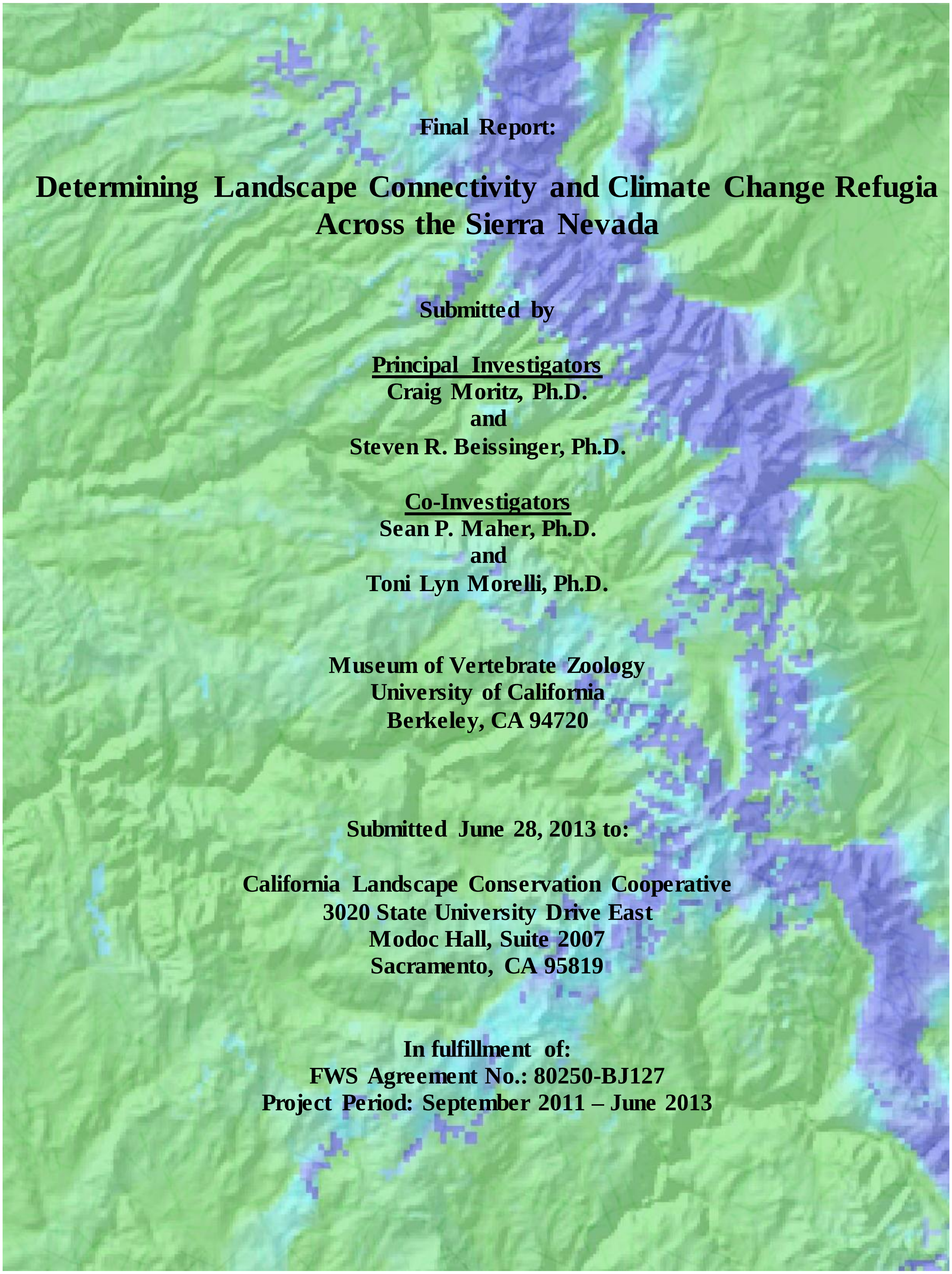

Final Report:

Determining Landscape Connectivity and Climate Change Refugia Across the Sierra Nevada

