Variation in Genetic Structure and Gene Flow Across the Range of *Sequoiadendron giganteum* (giant sequoia)[1]

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During this century, climate warming and altered precipitation patterns will lead to habitat changes that may be beneficial to some long-lived tree species and detrimental to others. Paleoendemics, with limited and disjunct distributions will face the greatest challenges, as migration rates will be too slow to keep pace with rapid environmental change and populations at the receding edges are eroded through mal-adaption. Giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz) is an iconic Sierra Nevada tree species with populations that tend to be small and highly fragmented (particularly in the northern range), making them especially vulnerable to environmental change. Maintenance of genetic variation is an important determinant of population persistence that, in part, depends on gene flow within and between populations. The research presented here describes: 1) the distribution of genetic diversity among population pairs distributed across the range of giant sequoia, and 2) the effective rates of gene flow across a highly fragmented habitat.

In 2015 and 2016, DNA was extracted from foliage collected from eight groves distributed across the range of giant sequoia, with the exception of Mariposa grove (leaf tissue from this grove originated from a clonal orchard at the University of California's Russell Research Station). For Placer rove, DNA was obtained from foliage of all trees and from seeds after germination. We used 11 microsatellite loci (DeSilva and Dodd 2014) to compare allelic diversity between population pairs, using the software STRUCTURE (Pritchard et al. 2000). We also used STRUCTURE to infer levels of historic gene-flow through assessing the degree of admixture between spatially separated population pairs. We inferred dispersal distances and size of effective mating groups within groves using SPAGeDI (Hardy and Vekemans 2002).

We found a prominent north-south divide at the Kings Canyon in spatial connectivity across *S. giganteum* groves. For the northern populations pairs, assignments of individuals to genetic clusters closely follow the grove of origin, indicating strong genetic structure (fig. 1). Rates of admixture (individuals showing evidence of shared genotypes from the two clusters) were low. This is surprising given the close proximity of members of each pair (i.e., ~4 km between Calaveras groves, ~3 km between Merced and Tuolumne , and ~7 km between Nelder and Mariposa groves. This indicates that even over short distances, groves in the northern range act as independent genetic units, with limited inter-grove gene flow. This is in contrast to populations in the southern part of *S. giganteum* range. For example, Long Meadow and Freeman Creek exhibited weak genetic and high rates of admixture (all individuals show equal ancestry from both assigned clusters) (fig. 1). These data indicate that these two southern groves exhibit little or no genetic divergence indicating recent or ongoing gene flow. This finding confirms the pattern noted in a range-wide study (Dodd and DeSilva 2016) that southern populations form a continual genetic unit. Given the distance between these two groves (about 20 km), we believe that genetic connectivity in the southern S. *giganteum* range may be maintained through a stepwise model of gene-flow.

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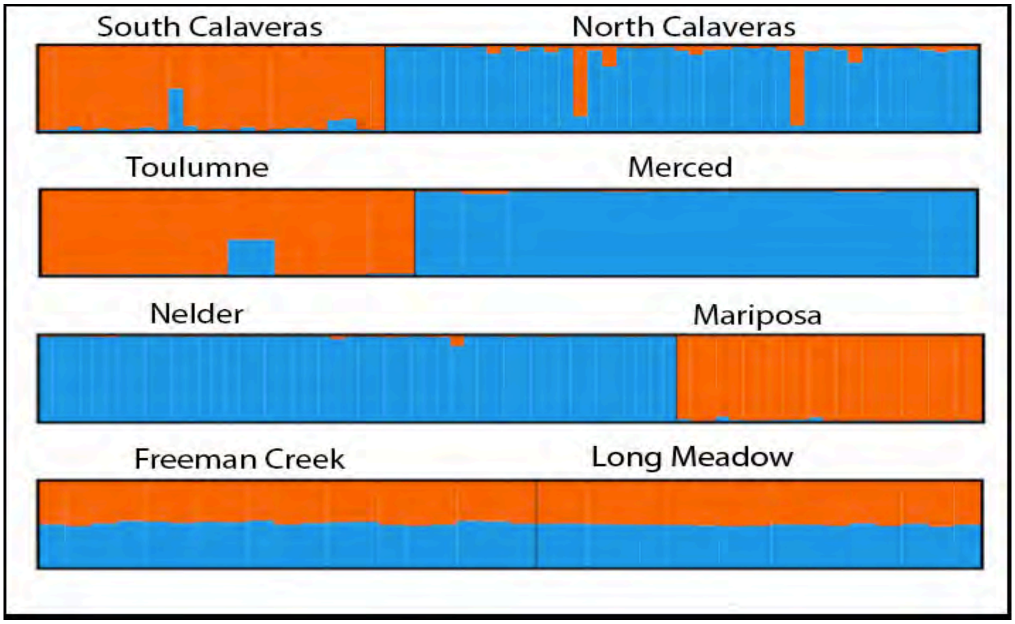

