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Review

Quercus Conservation Genetics and Genomics: Past, Present, and Future

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Abstract: *Quercus* species (oaks) have been an integral part of the landscape in the northern hemisphere for millions of years. Their ability to adapt and spread across different environments and their contributions to many ecosystem services is well documented. Human activity has placed many oak species in peril by eliminating or adversely modifying habitats through exploitative land usage and by practices that have exacerbated climate change. The goal of this review is to compile a list of oak species of conservation concern, evaluate the genetic data that is available for these species, and to highlight the gaps that exist. We compiled a list of 124 Oaks of Concern based on the Red List of Oaks 2020 and the Conservation Gap Analysis for Native U.S. Oaks and their evaluations of each species. Of these, 57% have been the subject of some genetic analysis, but for most threatened species (72%), the only genetic analysis was done as part of a phylogenetic study. While nearly half (49%) of published genetic studies involved population genetic analysis, only 16 species of concern (13%) have been the subject of these studies. This is a critical gap considering that analysis of intraspecific genetic variability and genetic structure are essential for designing conservation management strategies. We review the published population genetic studies to highlight their application to conservation. Finally, we discuss future directions in *Quercus* conservation genetics and genomics.

Keywords: conservation genetics; conservation genomics; *Quercus*; Oaks of Concern; endangered oaks

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1. Introduction

Oaks have evolved and adapted over the past 56 million years [1]. Their success has been attributed to high genetic diversity, rapid migration and adaptability, and their propensity for hybridization and introgression [2]. While the ecosystem services oaks provide support a multitude of species, humans in particular have interacted and benefited directly from oaks over many millennia. Acorns of *Quercus ithaburensis* and *Q. caliprinos*, identified by charcoal analysis, have been associated with early humans from 65,000–48,000 years ago and were likely included in their diet [3]. Oak wood, bark, leaves, and roots, as well as acorns, are part of traditional medicine in many parts of the world, and continue to be used as medicinal remedies [4–7]. Oaks figure in human folklore and culture [8] and have been perceived as sacred in numerous human societies [9]. Because of their abundance and high biomass they sequester carbon and so contribute to climate regulation [10]. Genomic studies are now illuminating the genetic basis behind humans' representation of oaks as symbolic of 'longevity, cohesiveness, and robustness' [11]. While this paper focuses on the species that have been adversely impacted by humans, the long relationship between humans and oaks has also had a positive effect on many species [2]. For example, fire regimes that have been used over human history to control undergrowth and enhance hunting areas have benefited oaks through reduced competition with understory vegetation and more shade-tolerant trees in the open areas maintained by such fires [12–14]. However, we are currently living in a time when many oak species are in danger.

The exact number of species in the genus *Quercus* is still open to clarification, as new species continue to be discovered in oak hot-spots such as Mexico/Central America and

China/Southeast Asia. Recent estimates are that approximately 430–435 differentiated species exist [2,15,16]. Oaks occur across the Northern Hemisphere from the equator to boreal regions and thrive in elevations from sea level to 4000 m on various soil types from alkaline to acidic. Species richness is especially high in North America and Asia, where oaks have adapted (and speciated) in response to varying ecological niches [2]. Some oaks, such as *Q. hinckleyi*, are as small as one meter at maturity and grow as clumps of long-lived clones. More familiar to most are large trees that dominate the landscape and live for hundreds of years, such as *Quercus macrocarpa*, *Q. petraea* and *Q. robur*. They can also be extremely rare and critically threatened (*Q. hinckleyi* [17,18]) or abundant with wide-spread distributions, like the other species just mentioned.

Effective conservation management benefits from genetic data to clarify species' identity and adaptations and to provide information on intraspecific diversity and population structure. Unfortunately, missing or incomplete genetic information limits comprehensive planning for many threatened oak species. A survey of conservation actions conducted as part of the Conservation Gap Analysis of Native U.S. Oaks [19] (hereafter Gap Analysis) found that genetic research was one of the least reported efforts, highlighting the need for genetic investigations for many oak species. Specific genetic gaps are seen for phylogenetics/taxonomy to clarify evolutionary significant units (ESU) and for population genetics to address diversity, gene flow, and hybridization/introgression. These findings motivated our effort here to evaluate the state of *Quercus* conservation genetics.