Submitted by

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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 shift 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, few studies have focused at a smaller scale to understand whether populations are connected across the expanse of the Sierra Nevada. Another mostly untested assumption is the existence of climate change refugia, 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 climate change refugia and connectivity between meadows across the Sierra Nevada and to use data on persistence, stability, and genetic diversity of mammal populations to validate these hypotheses. We addressed California Landscape Conservation Cooperative priorities of scale by analyzing across the Sierra Nevada. We involved state and federal natural resource managers throughout the project; some are already beginning to incorporate results. Our products focused on maps and tools that are user-friendly and that allow managers to make decisions and set landscape conservation priorities. We are communicating project outcomes directly to CA LCC partners to aid in decisions from immediate, small-scale adaptation projects to region-wide changes in use, development, and planning for state and federal land management. Our results will help managers to prioritize areas and landscapes that are critical to maintaining biodiversity in the Sierra Nevada in the face of climate change and to focus limited resources for effective adaptation efforts.

OVERALL RESULTS

Significant Activities and Results

The most important outcomes of this research were maps of refugial meadows and their connectivity across the Sierra Nevada. A unique aspect of this project is the use of species data to test, and ultimately validate, these hypothetical maps. We believe these maps will be important tools for professionals managing the natural resources of the Sierra Nevada in the face of climate change.

This project funded field surveys, genetic studies, and geospatial analysis by postdoctoral researchers and undergraduate students that produced the following:

1) Current Meadow Connectivity Maps across the Sierra Nevada
2) Projected Meadow Connectivity Maps across the Sierra Nevada using four criteria under two climate change models and two scenarios (48 outputs)
3) Current Climate Change Refugia Map across the Sierra Nevada (4 outputs)
4) Projected Climate Change Refugia Map across the Sierra Nevada under two climate change models and two scenarios (48 outputs)
5) Maps of genetic diversity for Belding’s ground squirrels (4 outputs)
6) A fine-scale analysis of meadows in the Yosemite National Park area providing managers with discrete estimates of connectivity and climate stability.

7) Results presented to the scientific and broader community in two peer-reviewed journal articles (to be submitted to *Molecular Ecology* and *Global Change Biology*)
8) A website for easy access to results by managers hosted by the Museum of Vertebrate Zoology, University of California, Berkeley (http://mvz.berkeley.edu/Grinnell/), available once our manuscripts are accepted.
9) Results presented to managers and scientists in the following meetings and public settings:
    a. Internal meetings with USFS, NPS & USGS (March 2013).
    b. The American Society of Mammalogists meeting in Philadelphia (June 2013).
    c. Follow-up meetings to 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.
    d. Webinar to be given through the CA LCC and/or a similar venue (Target August 2013).
    e. Results to be presented at future national meetings of professional societies such as the American Geophysical Union (San Francisco, CA, in December 2013), Ecological Society of America, Society of Conservation Biology, and The Wildlife Society.
10) Training opportunities for one full-time and one part-time postdoctoral researcher and three undergraduate students in the Departments of Environmental Science, Policy and Management and Integrative Biology and the Museum of Vertebrate Zoology at U.C. Berkeley.
11) Stronger collaborations built/reinforced between U.C. Berkeley and CADFW, FWS, NPS, USGS, and USFS

APPROACH AND SCOPE OF WORK

Based on discussions at U.C. Berkeley with natural resource managers and researchers in federal and California agencies, we focused the project on Sierra Nevada meadow systems. This provided an opportunity to map connectivity and refugia of discrete systems in the Sierra Nevada. The general framework used landscape and climate features to hypothesize connectivity between meadow systems, used landscape and climate features to identify hypothetical refugia, and used survey and genetic data to test these hypotheses.

The study focused on the Belding's ground squirrel (*Urocitellus beldingi*), a 250-g ground-dwelling sciurid found primarily in meadows in mid- to high-elevations from east-central California to Oregon in the north and Nevada and southern Idaho in the east. This species lives in family groups and feeds primarily on grass[6,7]. Previous research on this species has shown that its California range contracted considerably over the last century; 42% of sites surveyed in the first half of the 20th century are now unoccupied. These site extinctions appear to be linked to hotter and wetter climates, and are mitigated by human modification (i.e., "anthropogenic refugia") in the form of increased food or water[8]. However, Belding's ground squirrels have increased in size over the past century as measured by museum specimens. This was likely a response to milder winters, which could have improved food availability and lowered metabolic demands[9]. Thus, Belding's ground squirrels appear to be climate-sensitive. We hypothesized that strong temperature increases and extreme events can result in extinctions, although subtle warming over the last century appear to have had a positive effect on the species.

