

Determining Landscape Connectivity and Climate Change Refugia Across the Sierra Nevada

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INTERIM REPORT
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Project Description

Release of vast quantities of greenhouse gases into the atmosphere has increased annual mean temperatures, altered global precipitation, reduced polar ice caps, and changed plant composition^{1,2}. As California's climate rapidly changes, land managers need to know how species distributions might be shifting to design effective climate change adaptation strategies. Studies have begun to examine the effect of climate and land use change on Sierra Nevada birds and mammals^{3,4,5}. However, although most studies assume that the Sierra Nevada is a contiguous landscape with populations connected across its expanse, few studies have examined this assumption. Another mostly untested assumption is that there will exist climate change refugia, certain areas of more stable or buffered climate among heterogeneous landscapes, such as cold air drainages where cooler areas can be found at lower elevations. In this project, we sought to identify putative connectivity between meadows and climate change refugia across the Sierra Nevada and use data on persistence, stability, and genetic diversity of mammal populations to validate these hypotheses.

Through this study, we addressed California Landscape Conservation Cooperative priorities in terms of scale, analyzing across the Sierra Nevada; in terms of applicability, involving state and federal natural resource managers throughout the project who are already beginning to incorporate results; and in terms of products, focusing on maps and tools that are user-friendly and allow managers to make decisions and set priorities on the landscape. We are now working to communicate our results directly to CA LCC partners to aid in decisions from immediate, small-scale adaptation projects to region-wide changes in use, development, and planning of state and federal lands. Our results will help managers to prioritize areas and landscapes in the Sierra Nevada that are critical to maintaining biodiversity in the face of climate change and thus to focusing limited resources for effective adaptation efforts.

Basic Approach and Scope of Work

Based on discussions among natural resource managers and researchers in federal and California agencies and at U.C. Berkeley, we decided to narrow the project's focus to Sierra Nevada meadow systems. This provided an opportunity to map connectivity and refugia of discrete systems in the Sierra Nevada. The general framework was to use landscape and climate features to estimate connectivity between meadow systems, use climate features and species data to identify refugia among these, and use occupancy and genetic data to test these hypotheses.

Genetic Analysis

We used a microsatellite analysis of 188 Belding's ground squirrels from 16 sites across the Sierra Nevada and northern California to validate the hypotheses of meadow connectivity and climate change refugia. We optimized 12 polymorphic microsatellite markers for Belding's ground squirrels. Specifically, we examined population structure using the program STRUCTURE⁶ and the R⁷ package Geneland⁸ which allow for a geographic analysis of genetic diversity. A-priori geographic partitioning for STRUCTURE analysis split state-wide samples into four major areas: Northern California, Tahoe area, Yosemite, and southern Sierras. We used Genepop to test for population differentiation (F_{ST}). BayesAss was used to examine directional gene flow between populations.

Habitat Connectivity

We obtained a meadow dataset representing 17,039 meadow polygons in the Sierra Nevada⁹. The dataset was cross-referenced with a dataset of meadows in Yosemite obtained from Eric Berlow, which provided confidence in the relative accuracy. We assumed that polygons within the layer sufficiently represent available habitat for meadow-based species. However, in case of error in position and delineation and to reflect the likely interchange between

very close meadows, we buffered polygons by 150m and merged the resulting layer to create 7969 meadow systems, hereafter referred to as meadows.

We tested 5 hypotheses of connectivity:

1. Isolation by distance – Dispersal between meadows is limited by Euclidean (straight-line) distance between areas
2. Isolation by topography – Dispersal between meadows is limited by changes in topography, particularly by large changes in elevation.
3. Isolation by watercourses – Dispersal between meadows is limited by the presence of flowing water.
4. Isolation by roads – Dispersal between meadows is limited by the presence of major roads, used as a barrier of its own as well as a proxy for human development.
5. Isolation by environmental heterogeneity – Dispersal between habitats is limited by variability in the potential landscape composition, approximated with climate water deficit.