2. Developing a List of Oaks of Concern

For our review of the status of oak conservation genetics, we combine findings from The Red List of Oaks 2020 [16] (hereafter Red List) and the Gap Analysis to create a list of global species of concern. The Red List assessed 430 *Quercus* species. Species were evaluated based on current and projected population sizes, geographic range/endemism, population decline, and fragmentation. While the majority of oak species are not threatened, the study found that 41% are 'species of conservation concern' with 112 falling into the IUCN Threatened Categories: Critically Endangered (CR), Endangered (EN), or Vulnerable (VU) (see p. 9 and Appendix A in [16]) for descriptions and criteria of the IUCN categories. We use this list of species in our review. An additional 105 species are categorized as Near Threatened (NT) or Data Deficient (DD). If DD species are included in the analysis' calculations, the report estimates that globally 31% of oaks are in danger of extinction [16]; we did not include these additional 105 species in our literature review since few have been the subject of genetic studies.

The Red List identifies the U.S. as one of the areas with the highest number of threatened oaks, so we incorporated additional information from a detailed report on U.S. oaks, the Gap Analysis [19]. The Gap Analysis found that 31% of native U.S. oak species are 'species of concern' based on an assessment of data reported in The Red List of Oaks 2017 [20], the NatureServe conservation rankings [21], the USDA Forest Service risk assessment of vulnerability to climate change [22], and a survey of ex situ collections conducted as part of the gap report itself. Evaluation focused on risks of extinction, susceptibility to the effects of climate change, and presence of species in ex situ collections and considered both current and near-term threats. In addition to the criteria used in the Red List, the Gap Analysis looked at regeneration/recruitment and genetic variation/species integrity. Based on these criteria, it scored each species' level of vulnerability. Results show 28 U.S. oak species are 'species of concern', including 12 species not included in the Red List that we added to our list of 'Oaks of Concern'. Our combined list of threatened species is shown in Table 1 and contains 124 species.

Table 1. Species of Concern and genetic research focus.

Species of Concern [Cited Research]	**Conservation Classification**	**Country Distribution**	**Number of Ex Situ Collections**	***Quercus* Section**	**Citation Focus**
Quercus acerifolia [1]	EN	US	44	*Lobatae*	PT
Quercus acutifolia [1,23]	VU	BZ, GT, HN, MX	34	*Lobatae*	PT
Quercus afares [1,24–27]	VU	DZ, TN	18	*Cerris*	PT, PG
Quercus ajoensis [1,28]	VU	MX, US	5	*Quercus*	PT
Quercus albicaulis	CR	CN	0	*Cyclobalanopsis*	
Quercus arbutifolia [1,29,30]	EN	CN, VN	0	*Cyclobalanopsis*	PT, PG
Quercus argyrotricha	CR	N	4	*Cyclobalanopsis*	
Quercus arkansana [1]	VU	US	48	*Lobatae*	PT
Quercus asymmetrica	EN	CN, VN	0	*Cyclobalanopsis*	
Quercus austrina [1,28]	VU	US	25	*Quercus*	PT
Quercus austrocochinchinensis [1,30–34]	VU	CN, LA, TH, VN	0	*Cyclobalanopsis*	PT, PG, G
Quercus bambusifolia [35,36]	EN	CN, HK, VN	4	*Cyclobalanopsis*	PG
Quercus baniensis [33,34]	CR	VN	0	*Cyclobalanopsis*	PT
Quercus baolamensis [34]	CR	VN	0	*Cyclobalanopsis*	PT
Quercus bawanglingensis [37]	CR	CN	0	*Ilex*	PT, G
Quercus bidoupensis [34]	CR	VN	0	*Cyclobalanopsis*	PT
Quercus blaoensis [33,34]	CR	VN	0	*Cyclobalanopsis*	PT
Quercus boyntonii [1,28,38,39]	CR	US	21	*Quercus*	PT, PG, CON
Quercus braianensis [33,34]	VU	LA, VN	0	*Cyclobalanopsis*	PT
Quercus brandegeei [28,40]	EN	MX	9	*Virentes*	PT
Quercus cambodiensis [34]	CR	KH	0	*Cyclobalanopsis*	PT
Quercus camusiae [33,34]	CR	VN	0	*Cyclobalanopsis*	PT
Quercus carmenensis	EN	MX, US	3	*Quercus*	
Quercus cedrosensis [25,41]	VU	MX, US	2	*Protobalanus*	PT
Quercus chapmanii [1,28]	* LC	US	8	*Quercus*	PT
Quercus chrysotricha	EN	MY	0	*Cyclobalanopsis*	
Quercus costaricensis [1]	VU	CR, HN, PA	2	*Lobatae*	PT
Quercus cualensis	EN	MX	1	*Lobatae*	
Quercus cupreata	EN	MX	4	*Lobatae*	
Quercus daimingshanensis (*damingshanensis*) [1,30]	EN	CN	0	*Cyclobalanopsis*	PT
Quercus dankiaensis	CR	VN	0	*Cyclobalanopsis*	
Quercus delgadoana [1]	EN	MX	9	*Lobatae*	PT
Quercus delicatula	EN	CN	0	*Cyclobalanopsis*	
Quercus devia	EN	MX	0	*Lobatae*	
Quercus dilacerata [34]	CR	VN	0	*Cyclobalanopsis*	PT
Quercus dinghuensis	CR	CN	1	*Cyclobalanopsis*	
Quercus disciformis [33]	EN	CN	2	*Cyclobalanopsis*	PT
Quercus diversifolia [1]	EN	MX	3	*Quercus*	PT
Quercus donnaiensis [33,34]	CR	VN	0	*Cyclobalanopsis*	PT
Quercus dumosa [1,28,42–46]	EN	MX, US	30	*Quercus*	PT, PG
Quercus edithiae [33,47,48]	EN	CN, HK, VN	0	*Cyclobalanopsis*	PT
Quercus engelmannii [1,28,41,44,49–51]	EN	MX, US	36	*Quercus*	PT, PG
Quercus fimbriata	CR	CN	0	*Ilex*	