Study Location

We obtained a meadow dataset representing 17,039 meadow polygons in the Sierra Nevada[10]. We cross-referenced it with a dataset of meadows in Yosemite obtained from Eric Berlow (USGS), which provided confidence in its relative accuracy (i.e., location, extent, and density). We assumed that polygons within the layer sufficiently represented 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.

Climate Data and Potential Refugia

Climate data for all California hydrological units were estimated using 4km PRISM data[11] downscaled to 270-m (in collaboration with Flint and Flint, USGS[12]). These data represented minimum temperature, maximum temperature, and precipitation of each month of each year during the 20th century. Climate data were adjusted to incorporate cold-air pooling and were used in a fine-scale hydrologic model, Basin Characterization Model (Ver. 3), that provided monthly estimated values of snowpack (as snow-water-equivalent), runoff, and climatic water deficit (CWD) based on empirically derived parameters. CWD values for each water-year (October–September) were summed to provide the annual estimates of water availability to vegetation.

We define climate change refugia as areas on the landscape where the magnitude of change in climate and climate-derived measures was minimal between the historical and modern period, essentially attempting to capture regions that are stable in the face of recent climate change. We defined the historical period as 1910–1939, which coincides with the time of the original Grinnell Resurvey Project 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 represent temporally broad climate trends during each period, we used R[13] and the raster[14] and dismo[15] packages, particularly the function biovars, to generate summary variables that represent overall climate trends in each era. We particularly were interested in changes in mean annual temperature and total annual precipitation, maximum temperature of the warmest month, minimum temperature of the coldest month, and mean temperature of the coldest quarter; the latter was found to predict Belding's ground squirrel persistence in Morelli et al.[8] We also determined the mean of 1 April snowpack and CWD for each period. To represent the magnitude of change between eras, we used the simple difference for temperature-related variables, and the difference divided by the historical values for precipitation and hydrologically informed variables to measure proportional change (Figure 1). We note that for the difference in variables representing monthly or quarterly measures, the magnitude of values should be treated with caution because of the possibility that they represent non-analogue time periods (e.g., January in the historical period and February in the modern period). This may be relevant if specific phenologies are tied to daylight measures and not to environmental conditions.

In addition to changes in central tendencies, we examined the frequency of extreme modern values relative to variation in the historical period. We defined extreme values as exceeding the 95th quantile or below the 5th quantile; quantiles were calculated on a per pixel basis from the historical period. For minimum temperature, maximum temperature, and precipitation, the number of extreme years in the modern period were quantified per month, and these maps were summed to represent the overall stability of the local environment. We then used principle components analysis (with each month as a variable along with latitude and longitude) to identify seasonal and geographic patterns of stability. For snow pack corresponding to 1 April and CWD, we determined extreme years and present these as single maps.