Based on these hypotheses, we produced maps of connectivity across the mountains for eastern California, from the southern Sierra Nevada past the Warner Mountains to the Oregon border. For Hypothesis 1, we used simple Euclidean distance between genetic sample sites using the R package *sp*¹⁰. For Hypotheses 2–5, we generated at least one friction surface representing the cost of moving from one meadow to the next. We used the program *Circuitscape*¹¹ to estimate connectivity between meadow systems based on individual friction surfaces (Fig. 1). *Circuitscape* uses the principles of circuit theory to estimate habitat connectivity whereby habitat patches (i.e. meadows) are treated as electrical nodes, either "sources" and "grounds," and the friction surfaces provides resistance (or conductance) to the current across the landscape. Summary maps regarding the total current that would flow through each pixel represent the overall connectivity.

Next, in order to test between these hypotheses of connectivity, we calculated least cost distance values between genetic samples based on the connectivity maps using the R packages *raster*¹² and *gdistance*¹³, representing the relative isolation due to restriction. We then used Mantel tests to compare observed correlations between matrices of genetic distance and Euclidean or cost distances using the package *vegan*¹⁴. Mantel tests permute one of the matrices to generate a null distribution of values on which there can be a comparison of the observed value. Significant tests ($p < 0.05$) suggest a correlation that is more likely than random chance. When multiple hypotheses were supported, we used partial mantel tests to account for the correlation between Euclidean distance and the cost distance. In this case, correlation between the first and second matrix is compared to the third, and the null distribution is generated by permuting the first matrix. The effect of the third matrix, Euclidean distance, is controlled.

Climate Change Refugia

We determined climate change refugia in two time periods: a) historical to modern, to assess the existence of climate change refugia over the last century; and b) modern to future, to aid in prioritization for climate change adaptation strategies.

We examined trends in temperature and precipitation over the last century for the Sierra Nevada and surrounding areas using 4km PRISM data¹⁵ downscaled to 270-m (in collaboration with Flint and Flint, USGS¹⁶). These climate data were adjusted to specifically incorporate cold-air pooling¹⁴ and used in a fine-scale hydrologic model, Basin Characterization Model (Ver. 3), that provides monthly estimates values of snowpack, runoff, and climatic water deficit based on empirically derived parameters.

We defined the historical period as 1910–1939, which coincides with the time of the original surveys in the Sierra Nevada, and the modern period as 1970–1999, which represents the last 30 years of observed climate data available to us. To better understand the climate trends during each period, we used the function *biovars* in the R package *dismo*¹⁷ to generate the 19 bioclim layers. We particularly were interested in changes in mean annual temperature (Bio1) and total annual precipitation (Bio12); additionally maximum temperature of the warmest month (Bio05), minimum temperature of the coldest month (Bio06), and mean temperature of the coldest quarter (Bio11), the latter of which was found to predict well many of the persistent sites in Morelli et al. 2012¹⁸, were of interest but change in

value between periods should be treated with caution because of the possibility that values represent non-analogue time periods (i.e. January in the historic period and February in the modern period).

Climate may not be well represented by a single point estimate because of the inherent variation within years. As such, we calculated the 5th and 9th percentiles of each raw variable on a per cell basis for the historical period, focusing on the tails of each distribution as representative of extreme events. For minimum temperature, maximum temperature, precipitation and snow pack, quantiles were found on a monthly basis, whereas CWD was analyzed as yearly variation. We then determined the number of months (or years for CWD) in the modern period that exceeded the extreme values beyond expectation as a measure of magnitude of change.

To test the efficacy of the hypothesized climate change refugia, we examined species-specific data, predicting that higher rates of genetic diversity and persistence in those meadows would indicate refugial qualities. As such, we compared allelic richness for each of the population to the amount of change using Spearman's rank test. We also tested for an effect of connectivity by using generalized linear models to compare meadow connectivity to the number of alleles.

Species Responses to Climate Change

Finally, we examined patterns of local extinctions of small mammals using an occupancy modeling approach¹⁹. This framework includes an explicit estimate of the difficulty in detecting a given taxon, which is key in understanding rare and elusive species. Using the robust multi-season model, which first estimates historical occupancy and detection followed by estimates of colonization and extinction, we can test various covariates to uncover whether changes in climate have influenced extinction probability.

