003	2.54 E-003	2.91 E-003	3 E-003

$t$  scaled by a generational time of 25 years

## Discussion

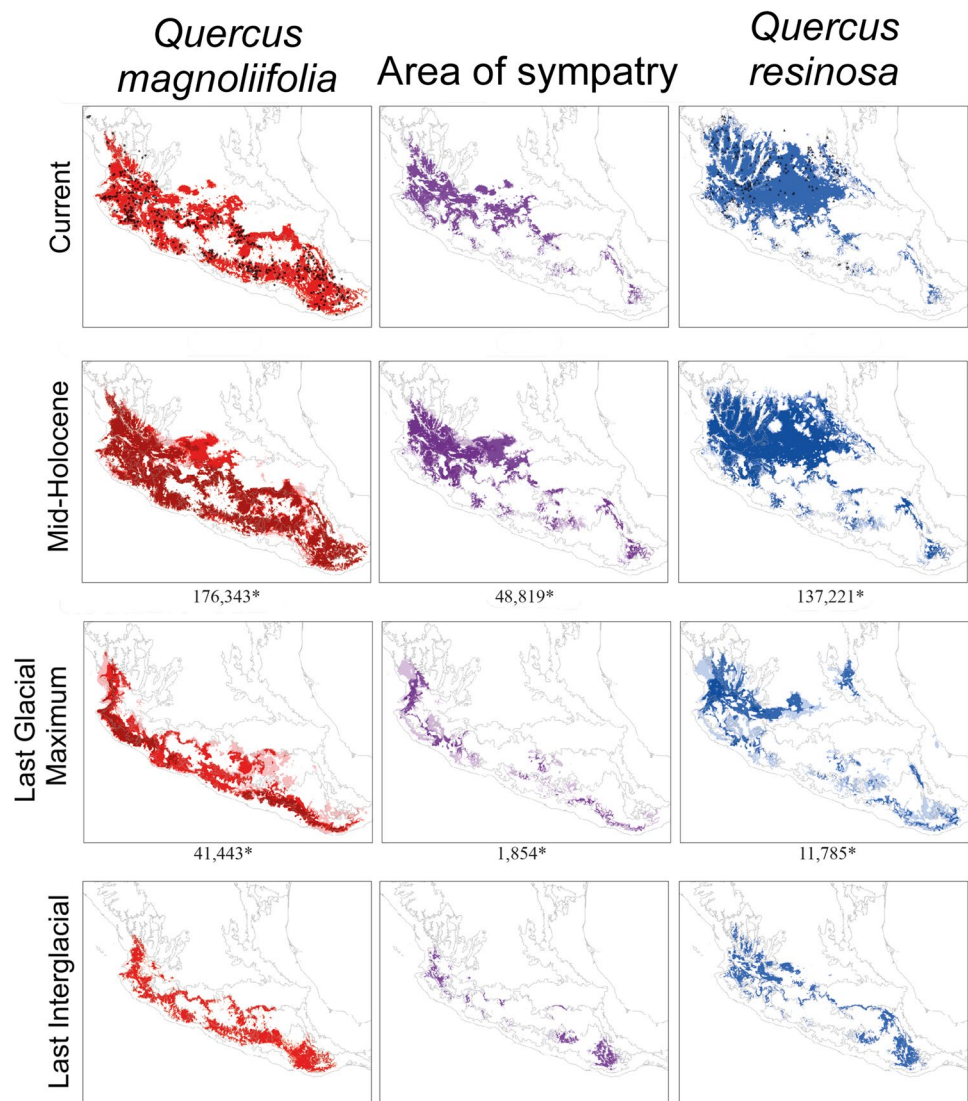
We investigated the patterns of genetic variation of two Mexican oaks, *Q. magnoliifolia* and *Q. resinosa*. We did not distinguish a unique genetic composition for each species; however, we found a chloroplast differentiation that was congruent with geography than the taxonomic status of each species or their previously described hybrids (Albarán-Lara et al. 2019). Our study revealed that after divergence (*c.* 10 Mya), high rates of introgression took place at the end of the Pleistocene (*c.* 35,000 years). Furthermore, past distribution models suggested that *Q. magnoliifolia* and *Q. resinosa* were largely in sympatry during the LGM, and during the Mid-Holocene, *Q. resinosa* likely expanded towards its current distribution. This was also supported by the migration models tested which suggested a recent establishment of *Q. resinosa* in the north of TMVB. In the light of this evidence, we propose that the pattern of genetic variation between both oak species reflect an

important role of not only introgression but also migration by means of historical seed dispersal events.