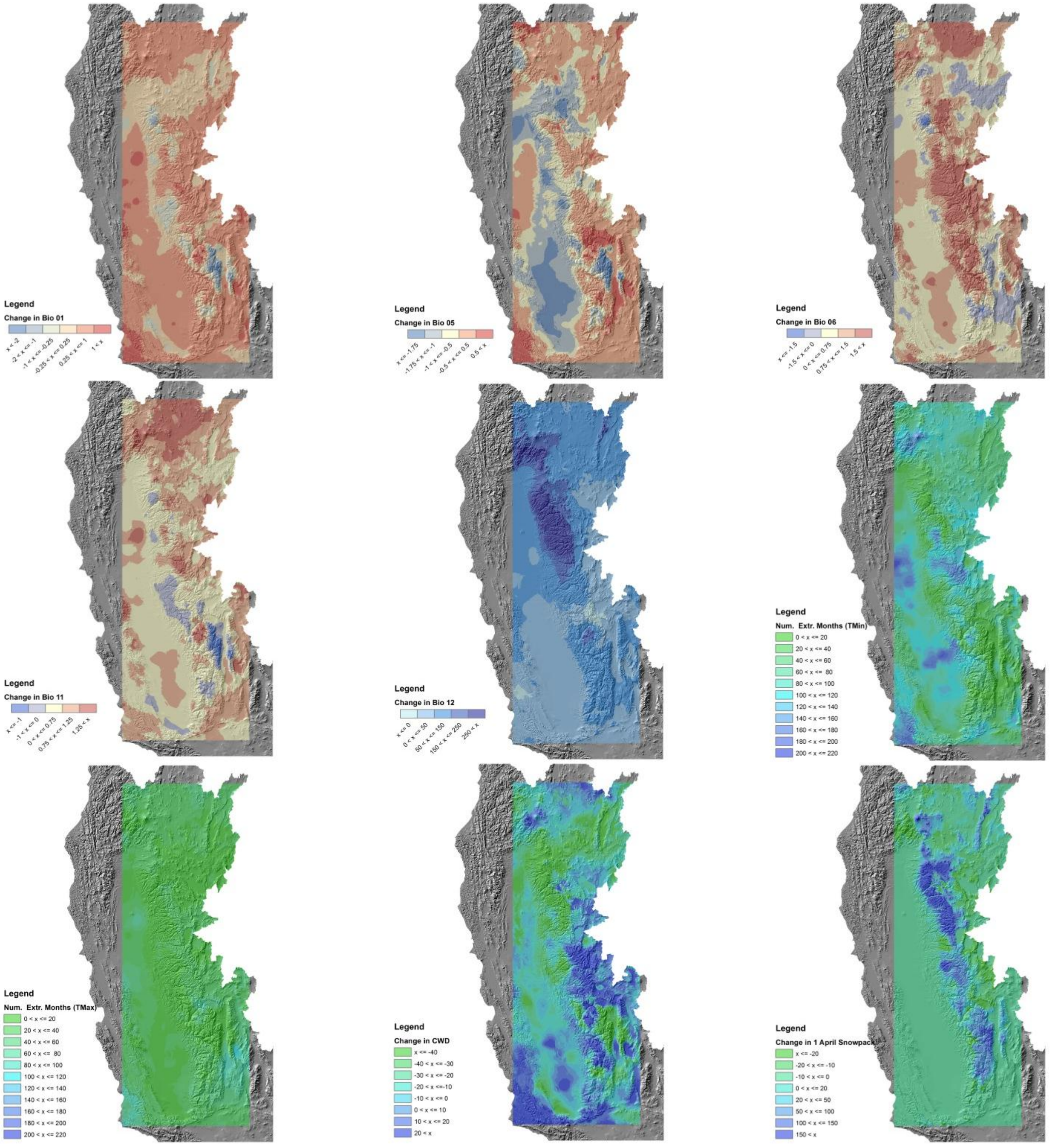

Figure 1: Climate Changes Across the Sierra Nevada. Differences between modern and historical periods are shown for variables of interest to delineate potential refugia. Values show general trends of annual warming (Bio01), mixed trends in the warmest months (Bio05), overall warming in the Sierra Nevada 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. We also present the number of months that minimum and maximum temperature that were extreme given the historical variability (see text for description). Finally, changes in climatic water deficit and 1 April snowpack show variable patterns of change.

To address the potential change in climate and estimate future refugia, we analyzed climate layers reflecting two emission scenarios (SRES A2 and B1, where A2 represents a higher emissions scenario with a more severe climate change forecast than B1) and two general circulation models (the NCAR Parallel Climate Model (PCM) and the NOAA Geophysical Fluids Dynamics Laboratory (GFDL)). These four projected/modeled data sets represented the same variables as in the observed data set, and incorporated aspects of cold-air pooling in the downscaling. Again we calculated summary values for 30-year periods representing early (2010–2039), middle (2040–2069), and late 21st century (2070–2099) using the biovars function in R, and totaled the number of months (or years for CWD) that exceeded the variation in the historical era.

Connectivity Surfaces
We identified 5 hypotheses of connectivity that could affect movement through the Sierra Nevada and would be reflected in patterns of occupancy and gene flow:

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

Based on Hypotheses 2–5, we produced maps (hereafter referred to as “friction surfaces”) across the mountains for eastern California, from the southern Sierra Nevada beyond the Warner Mountains to the Oregon border. For isolation by topography, we calculated an elevationally-weighted distance measure between meadows using the PathDistance tool in ArcGIS[16]. For isolation by watercourses, we generated a map of distances from these features and a binary map of their occurrence or absence in a given pixel. For isolation by roads, we generated a map of distance from these features. For isolation by environmental heterogeneity, we used a moving window to produce two maps representing the variability in CWD during the historical and modern periods.