Table 1. *Cont.*

Species of Concern [Cited Research]	Conservation Classification	Country Distribution	Number of Ex Situ Collections	*Quercus* Section	Citation Focus
Quercus flocculenta	EN	MX	3	*Lobatae*	
Quercus furfuracea	VU	MX	5	*Lobatae*	
Quercus gaharuensis	VU	ID, MY	0	*Cyclobalanopsis*	
Quercus galeanensis	EN	MX	8	*Lobatae*	
Quercus georgiana [1,39,52]	EN	US	55	*Lobatae*	PT, PG
Quercus graciliformis	CR	MX, US	21	*Lobatae*	
Quercus gulielmi-treleasei [23]	VU	CR, PA	2	*Lobatae*	PT
Quercus havardii [1,28,53]	EN	US	19	*Quercus*	PT, PG
Quercus hinckleyi [1,18,54,55]	CR	MX, US	12	*Quercus*	PT, PG, CON
Quercus hintonii [23]	EN	MX	3	*Lobatae*	PT
Quercus hintoniorum [23]	VU	MX	6	*Lobatae*	PT
Quercus hirtifolia	EN	MX	7	*Lobatae*	
Quercus honbaensis [34]	CR	VN	0	*Cyclobalanopsis*	PT
Quercus hondae [56]	VU	JP	2	*Cyclobalanopsis*	PT
Quercus inopina [1]	* LC	US	5	*Lobatae*	PT
Quercus insignis [1,28,57]	EN	BZ, CR, GT, HN, MX, NI, PA	27	*Quercus*	PT
Quercus kerangasensis	VU	BN, ID, MY	0	*Cyclobalanopsis*	
Quercus kinabaluensis	EN	MY	0	*Cyclobalanopsis*	
Quercus kingiana [58]	EN	CN, LA, MM, TH	0	*Ilex*	PT
Quercus kiukiangensis [30]	EN	CN	4	*Cyclobalanopsis*	PT
Quercus kotschyana [1,59]	EN	LB	0	*Quercus*	PT
Quercus kouangsiensis [1]	EN	CN	0	*Cyclobalanopsis*	PT
Quercus laceyi [1,28]	* LC	MX, US	16	*Quercus*	PT
Quercus lenticellata	EN	TH	0	*Cyclobalanopsis*	
Quercus liboensis	EN	CN	2	*Cyclobalanopsis*	
Quercus litseoides	VU	CN, HK	1	*Cyclobalanopsis*	
Quercus lobata [1,28,41,44,49,60–86]	* NT	US	41	*Quercus*	PT, PG, G, CON, GENOM
Quercus lobbii	EN	BD, CN, IN	0	*Cyclobalanopsis*	
Quercus lodicosa	EN	CN, IN, MM	0	*Ilex*	
Quercus look [1,59]	EN	LB, SY	16	*Cerris*	PT
Quercus lungmaiensis	CR	CN	1	*Cyclobalanopsis*	
Quercus macdougallii	EN	MX	0	*Quercus*	
Quercus marlipoensis	CR	CN	1	*Ilex*	
Quercus meavei	VU	MX	1	*Lobatae*	
Quercus merrillii	VU	ID, MY, PH	0	*Cyclobalanopsis*	
Quercus miquihuanensis [23]	EN	MX	12	*Lobatae*	PT
Quercus monnula	CR	CN	0	*Quercus*	
Quercus motuoensis	CR	CN	0	*Cyclobalanopsis*	
Quercus mulleri [87]	CR	MX	0	*Lobatae*	PG
Quercus nivea	EN	MY	0	*Cyclobalanopsis*	
Quercus nixoniana	EN	MX	0	*Lobatae*	
Quercus obconicus	EN	CN	0	*Cyclobalanopsis*	