### Introgression and migration events explain the present-day distribution of chloroplast diversity

Oak clades have a long evolutionary history in which their ancestors originated during the Paleocene (Zhou et al. 2022). In fact, fossil evidence indicated that *Quercus* had a long presence during this epoch in the Northern Hemisphere, forming a subtropical flora with temperate elements (Barrón et al. 2017). In North America, fossil records suggest that *Quercus* arrived in the middle Eocene (ca. 44 Ma) (Barrón et al. 2017). Later, as the climate cooled during the Eocene-Oligocene transition, oaks migrated southward and underwent a parallel diversification before and after colonizing Mexico around 14–20 Mya (Hipp et al. 2018). Since then, oaks have colonized a wide variety of environments from xeric scrublands to temperate forests of Mexico.

**Fig. 5** Species distribution models during the Mid-Holocene (6,000 years BP), Last Glacial Maximum (~ 21,000 years BP), and Last Interglacial (~ 120,000 years BP) for *Quercus magnoliifolia* (left), area of sympatry (middle), and *Quercus resinosa* (right). The intersection area of the replicates with the highest kappa index was projected as the distribution range of the species in each time horizon. Asterisks indicate the surface (km<sup>2</sup>) where the three models (MIROC, CCSM, and MPI) coincide for Last Glacial Maximum and Mid-Holocene



Within *Quercus*, colonization of new territories could be facilitated by interspecific gene exchanges and seed-dispersers (Petit et al. 2004; Kremer and Hipp 2020; Zhou et al. 2022). Evidence involving hybridization and long-distance dispersal in range expansions were earlier documented for European or North American oaks (Whittemore and Schaal 1991; Petit et al. 1997). Hybridization and its potential for facilitating

range expansion has been observed in Mexican oaks as well with the expansion of the subsection *Racemiflorae* at its northern edge (McCauley et al. 2019). In the case of *Q. robur* L. – *Q. petrea* (Matt.) Liebl. complex within Europe, Petit et al. (2004) established a model of continuous cycles of long-distance seed dispersal for the establishment of new populations of *Q. robur*, followed by interspecific pollen flow of *Q. petrea* into the newly formed populations. Repetitive introgression events and selection in favor to this successional species allowed the emergence of *Q. petrea* types into the new population bordered by *Q. robur*. Introgression-driven migration was an active mechanism during post-glacial colonization events in these oak species (Kremer and Hipp 2020).

In the light of our results and in the absence of nuclear differentiation previously reported by Albarrán-Lara et al. (2019), we propose that after *Q. magnoliifolia* and *Q. resinosa* diverged (~10 Mya) it is likely that repetitive cycles

**Table 5** Migration model comparison using Migrate-n

Model	Bezier approximation score	Log Bayes Factor (LBF)	Posterior probability	Choice
Model 1	-7065.12	-114.94	<0.000001	2
Model 2	-7007.65	0	0.99999	1
Model 3	-7105.45	-195.6	<0.000001	3

of long-distance seed dispersal and interspecific pollen flow may have played a role in the establishment of *Q. resinosa* in its current geographical distribution, and thus influence the present-day distribution of chloroplast diversity. According to many proxy reconstructions, temperatures during the LIG were warmer and wetter than present (reviewed by Suh et al. 2020), whereas during the last glacial period, dry and cool conditions prevailed in the tropics (Braconnot et al. 2007), suggesting that climatic conditions could favor the population persistence of both *Quercus* species during LGM, as was shown by our results (Fig. 5). As climate changed towards the Holocene, warmer and wetter conditions prevailed (Metcalf et al. 2000; Harrison et al. 2003). Due to wide preferences in temperature and annual precipitation regimens of *Q. magnoliifolia* (Albarrán-Lara et al. 2019), unidirectional introgression events at the end of the Pleistocene detected in this study could involve genetic variation that allowed *Q. resinosa* successfully overcome Holocene changes.