Using Grinnell Resurvey Project trapping data from throughout the Sierra Nevada^{3,20}, we identified 82 matching sites that represent exact, or practically the same, locations that were sampled during historical and modern surveys. From these data, we modeled potential local extinction responses for 15 taxa, representing various habitat preferences and life-history strategies. We examined 5 detection models based on trapping effort plus a null model, and a variation of the best-supported occupancy model for each species²⁰. We fit 32 extinction models based on changes in climate and isolation at the modern sampling site. The covariates include measures of climate stability and changes in local environmental and climate variables from the refugial analysis, as well as distance measures. To assess whether climate influenced extinction, we fit a null model for the extinction parameter and compared AIC values to models with covariates; if models with climate change performed better than the null model, we assume that climate influenced extinction. To fit and examine models, we used the function `colect` in the R package `unmarked`²¹.

Initial Results

Mantel tests of the complete genetic dataset show support for 4 of 5 hypotheses: isolation by distance, by topography, by roads, and by environmental heterogeneity (Table 1). Removal of the northern sites that the STRUCTURE analysis suggested are very separate populations and moreover are separated by such a great distance eliminates support for the isolation by roads (Table 2). Partial Mantel tests further eliminate support for the isolation by topography and environmental heterogeneity (Tables 3, 4).

We found changes in environmental variables consistent with an overall warming trend in the Sierra Nevada (Figure 2). There was a strong visual signal of geographic differences within and between variables, suggesting that species responses may vary across the Sierra Nevada. Environmental shifts away from the historical variation are also evident in the monthly raw climate variables and hydrological estimated values. In particular, there is a strong seasonal effect in monthly minimum temperature and monthly maximum temperature, based on the amount of variation explained by the first two component scores.

Discerning patterns of future change with respect of connectivity of meadows shows that well connected meadows may have not be subject to the maximum observed changes in summer maximum temperature, but minimum

temperatures may shift drastically (Figure 3). Overall, patterns change with different hypotheses of isolation and climate model and change scenario.

Of the 15 species we modeled using the occupancy approach, 12 species had signals of climate change effects on extinction. However there was a suite of variables that were well supported across these taxa, but frequently they were relatively consistent within a taxon. For instance, changes in summer precipitation were important in estimating probability of extinction for *Sorex palustris* and *Neotoma cinerea*, but changes in minimum temperature were associated with local extinctions of *Neotoma macrotis*. The three species in which local extinction was not well modeled were *Microtus longicaudus*, *Peromyscus truei*, and *Tamias alpinus*. In most species, models including a distance covariate were not the out-right best-supported model, but occasionally were within 2 AIC values, suggesting that isolation alone cannot explain extinctions.

Discussion

A primary challenge of our project was to devise an approach to address the interacting effects of connectivity, climate change, and individual species responses. We used meadows, as suggested by resource managers and federal researchers, as a focus because it is likely that connectivity between these important and sensitive habitats will be consistent for a variety of mammal taxa. Further, we expect that other taxonomic groups, such as amphibians and reptiles, likely are impacted by changes in the landscape and their populations will be influenced by isolation. The ability of species to move in response to the speed of climate change²² may be influenced by the ease at which they can move through the matrix of habitat and non-habitat.

Our results show a heterogeneous geography of climate change, particularly that aspects of seasonal dynamics will be in flux. Well-connected habitats should be able to maintain a metapopulation structure, particularly for vagile species that are able to move through a changing matrix. Our preliminary results suggest that Belding's ground squirrels are isolated by Euclidean distance, suggesting that well-connected habitats are those that are nearby. If meadow systems change due to decreases in moisture or encroaching trees, we expect that populations will become increasingly fragmented.

The occupancy modeling results suggest that local extinction events are well correlated with changing environmental conditions, particularly changes in precipitation and temperature. Changes in precipitation have been dramatic, particularly in the northern Sierra Nevada; the increase likely has an indirect effect on species through changes in available habitat and resources. The stability of the environment in regions with minimal change, as shown in our refugial maps, may facilitate persistence of species, especially for species that are environmentally sensitive or habitat specialists. A critical notion to consider is the interaction between variables in relation to differences in summer and winter patterns and how these may impact the response of species.