Table 1. *Cont.*

Species of Concern [Cited Research]	**Conservation Classification**	**Country Distribution**	**Number of Ex Situ Collections**	***Quercus* Section**	**Citation Focus**
Quercus oglethorpensis [1,28,39]	EN	US	47	*Quercus*	PT, PG
Quercus pacifica [1,28,43–46]	EN	US	22	*Quercus*	PT, PG
Quercus palmeri [1,28,41]	* NT	MX, US	18	*Protobalanus*	PT
Quercus parvula [1,88–90]	* NT	US	15	*Lobatae*	PT, PG
Quercus percoriacea	EN	MY	0	*Cyclobalanopsis*	
Quercus petelotii	EN	VN	0	*Cyclobalanopsis*	
Quercus phanera [1]	EN	CN	1	*Cyclobalanopsis*	PT
Quercus pinbianensis	CR	CN	0	*Cyclobalanopsis*	
Quercus pontica [1,25,28,61]	EN	GE, TR	91	*Ponticae*	PT
Quercus pseudosetulosa [58]	CR	CN	0	*Ilex*	PT
Quercus pseudoverticillata	CR	MY	0	*Cyclobalanopsis*	
Quercus pumila [23]	* LC	US	15	*Lobatae*	PT
Quercus quangtriensis [33]	VU	CN, LA, MM, TH, VN	0	*Cyclobalanopsis*	PT
Quercus radiata [1,91]	EN	MX	0	*Lobatae*	PT
Quercus ramsbottomii	EN	MM, TH	0	*Cyclobalanopsis*	
Quercus robusta	* DD	US	2	*Lobatae*	
Quercus rubramenta	VU	MX	0	*Lobatae*	
Quercus runcinatifolia	EN	MX	1	*Lobatae*	
Quercus rupestris	EN	VN	0	*Cyclobalanopsis*	
Quercus sadleriana [1,28,61]	* NT	US	14	*Ponticae*	PT
Quercus sagrana (sagraeana) [28]	EN	CU	1	*Virentes*	PT
Quercus semiserratoides	CR	CN	2	*Cyclobalanopsis*	
Quercus sichourensis [30,48,92]	CR	CN	1	*Cyclobalanopsis*	PT, G
Quercus similis [1,28]	* LC	US	2	*Quercus*	PT
Quercus steenisii	EN	ID	0	*Cyclobalanopsis*	
Quercus tardifolia	* DD	MX, US	0	*Lobatae*	
Quercus thomsoniana	CR	BD, BT, IN	0	*Cyclobalanopsis*	
Quercus tiaoloshanica [93]	EN	CN	0	*Cyclobalanopsis*	CON
Quercus tomentella [1,28,41,61,94–97]	EN	MX, US	33	*Protobalanus*	PT, PG
Quercus tomentosinervis	CR	CN	0	*Cyclobalanopsis*	
Quercus toumeyi [1,28]	* DD	MX, US	3	*Quercus*	PT
Quercus treubiana	VU	ID, MY	0	*Cyclobalanopsis*	
Quercus trungkhanhensis [33]	CR	VN	0	*Ilex*	PT
Quercus tuitensis	VU	MX	0	*Lobatae*	
Quercus tungmaiensis [58,98]	EN	CN, IN	3	*Ilex*	PT, G
Quercus utilis [1,48,58]	EN	CN	2	*Ilex*	PT
Quercus vicentensis	VU	MX, SV	1	*Quercus*	
Quercus xanthotricha	EN	CN, LA	0	*Cyclobalanopsis*	
Quercus xuanlienensis [33]	CR	VN	0	*Cyclobalanopsis*	PT

Conservation classification: CR—Critically Endangered, EN—Endangered, VU—Vulnerable, * NT—Near Threatened, * LC—Least Concern, * DD—Data Deficient (* Gap Analysis). (see [16] for descriptions and criteria of IUCN categories). Country distribution: BD—Bangladesh, BT—Bhutan, BZ—Belize, CN—China, CR—Costa Rica, CU—Cuba, DZ—Algeria, GE—Georgia, GT—Guatemala, HK—Hong Kong, HN—Honduras, ID—Indonesia, IN—India, JP—Japan, KH—Cambodia, LA—Lao People's Dem. Republic, LB—Lebanon, MM—Myanmar, MX—Mexico, MY—Malaysia, NI—Nicaragua, PA—Panama, PH—Philippines, SV—El Salvador, SY—Syrian Arab Republic, TH—Thailand, TN—Tunisia, TR—Turkey, US—United States, VN—Viet Nam. Citation focus: PT—phylogeny/taxonomy, PG—population genetics, CON—conservation, G—genome assembly, GENOM—genomic methods.