The friction surfaces were used as inputs in the program Circuitscape[17] to estimate movement between and among sites. Circuitscape uses the principles of circuit theory to estimate connectivity. Habitat patches (i.e., meadows) are treated as electrical nodes, either "sources" or "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 and were used to identify well-connected meadows. Alternatively, the program can also provide estimates of "electrical distance" between patches, which we used as a distance matrix between the genetic samples.

Table 1. Measures of potential refugia and support using field surveys. We compared measures of refugia with data collected in 2011 to determine which variables best explained occupancy. There were three categories of variables based on how change was measured (see text) or observed climate and climate-related measures. We report values of the Wilcoxon rank test comparisons and whether we used one-sided or two-sided tests (see text); significant tests were identified as refugial and we provide median values for occupied and unoccupied meadows.

Category	Variable	W	P-value	Test Direction	Refugial	Median Occupied	Median Unoccupied
Number of Extreme Months	Minimum Temp	264	0.0008	less	Yes	32.829	55.765
	Maximum Temp	264	0.9995	less	No		
	Precip (More)	96	0.0067	less	Yes	23.655	26.965
	Precip (Less)	235	0.9474	less	No		
	CWD (More)	203	0.7518	less	No		
	CWD (Less)	133	0.0880	less	No		
	Snowpack (More)	260	0.9910	less	No		
	Snowpack (Less)	313	1.0000	less	No		
	PC 2 Min. Temp	290	0.0009	two-sided			
	PC 2 Max Temp	206	0.4600	two-sided			
Mean Difference	Δ in Bio01	154	0.2302	less	No		
	Δ in Bio05	301	1.0000	less	No		
	Δ in Bio06	68	0.0004	less	Yes	1.280	1.712
	Δ in Bio11	133	0.0880	less	No		
	Abs Δ in Bio12	73	0.0007	less	Yes	-13.100	31.950
	Rel Δ in Bio12	70	0.0005	less	Yes	-0.013	0.029
	Abs Δ in CWD	252	0.9840	less	No		
	Rel Δ in CWD	276	0.9980	less	No		
	Abs Δ in Snowpack	45	0.0001	less	Yes	-2.097	79.992
	Rel Δ in Snowpack	36	0.0003	less	Yes	-0.003	0.972
Modern Value	Bio01	38	0.0004	less	Yes	2.307	4.946
	Bio05	59	0.0001	less	Yes	20.147	20.797
	Bio06	28	0.0005	less	Yes	-11.372	-6.305
	Bio11	33	0.0002	less	Yes	-5.304	-1.523
	Bio12	66	0.0006	two-sided	Yes	1019.940	1241.672
	CWD	56	0.0001	two-sided	Yes	155.659	238.291
	Snowpack	182	0.9654	two-sided	No		

Genetic Analysis of Belding's Ground Squirrel

We sampled 187 adult or sub-adult Belding's Ground Squirrel at 15 sites across California from Modoc County to the southern Sierra Nevada from 2003-2011 (Figure 2), with the majority of samples obtained in 2010 and 2011. Ground squirrels were trapped in Sherman or Tomahawk Live Traps. Genetic samples were collected through an ear snip or from a liver biopsy during preparation of museum skins.

DNA was extracted using standard methods and amplified using ten polymorphic microsatellite loci optimized from protocols developed based on other sciurid species[18–22]. We tested for and, where necessary, adjusted for null alleles, as well as Hardy-Weinberg equilibrium, and linkage disequilibrium. To assign individuals to populations, we ran an analysis in STRUCTURE 2.3.4[23], first across the entire study area based on the 15 sampling sites. Initially we split state-wide samples into four major areas: Northern California, Tahoe area, Yosemite, and southern Sierras. Then these four subpopulations were iteratively run on until samples grouped. A single genetic population (i.e., K = 1) had the strongest support based on the method by Evanno et al.[24]. Each run was replicated ten times with K set from 1 to 8 populations, with an initial burn-in of 10,000 iterations followed by 10^6 Markov chain Monte Carlo repetitions. We then calculated genetic differentiation (F_{ST}), adjusted for null alleles using Freena[25], and allelic richness (number of alleles per locus), controlled for sample size using FSTAT[26], in each of the resulting 9 populations. However, due to the wide geographic spread of the data and the particular interest of this project, we split some analyses into two geographic extents: state-wide (9 populations) and Central Sierra area (11 sample sites).