Project Outcomes

- 1) Two postdoctoral researchers were trained under this project, one part-time and one full-time
- 2) Three undergraduate researchers gained experience through this project, in the Departments of Environmental Science, Policy and Management and Integrative Biology and the Museum of Vertebrate Zoology.
- 3) Stronger collaborations were built/reinforced between U.C. Berkeley and CADFW, FWS, NPS, USGS, and USFS
- 4) Presentations, maps and other products were produced to aid natural resource conservation in the Sierra Nevada in the face of climate change

Products/Data Sharing

- 1) Current Meadow Connectivity Maps across the Sierra Nevada using 4 criteria**

- 2) Projected Meadow Connectivity Maps across the Sierra Nevada using 4 criteria under two climate change models and two scenarios (16 outputs)**
- 3) Current Climate Change Refugia Map across the Sierra Nevada**
- 4) Projected Climate Change Refugia Map across the Sierra Nevada under two climate change models and two scenarios (4 outputs)**
- 5) Spatially interpolated maps of genetic diversity for Belding's ground squirrels**
- 6) A fine-scale analysis of meadows in the Yosemite National Park area providing managers with more discrete estimates
- 7) Website on cal-adapt.org and on Climate Commons
- 8) 2 peer-reviewed journal articles (to be submitted to Molecular Ecology and Global Change Biology)
- 9) Presentation of results:
 - a. Preliminary results were already presented to USFS, NPS & USGS
 - b. Follow-up meetings will be held either remotely or, wherever possible, in-person with CA LCC Sierra Nevada partners such as staff of Yosemite National Park, Inyo National Forest, U.S. Forest Service - R&D and other NFS offices, CADFW, and FWS staff
 - c. Webinar will be given through the CA LCC and/or a similar venue
 - d. Results will be presented at the American Society of Mammalogists meeting (June 2013 in Philadelphia) as well as most likely The Wildlife Society, Society of Conservation Biology, and Ecological Society of America

***will be presented fully as appendices to next month's final report*

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Figure 2: Climate Changes Across the Sierra Nevada. Differences (modern minus historic periods) in bioclim variables. Bioclim variables essentially are summary variables that represent variability in climate, particularly aspects of temperature, precipitation, and their interactions. Values show general trends of annual warming (Bio01), mixed trends in the warmest months (Bio05), overall warming in the Sierra Nevada during cooler months (Bio06), and heterogeneous patterns of warming in the coldest quarter (Bio11). Additionally, there is an increase in annual precipitation (Bio12), especially in the northern Sierra Nevada.

