# Incorporating Genetic Information into Conservation Planning For California Valley Oak[1]

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## Abstract

Many plant species are of sufficient ecological importance to merit species-specific conservation plans. For species threatened by land use change, protected areas will be a key element of their conservation strategy. It can be particularly challenging to identify which sites to preserve for broadly distributed species such as California valley oak (*Quercus lobata* Née) that possess geographically structured genetic variation. Here, we investigate the use of molecular genetic markers to identify populations of high genetic diversity or high genetic uniqueness for designing a network of protected areas. In an earlier study, we sampled individuals from 32 valley oak populations distributed throughout the species range and determined their genotypes based on chloroplast haplotypes (six primers) and nuclear genetic markers (seven primers). Our findings from that study indicated a north-south gradient in genotypes and significant genetic differences between western and eastern populations. For this paper, we analyzed the data from a reserve design perspective. We conclude that a minimum of six of 32 locations would be needed to represent genetic variation as indicated by chloroplast DNA and at least 10 of 37 locations would be required to represent genetic variation as indicated by allelic variation in nuclear DNA. The analysis suggests that an efficient reserve network for protecting genetic variation in the species can be developed by including sites of high allelic diversity that are also complementary in their allelic composition. Many factors need to be considered in locating reserves, notably site biotic composition and condition, threatening processes, cost and opportunity. Incorporating genetic information enhances the description of site composition, providing a historical evolutionary perspective.

*Keywords*: biodiversity, genetic diversity, conservation plan, *Quercus*, reserve design

## Introduction

Biological diversity is manifested at many spatial scales and at many levels of organization, ranging from landscapes comprised of multiple ecosystems and species populations to genotypes within individual species (Noss 1990). Conservation planning in California and elsewhere has increasingly focused on landscape-scale, multi-species conservation (Groves and others 2002). At the same time, conservation biologists recognize the need to preserve genetic diversity within individual species,

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often by protecting populations in different parts of a species' range (Lomolino 2006). Conservation genetics has tended to focus on threatened or endangered species or species of commercial importance. For example, the Endangered Species Act includes a provision for listing "distinct population segments" of vertebrates, and the National Marine Fisheries Service has adopted the concept of "evolutionarily significant units" (ESUs) in designing conservation strategies for Pacific salmon species (Waples 2006). Additionally, it has provided a good vehicle for the preservation of plant species (Holsinger and Gottlieb 1991). Similarly, we would argue that it is important to consider genetic variation in devising conservation strategies for oak species that define California's threatened foothill oak woodland ecosystems.

In this paper, we focus on the use of genetic data for informing conservation planning for valley oak (*Quercus lobata* Née). Valley oak woodlands have been extensively converted and fragmented by agricultural and urban development (Pavlik and others 1991). Perhaps one-third of Valley oak savanna remains from its pre-European settlement distribution (Davis and others 1998). In the San Joaquin Valley roughly 95% of the riparian valley oak forest and valley oak woodland have been removed (Kelly and others 2005). Moreover, existing populations are experiencing significant loss of recruitment (Bolsinger 1988, Brown and Davis 1991, Tyler and others 2006). Conserving the ecological and evolutionary potential of valley oak will require habitat protection and restoration, attention to connectivity among fragmented sites, and enhancement of demographically viable local populations. An additional component of an effective strategy for valley oak will be a network of protected areas that is designed to conserve genetic diversity.