Additional surveys

In the summer of 2011, TLM and research assistants undertook additional surveys in Yosemite National Park to assess the current distribution of Belding's ground squirrels in meadows in an appropriate elevation band for the species (greater than 2100m). Surveys followed methods in Morelli et al.[8] and identified 20 additional sites that were occupied and 18 sites that were unoccupied (Figure 3).

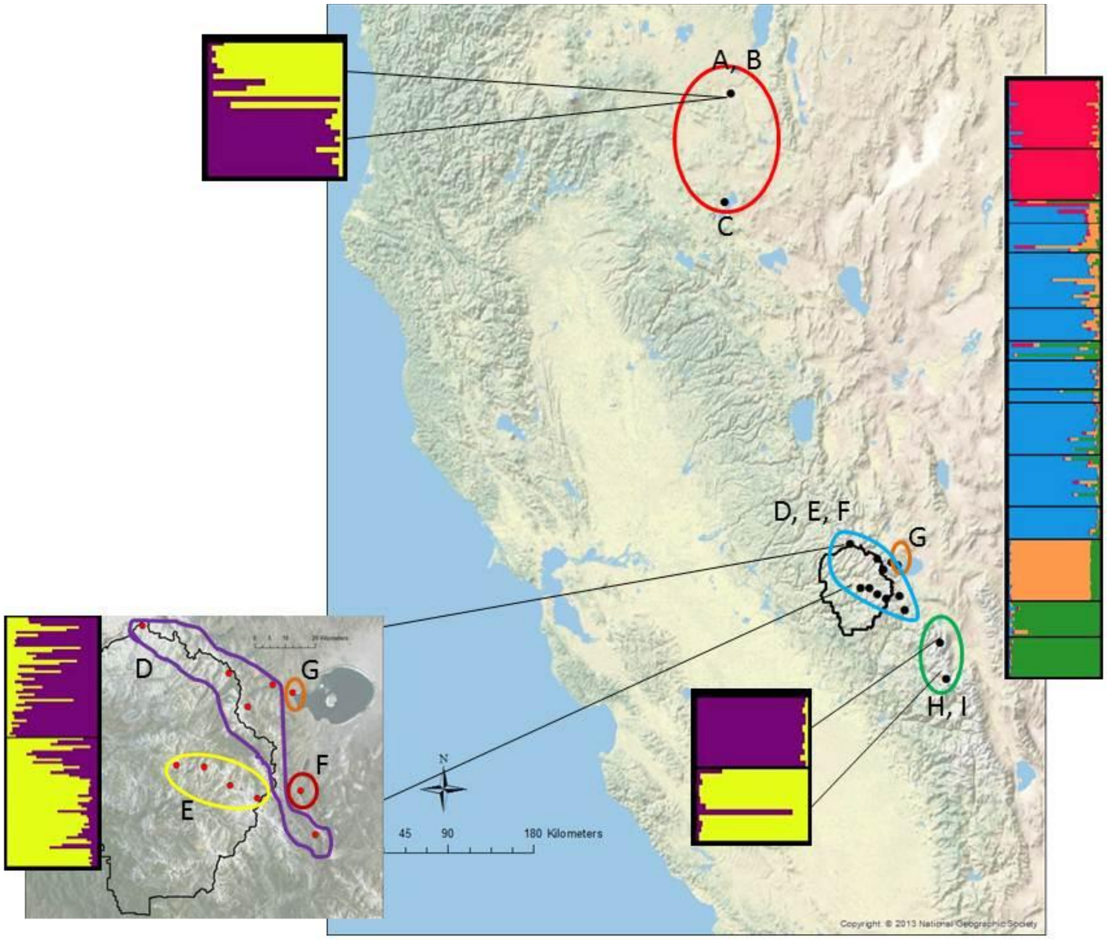

Figure 2. **Genetic samples and population structure.** Belding’s ground squirrel genetic sample sites mapped across California. Inset shows sampling in and just east of Yosemite National Park. STRUCTURE plot on right shows total California separation into four populations, corresponding to colored outlines on the map. Letters and yellow/purple STRUCTURE plots indicate further separation into nine populations after subsequent STRUCTURE runs.