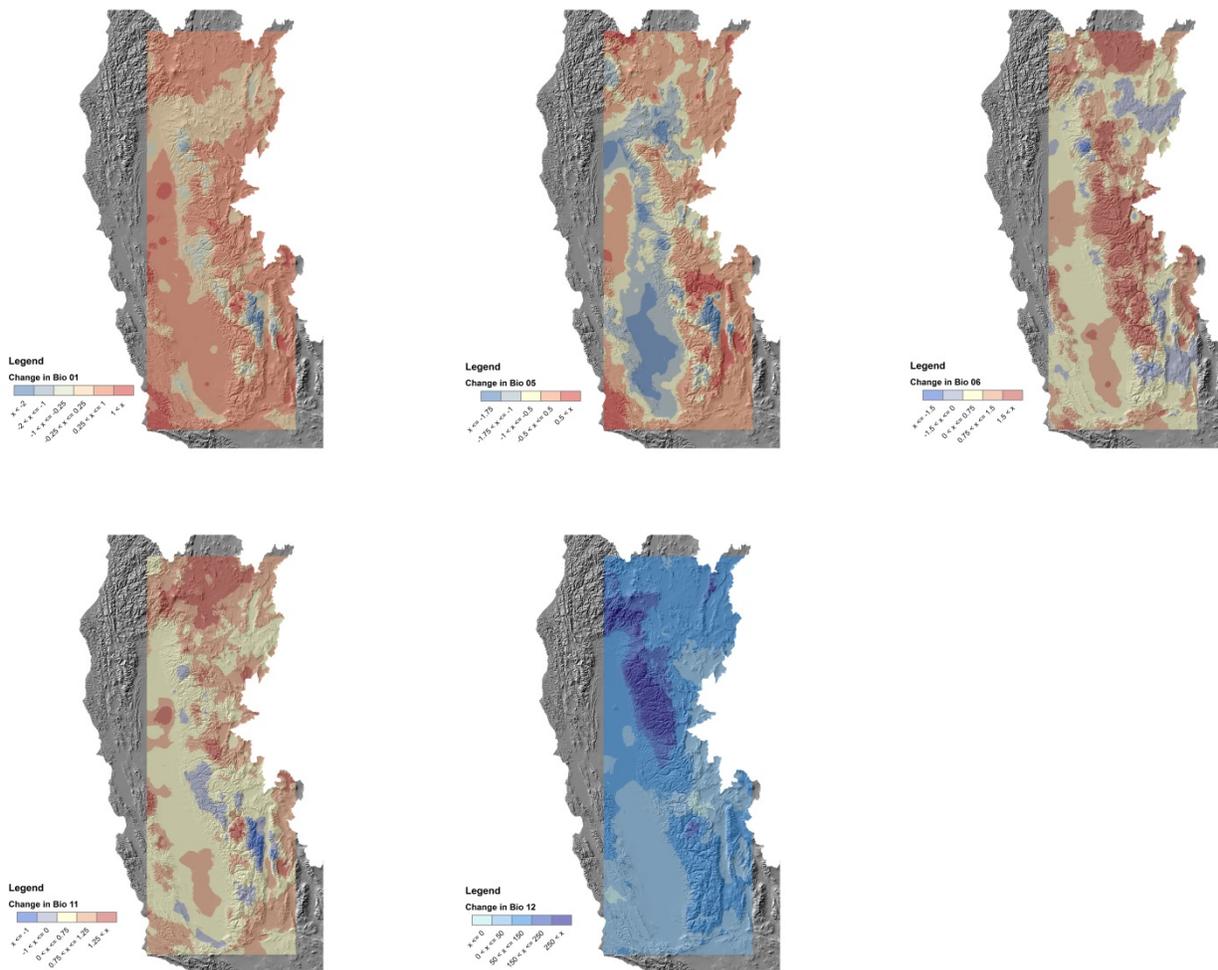


Figure 3: Connectivity and Change. Patterns estimate summer maximum monthly temperature (T_{max}) and minimum monthly temperature (T_{min}) and estimated connectivity. Values are measured in 30 year intervals using the GFDL general circulation model and change is measured between neighboring time periods. In each section, we plot the connectedness of meadows based on a hypothesis of isolation by topography and the mean value of the given variable and warming scenario (A2—increasing carbon dioxide, methane, and nitrous oxide concentration vs. B1—eventual leveling of carbon dioxide and nitrous oxide concentration, and reduction in methane). Of particular interest is the upper right quadrant of the change plots, which would designate whether well-connected meadows are likely to change dramatically. For additional perspective, we plot four meadows (red, blue, yellow, and green dots) in color to track how they are expected to change.