A similar scenario was hypothesized in a genome-wide sequencing study, suggesting that introgressed temperature tolerance alleles in co-occurring *Quercus* species were involved in the expansion of recipient species to higher latitudes (Leroy et al. 2020). If this is correct, *Q. resinosa* expanded northward parallel to sympatric areas (Fig. 5) by means of repetitive cycles of long-distance seed dispersal and interspecific pollen flow with *Q. magnoliifolia*, allowing *Q. resinosa* to reach its current geographical distribution and explain the low chloroplast differentiation. Although it has been suggested that *Quercus* species have lower seed dispersal potential, it has been reported that long distance dispersal also occurs mainly by bird species such as *Cyanocitta*, *Aphelocoma*, *Corvus* and *Pica* species (Steele and Smallwood 2002). Additionally, recent phylogenetic analysis has suggested close relationship with rodent (Sciuridae) and bird seed-dispersers in different periods of time: earlier following the split of *Quercus* ancestors, and after, during the Miocene (Zhou et al. 2022). This highlights that seed dispersers may be more important in determining the distribution of genetic variation in Mexican *Quercus* than previously thought. On the other hand, these repetitive cycles of hybridization and long-distance dispersal offer a plausible explanation for the wider geographical distribution of hybrids found in this study (Fig. S1), especially for those localities outside of the current area of sympatry proposed in a previous study (Albarrán-Lara et al. 2019).

Finally, past distribution models predicted that *Q. magnoliifolia* and *Q. resinosa* have been largely in sympatry since the LGM, providing the opportunity for genetic exchange, as is commonly found in *Quercus* species that co-occur in mixed stands (González-Rodríguez and Oyama 2005; Cavender-Bares et al. 2015; Hipp 2015; Sork et al. 2016; Hipp et al. 2018). Although, *Q. magnoliifolia* and

*Q. resinosa* today occur in different environments, they showed some degree of niche overlap in which a proportion of the niche of *Q. resinosa* was included into that of *Q. magnoliifolia* (Albarrán-Lara et al. 2019). In this sense, several studies have shown that climatic niche similarity promotes interspecific gene flow in diverse organisms (Arteaga et al. 2011; Andújar et al. 2014; Ortego et al. 2014; Wu et al. 2015), suggesting that ancient hybridization could be facilitated by the niche-overlap between oak species. From these hybrid zones, colonization events could also take place at great distances, invading new environments and differentiating in their current ecological niches (McCauley et al. 2019). The dispersal-migration processes are congruent with the model of invasion for *Quercus* species described by Petit et al. (2004).

### Genetic diversity patterns

There is no consensus about the patterns of genetic diversity in oaks worldwide. However, within the Neotropics, high numbers of haplotypes and within-population diversity is usually observed. For instance, populations of *Q. magnoliifolia* and *Q. resinosa* were characterized, in general, by comparable cpDNA diversity ( $H_s = 0.5–0.9$ ) to other *Quercus* distributed in Mexico, such as *Q. castanea*, *Q. insignis*, *Q. sapotifolia*, *Q. affinis–Q. laurina*, *Q. crassifolia–Q. crassipes* complex and oaks of the subsection *Racemiflorae* (Tovar-Sánchez et al. 2008; Ramos-Ortiz et al. 2016; Rodríguez-Correa et al. 2017; McCauley et al. 2019; Peñaloza-Ramírez et al. 2020). This level of chloroplast diversity attests for hybridization events as important drivers of high levels of genetic diversity observed, but also that species had persisted long enough to accumulate variation. Hybridization has prevented other factors being detectable, such as isolation by distance or associations between genetic diversity with latitude and altitude that track shifts in species distribution even in the absence of predictive distribution models.