Several approaches are available for the use of genetics in reserve design. Based on Fisher's (1930) principle that the amount of genetic variation is related to the evolutionary potential of a population, many conservation biologists emphasize the importance of maintaining genetic variation within and among populations (Ledig 1988, Frankham and others 2002). Most conservation strategies have used neutral markers as a surrogate of population evolutionary potential, but some biologists caution that assessment based on neutral genetic markers might overlook more important adaptive genetic variation (Lynch 1996, Reed and Frankham 2001). This concern is valid, and both molecular variation and adaptive traits can be integrated in conservation strategies, each of them providing complementary information (Toro and Caballero 2005). However, several limitations (e.g. cost, use of the appropriate molecular markers, development of statistical tools) hamper the use of adaptive markers in conservation (Luikart and others 2003, Gonzalez-Martinez and others 2006). A phylogeographic approach to reserve network design has been advocated to maximize genetic diversity and to retain populations representing the evolutionary history of the species (Moritz 1994, Avise 2000, Crandall and others 2000). Moritz (1994) argues that ESU's based on the organelle genome, such as mtDNA, would indicate appropriate management units for conservation. Newton *and others* (1999) counter that the ESU approach to tree's populations, using chloroplast markers, should be used with caution because phylogeographic studies may not always be ideal for conservation problems due to interspecific gene exchange in trees. Instead, they recommend that management units (MU's) based on nuclear genetic differences might be more informative. Meanwhile, several authors point out other limitations to the use of the ESU approach (Paetkau 1999, Avise 2000, Crandall and others 2000, Fraser and Bernatchez 2001). In sum, there is not yet consensus on the best way to obtain genetic data and incorporate it into land use planning (Moritz and Faith 1998).

In a separate paper, we applied a geographical genetic approach to valley oak. In that study, we conducted a multivariate analysis based on chloroplast and nuclear microsatellite genotypes to create a canonical trend across the species' range in order to test for geographical pattern of the genetic data (Grivet, Sork and Westfall, in review). Multivariate genotypes provide sensitive measures of genetic differences among populations (Westfall and Conkle 1992, Kremer and Zanetto 1997). The fact that they have been effectively used to identify seed zones in forestry suggests that at least some of those genetic differences are surrogates for adaptive genetic variation. In that paper, we identify geographic genetic trends in both the chloroplast and nuclear markers. Our findings show significant genetic differences on a north/south transect reflecting strong genetic differences across the species range. We also identify areas of sharp genetic gradients that are suggestive of high evolutionary interest and warrant more intensive sampling for future work.

Here, we use the genetic data described above to explore strategies for conserving genetic diversity in valley oak. We apply a "set covering algorithm" to identify the minimum number of locations needed to represent the allelic diversity documented at our sampling sites, as well as to measure how much diversity could be captured at a smaller number of locations by exploiting patterns of allelic richness and complementarity in allelic composition of different sites (Margules and Pressey 2000). We analyze both chloroplast and nuclear microsatellite alleles throughout the species range. By using the chloroplast markers, we incorporate longer-term evolutionary history into our analysis because the chloroplast is maternally inherited (Dumolin and others 1995) and its DNA is very conservative (Wolfe and others 1987). Specifically, we will ask the following questions: (1) How many sites are needed to represent *Quercus lobata* allelic diversity based on (a) chloroplast DNA, (b) nuclear DNA, and (c) both markers combined? (2) How are these sites distributed geographically? (3) How irreplaceable are sites in assembling a representative reserve network for valley oak genetic diversity? (4) Are there efficiencies in targeting certain areas based on patterns of allelic richness and complementarity?

## Methods

The study species, *Quercus lobata* Née, is a California endemic tree species. It mainly occurs in closed riparian forests of the Central Valley and at lower density in woodlands and savannas in low-elevation valleys and foothills of the Sierra Nevada, Coastal Ranges, and Transverse Ranges (Griffin and Critchfield 1972). Because of their extended latitudinal distribution (34-40˚ latitude) and the complex topography of California, *Q. lobata* populations are spread across various climatic and geographic regions. Valley oak is wind-pollinated and essentially 100% outcrossing (Sork and others 2002b). Dispersal agents include acorn woodpeckers, scrub jays, squirrels, and smaller rodents. Our laboratory has been involved in a series of genetic studies investigating contemporary pollen movement through pollen (Smouse and others 2001, Sork and others 2002a, Sork and others 2002b), contemporary acorn movement (Grivet and others 2005) and fine scale genetic structure (Dutech and others 2005). Collectively, these studies of contemporary and recent historical gene flow indicate that the scale of dispersal determining a genetic neighborhood is ca 100-300 m, but these estimates do not preclude occasional long distant pollen or seed dispersal.