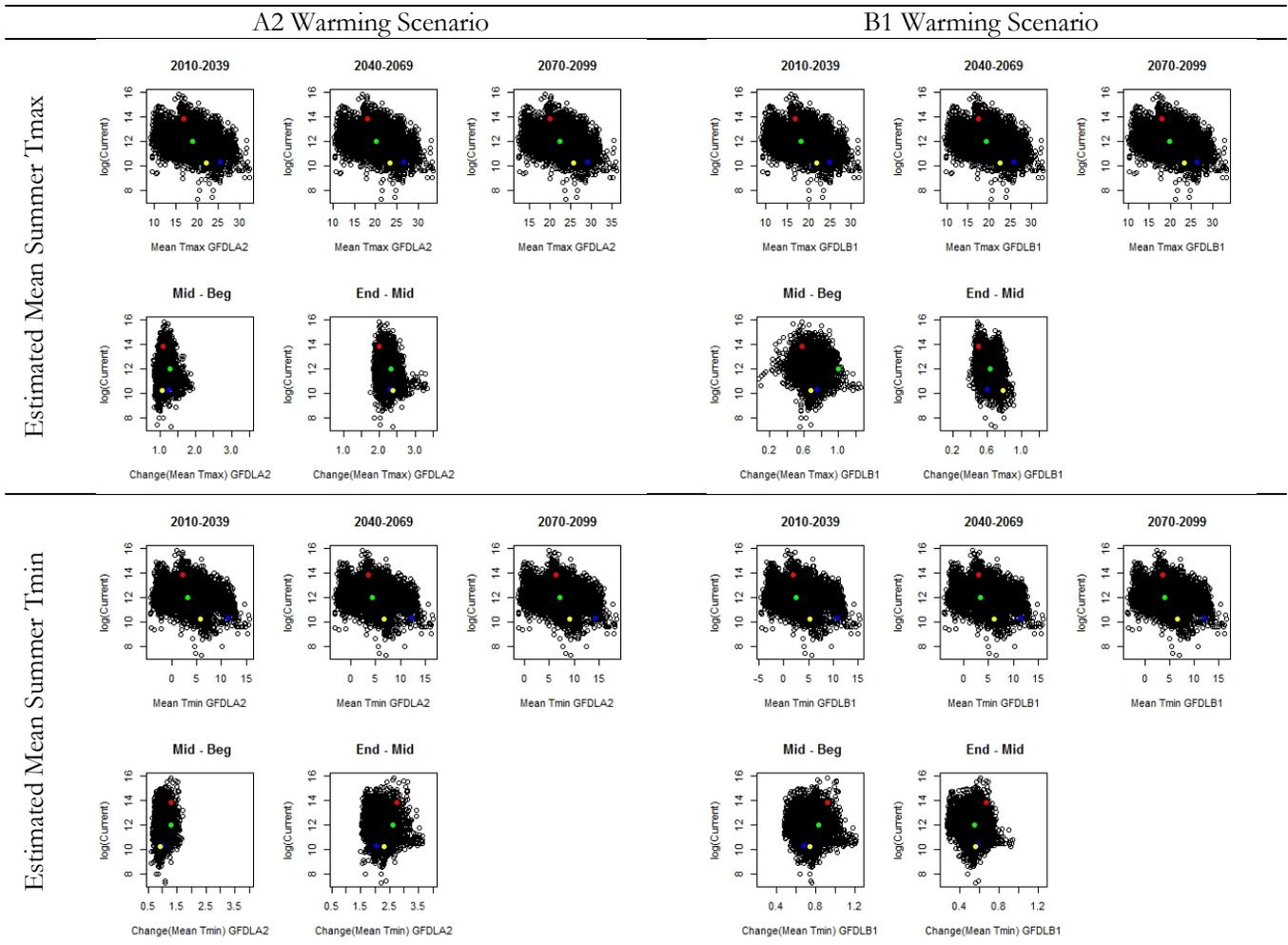


Table 1: Mantel tests of the complete genetic dataset show support for 4 of 5 hypotheses: isolation by distance, by topography, by roads, and by environmental heterogeneity (n =16)

GIS Layer	Distance Measure	Mantel r	P-value
None	Euclidean	0.6954	0.001
PathDistance	Least Cost	0.8625	0.001
Connectivity by Path Distance	Least Cost	-0.1721	0.788
Connectivity by His CWD	Least Cost	0.5661	0.003
Connectivity by Mod CWD	Least Cost	0.5849	0.001
Connectivity by Roads	Least Cost	0.4374	0.029
Connectivity by River (continuous)	Least Cost	-0.1907	0.793
Connectivity by River (binary)	Least Cost	-0.197	0.821

Table 2: Mantel tests of the genetic dataset minus northern populations show support for 3 of 5 hypotheses: isolation by distance, by topography, and by environmental heterogeneity (n =14)

GIS Layer	Distance Measure	Mantel r	P-value
None	Euclidean	0.6706	0.001
PathDistance	Least Cost	0.6500	0.002
Connectivity by Path Distance	Least Cost	0.1238	0.300
Connectivity by His CWD	Least Cost	0.5414	0.004
Connectivity by Mod CWD	Least Cost	0.5184	0.007
Connectivity by Roads	Least Cost	0.1553	0.254
Connectivity by River (continuous)	Least Cost	-0.1344	0.703
Connectivity by River (binary)	Least Cost	-0.1664	0.742

Table 3: Partial Mantel tests eliminate support for the isolation by topography, by roads, and environmental heterogeneity hypotheses (n=16)

GIS layer	Distance Measure	Mantel r	P-value
PathDistance	Least Cost	0.7431	0.059
Connectivity by His CWD	Least Cost	-0.4989	0.996
Connectivity by Mod CWD	Least Cost	-0.3686	0.969
Connectivity by Roads	Least Cost	-0.2595	0.868

Table 4: Partial Mantel tests of the genetic dataset minus northern populations eliminate support for the isolation by topography and environmental heterogeneity hypotheses (n=16)

GIS layer	Distance Measure	Mantel r	P-value
PathDistance	Least Cost	0.2878	0.111
Connectivity by His CWD	Least Cost	-0.299	0.908
Connectivity by Mod CWD	Least Cost	-0.2269	0.849