The countries with the highest numbers of threatened oak species are China with 36, Mexico with 32, and the United States with 28. Not surprisingly these are the three countries with the highest oak species richness. Other regions of concern are Viet Nam with 20 threatened oak species and Malaysia with nine. Chinese, Mexican, and Vietnamese oaks are mainly threatened by loss of habitat due to logging, agriculture, and urbanization, while in the United States, climate change and invasive species are the major concerns [16].

3. Genetic Research on Oaks of Concern

We used citations in the Red List, the Gap Analysis, Google Scholar Searches (filtering on species name and the word 'genetics' for a date range of 2000 to present), and citations contained within these studies, to identify genetic studies that have been conducted on the species on our list, with the caveat that the results represent a 'point in time' and that new research is constantly being added, may not yet be published, or was not found by this search protocol. Citations to genetic studies are included in Table 1.

We found a total of 78 references that included analysis of one or more species on the list. We classified each of the cited papers by the main focus of the research: phylogeny/taxonomy (PT), population genetics (PG), conservation (CON), genome assembly (G), and genomic methods (GENOM). Of the 124 species, 71 (57%) had one or more published research papers involving a genetic study. *Quercus* sections with the highest numbers of listed species are *Cyclobalanopsis*, *Lobatae*, and *Quercus*. Of the Oaks of Concern in each of these sections, 24 of 55 (44%) of *Cyclobalanopsis*, 15 of 30 (50%) of *Lobatae*, and 16 of 21 (76%) of *Quercus* taxa have cited genetic research.

Of the published genetic papers, 24 of 78 (31%) are phylogeny/taxonomy related (PT) with a number dealing with macroevolution of the *Quercus* genus (such as [1,28]), while others focus on phylogenies within *Quercus* sections (such as [23,40,41,61]), and still others look at regional phylogenies (such as [30,33,34,46–48,56,58,59,88,91]). It is notable that for 51 of the 71 (72%) species with cited works, the *only* genetic research was phylogeny/taxonomy related (see Table 1). The rise of genomic analysis in phylogenetics over the last few years (phylogenomics [99]) has provided better tools for clarifying enigmatic relationships within *Quercus*. In particular, with the application of RAD-seq methods, it has been possible to use tens of thousands of genetic markers to get good phylogenetic signal and provide insights into the evolutionary diversification of the *Quercus* genus [1,2]. Phylogenetic research is important in delineating conservation units (ESUs), a critical component in establishing a starting point for conservation planning. Phylogenetics/phylogenomics has been used to answer many questions about Oaks of Concern, such as confirming species' identity and addressing introgression. Additionally, many of these papers include other pertinent data relating to conservation, for example, to hybridization and biogeography. While elucidating the evolutionary history of oaks is certainly an important endeavor, direct implications of phylogenetic reconstruction for conservation management are limited. Most phylogenetic studies include only one or a very few representatives of each species, so provide little insight into many issues most pertinent to conservation management.

4. Population Genetics for Oaks of Concern

We found that a critical area of conservation research, population genetics studies (PG), are missing for the vast majority of Oaks of Concern. Population genetics studies assess intraspecific genetic diversity and population structure and form the foundation of the field of conservation genetics. While we found 39 of 78 (50%) papers focused on population genetic (PG) questions, only 16 different species were investigated in these papers (Table 2), leaving 87% of the species with no information on intraspecific diversity. Five papers examined specific conservation (CON) questions, such as ex situ conservation [100], habitat destruction [93], and genetics as input to conservation planning in response to climate change [73,76,85]. Five dealt with genomic methods (GENOM) such as epigenetics [79,80,86], ecological niche modeling [84], and landscape genomics [81].

Table 2. Population genetics studies involving Oaks of Concern.