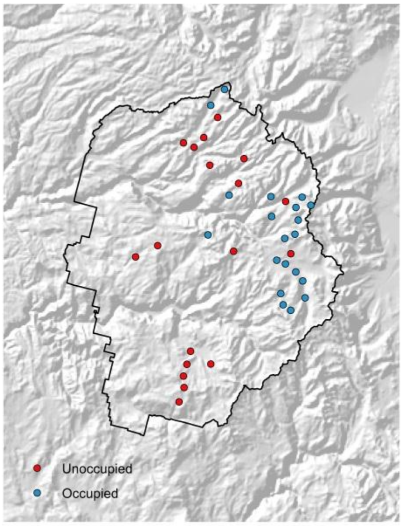

Figure 3. Locations of 2011 Surveys with Observational Results. The 38 survey sites were distributed throughout Yosemite National Park, with the 20 occupied sites more frequent in the east and northeast than the 18 unoccupied sites. Occupied sites had higher levels of connecitivity and were more often in regions that did not experience as much as environmental change as the unoccupied sites.

Analysis of Meadow Connectivity and Refugia

To test if the meadow connectivity layers and potential refugia explained patterns in occupancy, we overlaid the locations of the 2011 surveys, buffered by 2km, using R packages sp[27], maptools[28], rgdal[29], and rgeos[30]. We extracted the expected connectivity of surfaces corresponding to Hypotheses 2–4, as well as values from the putative refugia maps using the raster package. We used a one-sided Welch two sample t-test to ask whether mean connectivity of occupied sites was greater than unoccupied sites. We excluded Hypotheses 1 and 5 from this analysis because of potential issues of transferring resistance surfaces through time. We used Wilcoxon rank tests to examine whether occupied sites changed less than unoccupied sites, and whether observed modern climate and hydrological variables differed between sites (Table 1).

After validation of our hypotheses, connectivity and change values for each meadow were determined by overlay. We then identified the meadows that were in the upper quartile of connectivity in all of the resistance surfaces and classified these as "well-connected". Meadows that were in the upper quartile of at least one of the four surfaces were classified as "relatively well-connected". We analyzed the elevation and size of well-connected and relatively well-connected meadows compared to the unclassified set by plotting stacked histograms. If our classifications are random draws of meadows, then we expected them to have similar size and elevational distributions. Maps of the classified meadows were generated (Figure 4). We also identified those larger meadows that were not well-connected to determine their geographic position within the Sierra Nevada.

Meadows were then classified as refugial or non-refugial based on the values extracted in the change maps. We used the following thresholds to define climate change refugia: temperature changes within 1°C, relative precipitation, snowpack, and CWD changes within 10%, and no more than 30 or 60 months above the extreme historical minimum temperatures. While these criteria were not based on statistical models, they do identify sites undergoing little change. To aid in prioritization for climate change adaptation strategies, we extracted values from the future scenario change maps and applied the same thresholds.

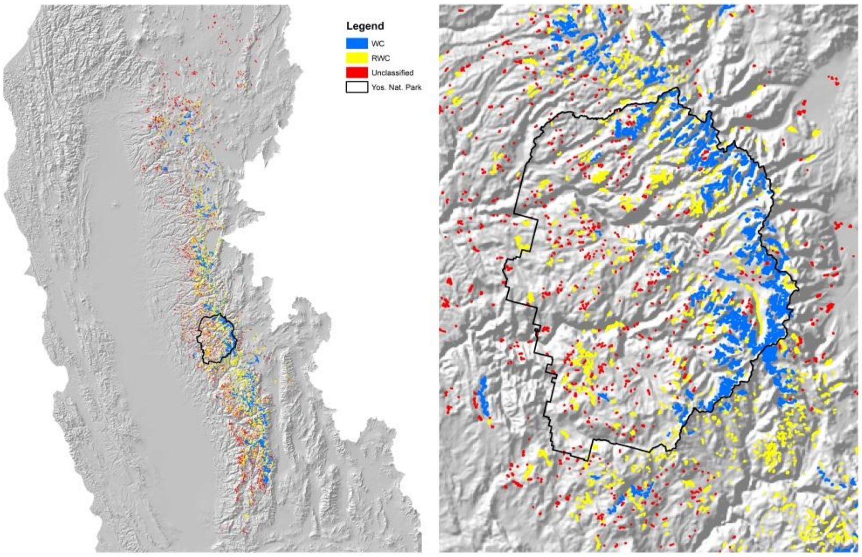

Figure 4. Geographic distribution of well-connected meadows. Meadows in blue were the most well-connected (see text for definition) of the four non-climate related resistance surfaces, whereas relatively well-connected meadows are show in yellow. The remaining meadows are show in red. Maps are presented for the entire Sierra Nevada, as well as a focal map around Yosemite National Park to demonstrate the finer-scale variability in position.