The data used for this paper were collected in 2003 and 2004 as part of an ongoing genetic analysis of the biogeographical patterns of California valley oak

(Grivet and others 2006; Grivet, Sork and Westfall, in review). We mainly sampled valley oaks in oak woodlands and savannas in foothill environments around the Central Valley as opposed to oaks in remnant gallery forests of the Central Valley floodplains. We sampled 37 populations with 3-4 individual trees per site for a total of 113 individuals (*fig.* 1, Table 1). The chloroplast (cp) data set includes 32 populations and 97 individuals (Table 1). The methods of DNA extraction as well as PCR conditions are described in Grivet *and others* (2006). These samples were genotyped for six chloroplast microsatellites: ccmp10 was designed from *Nicotiana tabacum* DNA (Weising and Gardner 1999), while μdt1, μdt3, μdt4, μcd4, and μcd5 were designed from *Quercus robur* DNA (Deguilloux and others 2003).

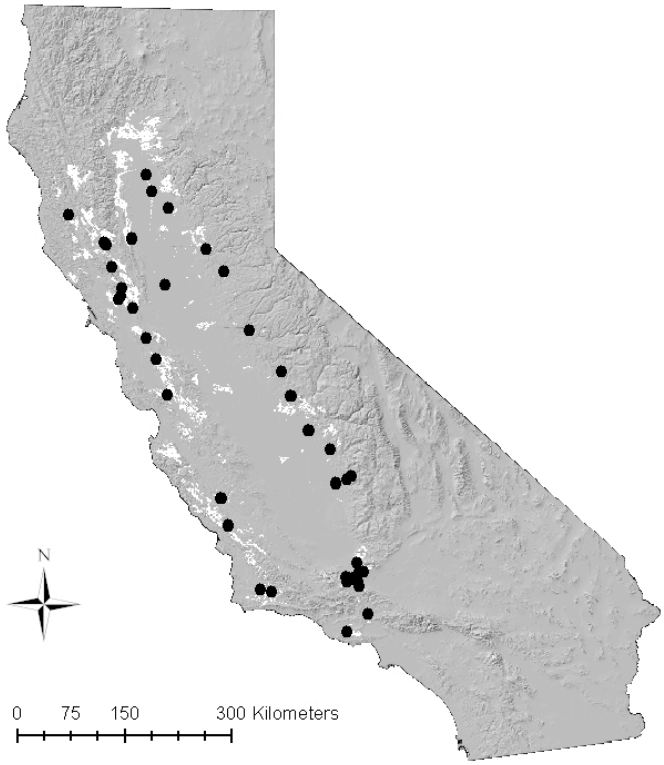


**Figure 1** – Location of 37 sampling sites for California valley oak (*Quercus lobata*). White regions indicate contemporary distribution of valley oak.

The nuclear (n) data set includes 113 individuals from all 37 populations (*fig.* 1; Table 1). The methods for DNA extraction and PCR conditions are described in Grivet and others (in review). We used seven nuclear microsatellites: MSQ4 (Dow and others 1995), QpZAG1/5, QpZAG9, QpZAG36, QpZAG110 (Steinkellner and others 1997), QrZAG11, and QrZAG20 (Kampfer and others 1998). We measured the length of the amplified sequence by running an aliquot of each PCR product on an ABI 3700 capillary sequencer at the UCLA Sequencing & Genotyping Core Facility (http://www.genetics.ucla.edu/sequencing/index.php). To check repeatability, each sample was re-genotyped, after repeating the PCR reactions.

**Table 1**: characterization of valley oak populations (n = 37). Each population is characterized by three individuals, except for populations 37 and 55 that have four individuals. Populations in bold were analyzed for nuclear markers only.