Figure 1—STRUCTURE (Pritchard et al. 2000) clusters for population pairs: Vertical bars represent a sampled individual, color-coded for assigned cluster. Northern range of giant sequoia represented by: North–South Calaveras, Tuolumne–Merced, and Nelder–Mariposa. Southern range: Freeman Creek–Long Meadow.

We estimated the fine-scale genetic parameters of neighborhood size (the number of effectively reproducing individuals occupying a deme around a parent tree) and sigma (the bulk dispersal distance of genes). We found dispersal dynamics to be highly variable across populations studied so far (table 1). In North Calaveras, gamete dispersal (sigma) likely occurs over a spatial scale of (0.22 km) and mating groups are not dramatically smaller than the mature census population. For Nelder, average dispersal distance is 0.29 km; however, the neighborhood only contains 10 individuals. We believe this difference is due to the variation in density across these two groves and the fact that Nelder grove is spread over a large area, with many areas where giant sequoia is absent. Thus, Nelder exhibits increased grove edge and spatial separation of demes. In contrast, within Giant Forest, a large grove in the southern section of *S. giganteum* range, the genetic neighborhoods are large in both area and number of individuals. The larger dispersal distance found in Giant Forest can be accounted for, in part, by the larger grove area. Larger groves contain more overlapping genetic neighborhoods and less edge, which allows gene flow to occur in all directions.

Table 1—Neighborhood size for three populations distributed across the range of giant sequoia

Population	Number of individuals within neighborhood	Radius (km) of neighborhood (sigma)
North Calaveras	51	0.22
Nelder	10	0.29
Giant Forest	174	1.6

Placer is the northernmost *S. giganteum* grove, and is separated from the nearest natural grove at North Calaveras by approximately 90 km. There are six mature individuals in this grove and two young individuals, which we determined by genetic analysis to be a result of human planting, rather than natural reproduction. Placer grove exhibited extremely low genetic diversity; of the 11 loci, five were monomorphic and three others had only two alleles each. Interestingly, we found evidence of an influx of exogenous pollen at Placer; preliminary results from seed arrays showed some seeds that were heterozygous with an allele that did not occur in any of the mature trees in the Placer grove. This cannot occur without the introduction of an outside pollen source. Considering that the nearest grove to Placer is ~90 km to the south, we determined that the likely source for this exogenous pollen is either one of the two young individuals (within the grove of planted origin) or the nearby plantation of *S. giganteum* (planted by the Auburn Lions Club in 1951 approximately 15.2 m to 30.5 m from the grove edge).

In conclusion, our research suggests that the northern populations of S. *giganteum* should be considered a high conservation priority, due to their small size, unique genetic composition, and lack of genetic continuity with other groves. In contrast, southern S. *giganteum* groves will likely be more resilient to genetic diversity loss due to genetic exchange with adjacent groves. Our previous work also indicates that giant sequoia is suffering from a long-term decline in population size and exhibits low levels of genetic diversity (Dodd and DeSilva 2016), making it crucial to protect the remaining diversity within the species. The fine-scale spatial structure analyses presented here can be used to direct conservation efforts. For instance, groves like Nelder that have strong within-population structure, are highly vulnerable to loss of genetic diversity. Moreover, incorporating genetic neighborhood size into ongoing seed collection strategies can maximize the capture of genetic diversity across the range. With the onset of climate change, genetically diverse seed banks may become invaluable if and when land managers begin to undertake widespread S. *giganteum* planting or assisted migration.

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