Species of Concern	Citation	Focus of Study	Method Used
Q. afares	Mir et al. [24]	hybridization	nuclear allozymes, chloroplast markers
Q. arbutifolia	Xu et al. [29]	genetic diversity	chloroplast (cpDNA), nuclear (ITS) DNA sequences
Q. austrocochinchinensis	An et al. [31]	introgression	AFLP markers, nu-SSRs
Q. bambusifolia	Zeng et al. [35,36]	inbreeding, genetic diversity, population structure	nu-SSRs
Q. boyntonii	Spence et al. [39]	fragmentation, ex situ collections, inbreeding, heterozygosity	nu-SSRs and EST-SRRs
Q. dumosa	Backs et al. [43]	introgression	nu-SSR
	Burge et al. [42]	gene flow/environmental gradients	RAD-seq
	Ortego et al. [45]	genetic differentiation, population structure	nu-SSR
Q. engelmannii	Oney-Birol et al. [51]	hybridization/introgression	RNA-seq
	Ortego et al. [50]	ecological niche modeling	nu-SSR
	Riordan et al. [49]	responses to geography and climate	nu-SSR
Q. georgiana	Kadav [52]	genetic diversity, population structure	EST-SSRs
	Spence et al. [39]	fragmentation, ex situ collections, inbreeding, heterozygosity	nu-SSRs and EST-SRRs
Q. havardii	Zumwalde et al. [53]	genetic diversity, population structure	nu-SSRs
Q. hinckleyi	Backs et al. [18]	genetic diversity, population structure	nu-SSRs
	Backs et al. [55]	hybridization	nu-SSRs
	Backs et al. [54]	genetic diversity, in situ/ex situ	nu-SSRs
Q. lobata	Abraham et al. [68]	hybridization	nu-SSRs
	Ashley et al. [65]	landscape genetics, population structure	nu-SSRs
	Browne at al. [66]	adaptational lag/temperature	genome-wide sequencing
	Craft et al. [69]	hybridization	nu-SSRs
	Dutech et al. [67]	gene flow, genetic diversity, population structure	nu-SSRs
	Gharehaghaji et al. [70]	gene flow	nu-SSRs
	Grivet et al. [73]	gene flow	nu-SSRs
	Gugger et al. [60]	sequence variation/climate gradients	whole-transcriptome sequencing (mRNA-Seq)
	Mead et al. [64]	ecophysiological traits/gene expression	RNA-seq
	Pluess et al. [74]	gene flow	nu-SSRs
	Scofield et al. [75]	gene flow	nu-SSRs
	Sork et al. [77]	gene flow, pollen movement	allozymes, nu-SSRs
	Sork et al. [78]	gene flow, population structure	nu-SSRs
	Sork et al. [63]	gene flow, environmental gradients	chloroplast and nuclear microsatellite
	Sork et al. [46]	hybridization, introgression	nu-SSRs, RADseq-based sequences

Table 2. *Cont.*

Species of Concern	Citation	Focus of Study	Method Used
Q. mulleri	Pingarroni et al. [87]	genetic diversity	nu-SSRs
Q. oglethorpensis	Spence et al. [39]	fragmentation, ex situ collections, inbreeding, heterozygosity	nu-SSRs and EST-SRRs
Q. pacifica	Backs et al. [43]	gene flow, population structure, introgression	nu-SSRs
	Ortego et al. [45]	evolutionary history, demographics	nu-SSRs, cpSSRs
Q. parvula	Dodd et al. [90]	species differentiation	AFLP genetic markers
	Kashani et al. [89]	genetic differentiation, introgression	AFLP genetic markers
Q. tomentella	Ashley et al. [94,95]	genetic variation, structure	nu-SSRs
	Ashley et al. [95]	landscape and conservation genetics	nu-SSRs
	Ashley et al. [96]	genetic variation, population structure	nu-SSRs

While it is discouraging that only 16 Oaks of Concern have population genetics (PG) related citations (Table 2), these studies provide important examples of the work that has been done, as well as highlighting the somewhat limited breadth of the population genetics research for endangered oaks to date. Of those species that have been studied using population genetic approaches, twelve are in Mexico or the U.S., three in China or Southeast Asia, and one in North Africa. China has the largest number of threatened species on our Oaks of Concern list (36), but only a handful of species have been studied (Table 1) and only three have been the subject of population genetic research (Table 2). These three species are members of the *Cyclobalanopsis* section occurring in Southeast Asia. *Quercus arbutifolia* is an Endangered species found in the mountain cloud forests of southern China and Viet Nam. Xu et al. [29], used chloroplast (cpDNA) and nuclear (ITS) DNA sequences to examine *Q. arbutifolia*'s genetic diversity, phylogeographic structure, and evolutionary history. The authors acknowledge the highly threatened status of this species, but highlight how their findings on genetic diversity, which they found to be unexpectedly high, and population dynamics are critical to developing effective conservation plans. *Quercus austrocochinchinensis* is a Vulnerable species found in China, The Lao People's Democratic Republic, Thailand, and Viet Nam. It is referenced in six genetic research papers, but only one population genetics paper. Possible hybridization between *Q. austrocochinchinensis* and a sympatric species, *Q. kerrii,* was investigated using AFLP markers and nu-SSRs, providing information for long-term conservation and restoration of the tropical ravine rainforest environment in the Indo-China area [31]. *Quercus bambusifolia* is an Endangered species found in China, Hong Kong, and Viet Nam. Using population genetics analyses of nu-SSR data, Zeng et al. [35,36] examined inbreeding, genetic diversity, and population structure, and provide data applicable to restoration of severely fragmented tropical landscapes.