| Population ID | Latitude (decimal degrees) | Longitude | Elevation (meters) |
|---|---|---|---|
| 1 | 34.8156 | -118.8251 | 1201 |
| 2 | 36.0479 | -119.0344 | 138 |
| 3 | 36.0979 | -118.8654 | 216 |
| 4 | 36.1122 | -118.8440 | 320 |
| 5 | 36.4850 | -119.1205 | 153 |
| 8 | 36.7253 | -119.4596 | 118 |
| 9 | 37.1534 | -119.7341 | 359 |
| 10 | 37.4619 | -119.8798 | 656 |
| 11 | 37.9798 | -120.3884 | 537 |
| 13 | 38.7139 | -120.8115 | 539 |
| 14 | 38.9963 | -121.1085 | 453 |
| 16 | 39.4984 | -121.7289 | 44 |
| 17 | 39.7115 | -122.0043 | 43 |
| 25 | 39.3836 | -123.3433 | 450 |
| 26 | 39.0364 | -122.7402 | 427 |
| 27 | 39.1068 | -122.3079 | 127 |
| 28 | 38.7476 | -122.6186 | 332 |
| 29 | 38.4831 | -122.4434 | 58 |
| 30 | 38.2392 | -122.2675 | 19 |
| 31 | 37.8646 | -122.0346 | 77 |
| 32 | 37.6018 | -121.8731 | 84 |
| 33 | 37.1556 | -121.6904 | 295 |
| 34 | 35.8679 | -120.8211 | 129 |
| 35 | 35.5275 | -120.7039 | 221 |
| 36 | 34.7231 | -120.2160 | 239 |
| 37 | 38.5351 | -121.7494 | 18 |
| 40 | 38.3538 | -122.4817 | 73 |
| 42 | 39.9094 | -122.0897 | 58 |
| 45 | 34.8742 | -118.8948 | 988 |
| 46 | 34.4099 | -118.5741 | 359 |
| 47 | 34.1871 | -118.8909 | 202 |
| 48 | 34.6963 | -120.0401 | 337 |
| **49** | 34.7548 | -118.7095 | 1119 |
| **50** | 34.8451 | -118.8302 | 1088 |
| **51** | 34.9173 | -118.7169 | 1536 |
| **52** | 34.9416 | -118.6321 | 1409 |
| **55** | 35.0520 | -118.7340 | 406 |

For the cpDNA data set, we documented 22 total alleles across six microsatellite loci. For the nuclear DNA data set, we catalogued 78 alleles from seven microsatellite loci. For the set covering analysis, each sample site was characterized by the presence or absence of each allele. We used MARXAN 1.8 reserve design software to identify sets of sites that captured the greatest number of alleles for a specified set size, as well as the minimum number of sites needed to satisfy the goal of representing every allele at least once in the final set (Possingham and others 2000). We used the simulated annealing search option, a stochastic search procedure that iteratively creates and compares sets of sites and selects the set that best achieves the specified conservation targets at the lowest cost. Here we set a target of

representing each allele at least once in the final set. All sites were assigned an arbitrary equal cost and all alleles were weighted equally. We assumed that all sites were unprotected unless selected and also ignored site differences in threat from future landscape change. MARXAN 1.8 also allows spatial design parameters (e.g., clustering of sites) but we did not include any spatial weighting. We selected the best set for site networks ranging in size from one site to as many as needed to represent all alleles by varying cost and penalty functions (see Possingham and others 2000). For each network size, we selected the best set from 100 model runs of 1 million iterations each. We first analyzed the chloroplast and nuclear datasets separately and then we examined the pooled data for sites where both cpDNA and nDNA were sampled (n=32).

## Results

Out of 32 sites with cpDNA data, site 31 has the highest allelic richness and represents 12 of 22 alleles. Twenty of 22 alleles can be represented with three of the 32 sites indicating that there are other high diversity sites that are relatively complementary in their composition. To represent all 22 alleles, including three rare alleles that occur at only one site each, requires six sites. One site (27) is irreplaceable and four sites (sites 27, 25, 33, 46) appear in more than half of the best set of solutions (*fig*. 2). These sites are all found in the western range of the species distribution and most of them in the north (*fig*. 2).