The geographic distribution of hap-12 at the north of TMVB and their derived position from ancestral hap-9 (Fig. S3; Fig. 2) suggested colonization events that were supported by the migration model, indicating a recent establishment of *Q. resinosa* at the north of TMVB. This highlights the relevance of TMVB as a bridge between biogeographic provinces directly influencing the genetic variation of co-distributed taxa (Tovar-Sánchez et al. 2008; Bryson et al. 2018). Results from migration models indicated that *Q. resinosa* dispersed from the western part of TMBV northward into the Sierra Madre Occidental and Central Mexican Plateau, probably very recently in geological time. The derived condition of hap-12 and its geographic distribution were also consistent with this colonization route. The TMVB was previously proposed as well as an important hotspot for oak species diversity, as well as important zone for hybridization



and introgression processes (Tovar-Sánchez et al. 2008; Bryson et al. 2018; Albarrán-Lara et al. 2019), allowing the contact between previously isolated oak species in other biogeographic regions, and thus, acquired new haplotypes by secondary contact. Interestingly, the pattern of shared haplotypes among *Q. magnoliifolia*-*Q. resinosa* and hybrids further supported, as explain in the previous section, that hybridization may have occurred more than once, since both ancestral haplotypes and relatively more recent haplotypes (Fig. 2) were shared between species.

Finally, our results together with previously reported nuclear variation (Albarrán-Lara et al. 2019) suggest that *Q. magnoliifolia* and *Q. resinosa* do not represent isolated gene pools. This contrasts with other *Quercus* species from other sections inhabiting Mexico, in which despite frequent hybridization remain genetically, morphological, and ecologically distinct (e.g., Tovar-Sánchez et al. 2008; Rodríguez-Correa et al. 2017). Notwithstanding, a similar pattern was observed previously between *Q. minima* (Sarg.) Small and *Q. geminata* Small in southeastern United States (Cavender-Bares et al. 2015). Some authors argue that species boundaries are semi-permeable with permeability varying as a function of genome region (Harrison and Larson 2014). Thus, hybridizing taxa often remain distinct for only part of the genome. Barton and Hewitt (1985) suggested that sequences on a chromosome become homogenized over time by gene flow, except in small regions subject to divergent directional selection. Later, Wu (2001) proposed that for recently diverged species few genes contribute to reproductive isolation, whereas gene exchange can occur in other parts of the genome. In this way, chloroplast loci studied here and those previously assessed with nuclear loci, probably exchanged between *Q. magnoliifolia* and *Q. resinosa*, leading to large genetic admixture between them. Thus, it is likely that divergence between these *Quercus* species remains only in loci under natural selection. Scanning a large proportion of the genome to detect genome-wide patterns of divergence during reproductive isolation may improve our understanding about how *Quercus* species evolve in the face of gene flow (Nosil and Feder 2012).

## Conclusions

To study the evolutionary history of *Q. magnoliifolia* and *Q. resinosa*, we assessed the genetic variation of chloroplast molecular markers implementing different approaches. Although we did not recognize a gene pool for each species, we found evidence that suggested an evolutionary history involving colonization by hybridization and long-distance seed dispersal between these two oak species. It is likely that by means of these mechanisms both *Q. magnoliifolia* and *Q. resinosa* show their current population genetic structure and distribution preventing strong signals of genetic divergence.

In the face of such complex phylogeographic pattern, we assume that divergence between species remains mainly on loci under natural selection, providing evidence about the “porous” nature of species boundaries among oaks.

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**Author contribution** AAL, PDA, and KO designed the study and supervised the whole project. AAL and JMPR performed the field and molecular work. AAL, MOZ, CTM, JMPR, IMD-C, HRC, and KO analyzed the data and interpret the results. The manuscript was written and revised by all authors.

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## Declarations

**Conflict of interest** The authors declare no competing interests.

**Data Archiving Statement** The datasets generated and analyzed during the current study will be public available in the open access repository of Zenodo [<https://doi.org/10.5281/zenodo.7641524>, <https://doi.org/10.5281/zenodo.7641499>].

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