The only North African species on our list of Oaks of Concern is *Q. afares*, the African Oak, a Vulnerable species with a limited distribution in the coastal mountains of Algeria and Tunisia. With genetic analysis using nuclear allozymes and chloroplast markers, Mir et al. [24] confirmed its identity as a stable hybrid of two sympatric but phylogenetically distant species, *Q. suber* and *Q. canariensis*. *Q. afarensis* combines traits of these two species, suggesting one or more hybridization events.

Quercus mulleri (section *Lobatae*) is a microendemic oak found in the Sierra Sur de Oaxaca of Mexico. In the first report on this species since it was identified 60 years ago, a population genetics study (PG) examined genetic diversity and population structure using nu-SSRs with the goal of providing information to enhance conservation strategies [87].

The western United Sates, particularly California, has been the focus of numerous studies of oak population genetics, including several studies of Oaks of Concern. *Quercus dumosa* is an endangered oak (section *Quercus*) found in Baja California, Mexico, and

California. Three population genetics studies (PG) examined genetic exchange between this species and its close relatives. One study focused on the influence of environmental gradients using RAD-seq [42], another examined introgression and species' integrity related to neighboring species using nu-SSR [43], and a third examined genetic differentiation and population structure to examine evolutionary history of sympatric species using nu-SSR [45]. *Quercus engelmanii* is also an endangered species distributed in Baja California, Mexico and southern California, US. Population genetic studies have examined responses to geography and climate [49], ecological niche modeling [50], and hybridization/introgression using RNA-seq [51].

Valley oak, *Q. lobata*, a California endemic listed as Near Threatened, is by far the most thoroughly investigated species on our list. Seven papers report on phylogeny/taxonomy [1,28,44,61,62,71,83], one paper reports on genome assembly [62], and five (including one in this special edition [86]) investigate new genomic methods 79–81,84,86]. A number of population genetic papers have also focused on *Q. lobata*. Several studies have investigated gene flow, hybridization, and population structure [46,65,67–70,72,74,75,77,78]. One study used whole-transcriptome sequencing (mRNA-Seq) to investigate sequence variation with climate gradients [60] and another looked at geographic patterns of genetic variation in relation to climate change using chloroplast and nu-SSRs [63]. Drought response was measured using ecophysiological traits and gene expression (RNA-seq) [64]. A common garden experiment and genome-wide sequencing were used to examine adaptational lag to temperature, with potential application to identifying genotypes preadapted to future climate change conditions [66]. Valley oak provides a model of how different genetic approaches can be used to investigate the ecological and evolutionary genetics of a threatened tree species, predict future trends, and assist in developing strategies to manage the risks a species is facing.

Two species of oaks on our list are endemic to the California Channel Islands, *Q. pacifica* and *Q. tomentella*. *Quercus pacifica* is an Endangered species, and researchers have investigated gene flow, population structure, and relationships to two mainland oaks using nu-SSRs [43] and evolutionary history and demographics using nu-SSRs and cpSSRs [45]. *Quercus tomentella*, also listed as Endangered, is a member of the small section *Protobalanus*. Population genetics papers cover genetic variation and population structure [94], landscape and conservation genetics [95] and genetic variation and population structure [96] all using nu-SSRs. Another species, *Quercus parvula* is found on Santa Cruz Island and in the California Coast Ranges and is classified as Near Threatened. Two population genetics papers report on genetic differentiation and introgression [89] and species differentiation [90], both using AFLP genetic markers.

Quercus hinckleyi is a Critically Endangered species with an extremely limited distribution in Texas, USA. Population genetic studies have examined clonality, diversity and population structure [18], hybridization [55], and genetic diversity assessment of in situ and ex situ populations [54]. Important for conservation, Backs et al. [18] reported a high level of clonality at some sites, with the number of genetically unique individuals being substantially lower than previously assumed from population counts.

The other Oaks of Concern that have had population genetic studies are primarily in the Eastern United States. One paper in this Special Issue examines genetic diversity and population structure in the Endangered *Q. havardii* [53]. Another paper in this Special Issue conducted population assessments of three Oaks of Concern, *Q. georgiana*, *Q. oglethorpensis*, and *Q. boyntonii*, and reports that these species have lower genetic diversity than more abundant oaks [39]. Another paper covers genetic diversity and population structure of *Q. georgiana* using EST-SSRs [52].

One question recently explored for several North America species is how well the genetic diversity of the species is captured in ex situ collections. Oak seeds (acorns) are not candidates for seed banks; they lose viability when desiccated. Desiccation is part of the standard protocol of conventional seed-banking [101–104]. Conservation of living oaks in ex situ collections can be constrained by space limitations, long generation times, and their proclivity to hybridize [54]. A recent paper by Backs et al. [54] reported that ex situ collections of *Q. hinckleyi* were likely sampled from only one of the remaining in situ genetic clusters and missed much of the in situ diversity. The study of *Quercus georgiana*, *Q. oglethorpensis*, and *Q. boyntonii* mentioned above reports that while common alleles are well preserved in ex situ collection, low frequency and rare alleles are not [39].