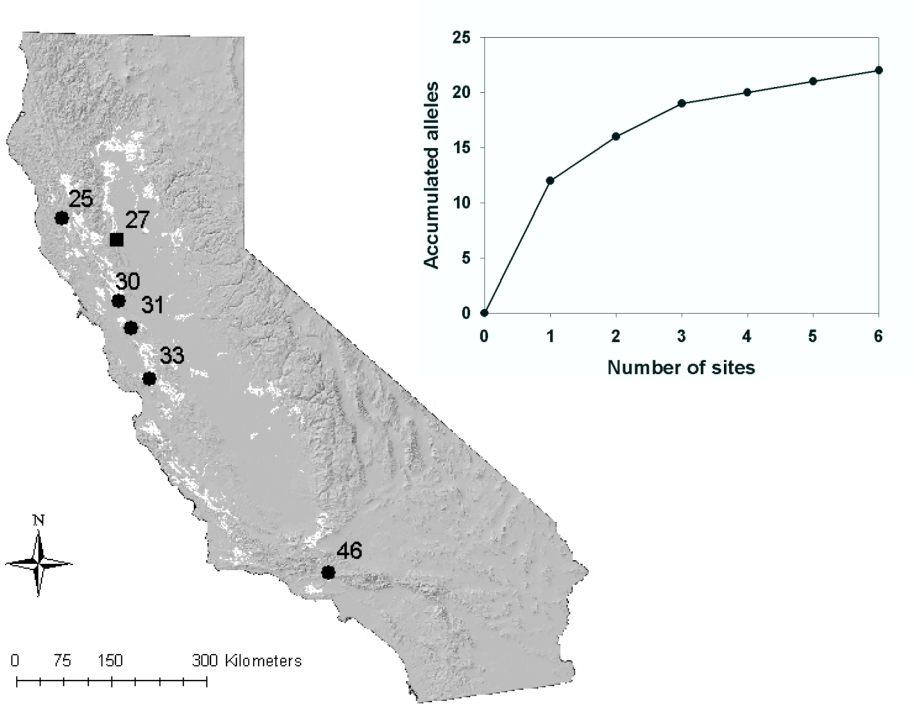


**Figure 2** – Map of set of **six** sites that capture most of the **chloroplast** allelic diversity in *Quercus lobata*. Embedded chart indicates accumulation of chloroplast alleles. Squared symbols represent irreplaceable sites.

For the nDNA alleles, 10 sites are required to obtain complete coverage of 78 alleles (*fig*. 3). The accumulation curve is steep at first, indicating the occurrence of rich and complementary sites. The last additional sites are needed to capture rare alleles. Three sites are perfectly irreplaceable (sites 52, 48, and 47 occur in all 100 solutions) and are widely distributed (*fig*. 3): one in the Tehachapi Range, one in the Santa Inez Valley, and one in the Southwest respectively. In contrast to the cpDNA analysis, the sites needed for full representation of nDNA are distributed throughout the range of valley oak (*fig*. 3), with a slight bias towards sites in the southern part of the range.

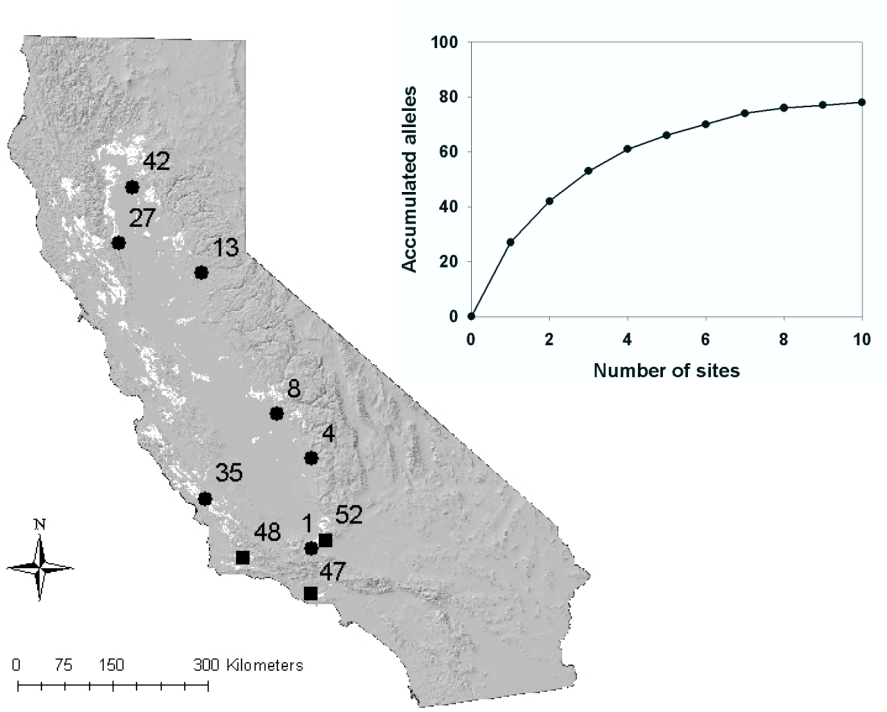


**Figure 3** – Map of set of **ten** sites that capture most of the **nuclear** allelic diversity in *Quercus lobata*. Embedded chart indicates accumulated nuclear alleles.

To evaluate reserve design based on the combined markers, we used 32 populations and 100 total alleles. In this final analysis, 11 sites are required for a complete solution and two sites capture more than 50% of alleles (*fig*. 4). Solutions with at least six sites capture all chloroplast alleles and most nuclear alleles. We found two sites to be perfectly irreplaceable (*fig*. 4): one in the Sierra foothills (13) and one in the San Inez Valley (48). The ten sites occurring most often in the solution to capture the most alleles are distributed through the entire species range (*fig*. 4). Generally the solution for cpDNA can be nested inside the solution for nDNA.

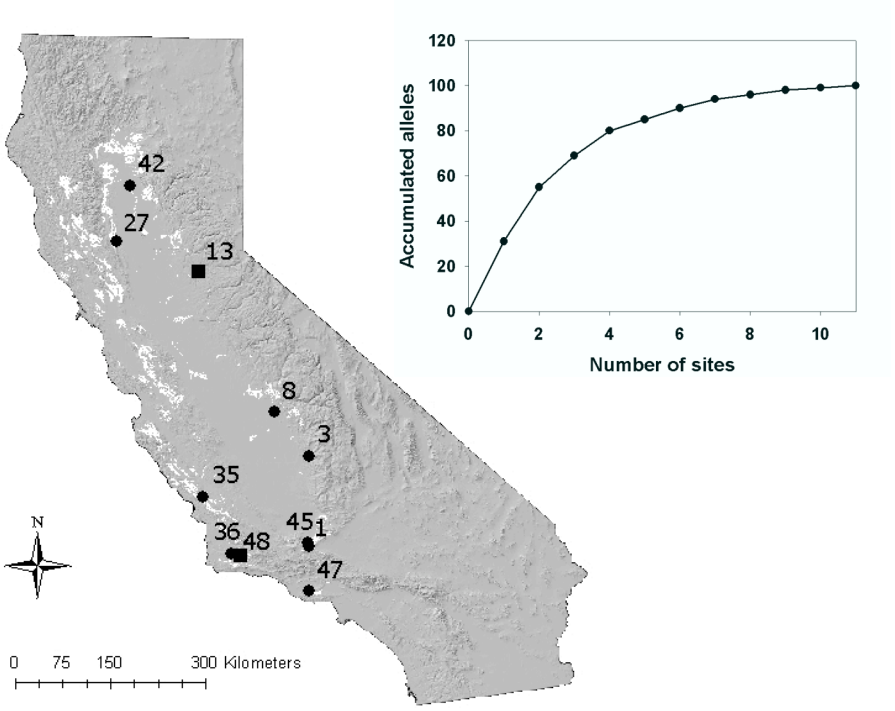


**Figure 4** – Map of set of **eleven** sites that capture most of the allelic diversity when pooling chloroplast and nuclear microsatellite alleles. Embedded chart indicates rate of accumulation.

## Discussion

Many factors must be considered in designing biodiversity reserve networks in the real world, notably social goals, the quality and condition of biological resources, threats, costs and opportunities (Prendergast and others 1999, Davis and others 2006). Representation of existing diversity is a basic goal of systematic conservation planning (Margules and Pressey 2000). Without considering the many other dimensions of reserve network design, we have analyzed valley oak genetic data to explore what a representative network of sites to protect genetic diversity in valley oak might look like in terms of number of sites, geographic distribution and site irreplaceability.