For many other species on our Oaks of Concern list, there are immediate questions that can be addressed through genetic and/or genomic analysis, such as confirming taxa, identifying clones, examining levels of diversity, and measuring gene flow [105]. *Quercus tardifolia*, is a good example. It is described as Data Deficient, requiring both field research and taxonomic clarification and lacking demographic data and diversity information [19]. Other species of concern are not so lacking in information, but still have genetic gaps in their conservation portfolios. *Quercus robusta* needs research to distinguish spontaneous hybrids from historic hybrids that have evolved into true species [106]. For *Q. acerifolia*, there is a need to identify genetic structure of populations [107] and for *Q. carmenensis* there is a need to verify species integrity and/or levels of introgression [108].

To summarize, our survey of genetic studies shows that while some Oaks of Concern have benefited from population genetic research, most are lacking basic conservation-focused data. This need can be addressed through population genetic analysis looking at species integrity, intraspecific diversity, population structure, gene flow, hybridization levels, and diversity capture in ex situ collections. Only with this information can comprehensive conservation strategies be developed.

5. Future Directions

Some exciting new genetic methods that have application to conservation questions can be characterized as ‘genomic research’. The ability to look across an entire oak genome or use ‘reduced representation’ genome sampling has been made possible in recent years by advances in DNA sequencing as well as through better ‘big data’ manipulation due to increased computing power, storage capabilities, and robust analytic applications. A sampling of genomic research that has been directed toward oak conservation includes phylogenomics [83], epigenetics [80], QTL (quantitative trait loci) [109], and landscape genomics [110]. While phylogenomics provides a broad evolutionary picture of oaks and helps define ESU’s, epigenetics, QTL, and landscape genomics have the potential to investigate the genomic basis of adaptive traits and apply this knowledge to developing conservation strategies for Oaks of Concern. These new genomic research methods will provide information on plant and species adaptive responses, data needed for flexible conservation efforts that may include plant migration and/or reintroduction.

Epigenetics is the study of heritable phenotypic changes in an organism that do not involve alterations in the DNA code itself. It is emerging as an important field of research for understanding plant adaptability and plasticity and for identifying the ‘ecological background’ of individuals [111]. The shortfall in oak-related research in these areas is exemplified by a survey of epigenetic research which found of approximately 20,000 epigenetic studies published in 2019, only 3% of the papers were plant-related, and of those only 5% focused on forest species [112]. Of tree-related papers, only a handful reference *Quercus* species, for example, [80,113,114].

Epigenetic modification can be created by biotic or abiotic environmental stresses, stochastic “epigenetic mutations” [111,115] or natural processes such as hybridization [116]. They can be reset when a stress is relieved or may result in heritable epigenetic marks that can be passed on as ‘molecular memory’ persisting through several subsequent generations and potentially becoming evolutionarily viable [116–118]. Oaks as long lived organisms have the time to enhance their epigenetic responses through a number of stressful events before passing along these responses through their germlines [119]. Some work has been done with oaks and epigenetics [114,120] including a paper in this Special Issue that examines experimental DNA methylation using the Near Threatened *Q. lobata* [86]. This is an area of conservation interest that should be explored both for planning conservation strategies and basic research into underlying adaptive mechanisms.

Current data processing capabilities have also made it possible to search genome-wide for QTL (quantitative trait loci) [109]. QTL mapping seeks to identify the relationship between various genomic locations and a set of quantitative traits, leading to a chromosomal location and ultimately to identification of gene(s) with the final goal of looking at gene expression. Among other things, this will lead to a better understanding of genetic mechanisms of variation and adaptation [121]. Results can then be applied to adjust conservation measures in response to rapid change, for example, by identifying the genetic adaptability potential of individuals to be used in assisted migration or reintroduction [122,123].

Landscape genomics examines the relationship and interaction between adaptive genetic loci on genomes and landscape variations across which natural populations exist [110]. It seeks to identify the aspects of the environment that affect genetic variation and how that variation in turn affects adaptation [124,125]. It is a valuable tool in understanding oaks' responses to environmental stresses and evaluating alleles that occur under certain climate and habitat conditions. These correlations will aid in conservation planning for plant migration or restoration by identifying populations or individuals that are currently responding favorably to conditions that are anticipated in the climatic future [81,126,127].

These emerging genomic tools as well as more traditional population genetic analyses can and should provide vital input to developing effective oak conservation strategies. Our review highlighted important gaps in our knowledge of many species that are or may soon be facing extinction. For geneticists, there is much work and many opportunities to address conservation needs of the Oaks of Concern.

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