Our results are preliminary because we would like to sample more individuals per site and more sites, especially in under-sampled regions and environments such as the gallery forests of the Sacramento and San Joaquin river basins and in areas identified by Grivet and others (in review) as having sharp genotypic gradients. Moreover, our sample design (i.e. few individuals per population) is appropriate for chloroplast markers because they present low level of genetic diversity within most of the sites, but it would be preferable to include more nuclear genotypes per site for the interpretation of the nuclear results. With these caveats, these findings based on a widely distributed set of populations present a useful analysis of a reserve design network for valley oak. It appears that a representative network will necessarily require distributing sites across the geographic distribution of the species. The number of sites will depend on whether the system is designed to exploit efficiencies

obtained through selection of areas that have high diversity and are also complementary in composition to other sites. The steep accumulation curves for both cpDNA and nDNA argue in favor of such a systematic approach. It also appears that a network design based on cpDNA will differ from that based on nDNA markers, possibly because one set is more based on colonization history and the second is the outcome of multiple evolutionary pressures. This finding supports the recommendation of Fraser and Bernatchez (2001) to utilize more than one kind of genetic information. The combined analysis is a good way of developing a reserve design that integrates the two sets of genetic markers, and, in this study, it seems that we can preserve much of the cpDNA diversity within the sampling scheme for the nDNA markers. The current analysis constitutes the first step in designing a network by incorporating neutral markers from two genomes with different evolutionary histories. Future work should include both more sites, especially in ecosystems that we have not yet sample such as riparian forests, as well as more individuals per site. Moreover, it would be valuable to include genes that are linked to adaptive traits, although such loci are not yet available.

It is reassuring that the interpretation based on a very simple genetic model of simply maximizing genetic variation across the species range captures the areas of genetic interest that we identified in our multivariate genetic approach (Grivet, Sork and Westfall, in review). In that paper based on the same sets of data, we found a latitudinal gradient of chloroplast and nuclear multivariate genotypes, with genetically distinct northern and southern areas. Based on those patterns, we advised that it appears that there would be a need for more reserves in the north and in the south when taking into account both markers, but we did not translate that interpretation into a reserve design. Here, we use a formal reserve design approach with simple assumptions of allelic sampling and arrive at similar conclusions.

To compare the reserve solution observed here with that based on a phylogeographic approach, it will be necessary to use DNA sequence data for multiple genes of valley oak. Such work would be costly but it would yield an effective scrutiny of analyses based on microsatellite data. In addition, it would present a more precise genetic history of valley oak, both for its own sake, and it would reveal whether the set covering solution is capturing evolutionary lineages and history. If so, future studies could deploy a molecular approach to reserve design based on the less expensive allelic approach rather than a sequence approach.

The next step in modeling the analysis of reserve design, once we have more data, would be to incorporate other factors that influence decision-making around site selection (Davis and others 2006). Before setting conservation priorities simply based on the biological analysis, it would be practical to consider the value of a site based on resource quality, threats to resource quality, and costs. For example, threats to resource quality are of major concern in California. An analysis of site vulnerability to land conversion indicates that almost the entire distribution of valley oak is in areas of high vulnerability to land conversion (Davis and others 1998). Future work would yield much more practical results if it integrated both biological and socioeconomic considerations. Our preliminary analysis indicates some flexibility in site location and California has enough extant populations that reserve design could take into account these other factors. However, the choice of sites will decline with time and critical areas from a genetic standpoint could be lost as well.

Finally, we point out that a robust reserve design will need to account for other factors associated with site quality such as proximity to other populations outside the "reserve." Lack of connectivity and/or small population size could result in loss of genetic diversity within the reserve. Ongoing studies in our laboratory are attempting to understand gene flow within and among fragments that could help assess resource quality of a habitat based on this process.

Valley oak is a significant element of California's biodiversity that is threatened by landscape change and population attrition. Public agencies and private organizations like The Nature Conservancy and the California Oak Foundation are already engaged in many conservation and restoration efforts throughout the range of the species. Due to the habitat importance of valley oak, a preservation plan is likely to include far more sites than those needed to preserve genetic and evolutional processes. Nonetheless, a systematic analysis of genetic diversity in existing and candidate reserve sites using the kind of tools demonstrated here could help to more fully characterize the current network of protected areas and help these organizations prioritize future investments in conservation and restoration projects.

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