Analysis of Connectivity and Refugia on Patterns of Genetic Diversity

Patterns of genetic diversity were analyzed with respect to refugia and connectivity in two ways. First, we addressed Hypotheses 2–5 using values of Fst and the matrices from the site-level Circuitscape analysis. For Hypothesis 1, we calculated the minimum Euclidean distance between populations using the package sp. We used the Multiple Matrix Regression R (MMRR) method developed by Wang[31] and backward selection to test whether a combination of distance matrices could explain the Fst patterns. The advantage of this approach, as opposed to Mantel tests, is that it allowed the comparison of several distances matrices simultaneously as well as the amount of variation explained by the given model.

Second, we examined the pattern of allelic richness for four well-supported populations within and around Yosemite National Park. We used measures of connectivity and values from our change maps for these sites as predictor variables with allelic richness as the response variable in general linear models. We expected that more connected sites and those sites that experienced minimal environmental change would have higher values of allelic richness.

We interpolated allelic richness across the Sierra Nevada to provide a visual representation of genetic diversity using spatial and model-based approaches using ArcGIS and the Geostatistical Analyst and Spatial Analyst extensions. For spatial methods, we used the 15 genetically sampled locations, and either estimated spatial decay relationships using semi-variograms or assumed decay based on the distance from sites. The latter approach allows for a relatively naïve and parsimonious interpolation using inverse-distance-weighting. Assuming that the trend in allelic richness is due to distance alone, we estimated a semi-variogram of allelic richness using 12 20-km lags, allowed for anisotropy, and interpolated values using ordinary kriging. We then estimated the spatial decay based on patterns of potential refugia, using results from the fine scale analysis of the Central Sierra Nevada, and interpolated values using ordinary co-kriging. We also applied the results of regression analysis on the raster grids to provide a non-spatially determined interpolation. Accuracy was assessed using root mean square error (RMSE) which varies from unity (perfect assessment), with larger values suggesting more error.

Analysis of Individual Species Responses to Climate Change
Finally, we examined patterns of local extinctions of small mammals using an occupancy modeling approach[32]. This framework includes an explicit estimate of the probability of detecting each taxon, which is key to understand distributional change of rare and elusive species. Using the robust multi-season model, which first estimates historical occupancy and detection and then estimates colonization and extinction, we tested various covariates to uncover whether changes in climate-influenced extinction probability.

Using Grinnell Resurvey Project trapping data from across the Sierra Nevada[3,33], we identified 82 matching sites that represented either overlapping locations or non-overlapping locations at similar elevation and with similar vegetative composition that were sampled during historical and modern surveys. From these data, we modeled local extinction responses for 17 small mammal species (Table 2), representing a variety of 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 species[33]. We fit 32 extinction models based on changes in climate and isolation at the modern sampling site. The covariates included 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 among 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 colext in the R package unmarked[34].

Table 2. The number of sites where small mammals were sampled. Naïve states do not account for detectability, and will overestimate colonization, extinctions, and naïve absences.

Species	Naïve Absence (Both Periods)	Naïve Colonizations	Naïve Extinctions	Naïve Occupancy (Both Periods)
Callospermophilus lateralis	43	6	11	22
Dipodomys heermanni	76	0	6	0
Microtus californicus	61	3	7	11
Microtus longicaudus	33	8	10	31
Microtus montanus	49	11	10	12
Neotoma cinerea	47	4	16	15
Neotoma macrotis	60	7	6	9
Peromyscus boylii	45	5	12	20
Peromyscus maniculatus	3	3	10	66
Peromyscus truei	48	10	8	16
Reithrodontomys megalotis	56	5	9	12
Sorex palustris	60	1	15	6
Sorex trowbridgii	65	6	5	6
Tamias alpinus	67	0	10	5
Tamias senex	66	5	6	5
Tamias speciosus	43	6	12	21
Zapus princeps	54	8	9	11

RESULTS

Environmental variables consistently indicated 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 were also evident in the monthly raw climate variables and hydrological estimated values. In particular, there was 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.

Meadow Connectivity and Refugia

Maps for Hypotheses 2–5 for meadows generally showed different patterns of connectivity across the landscape (Figure 5). Environmental heterogeneity had patchily distributed regions of high values,

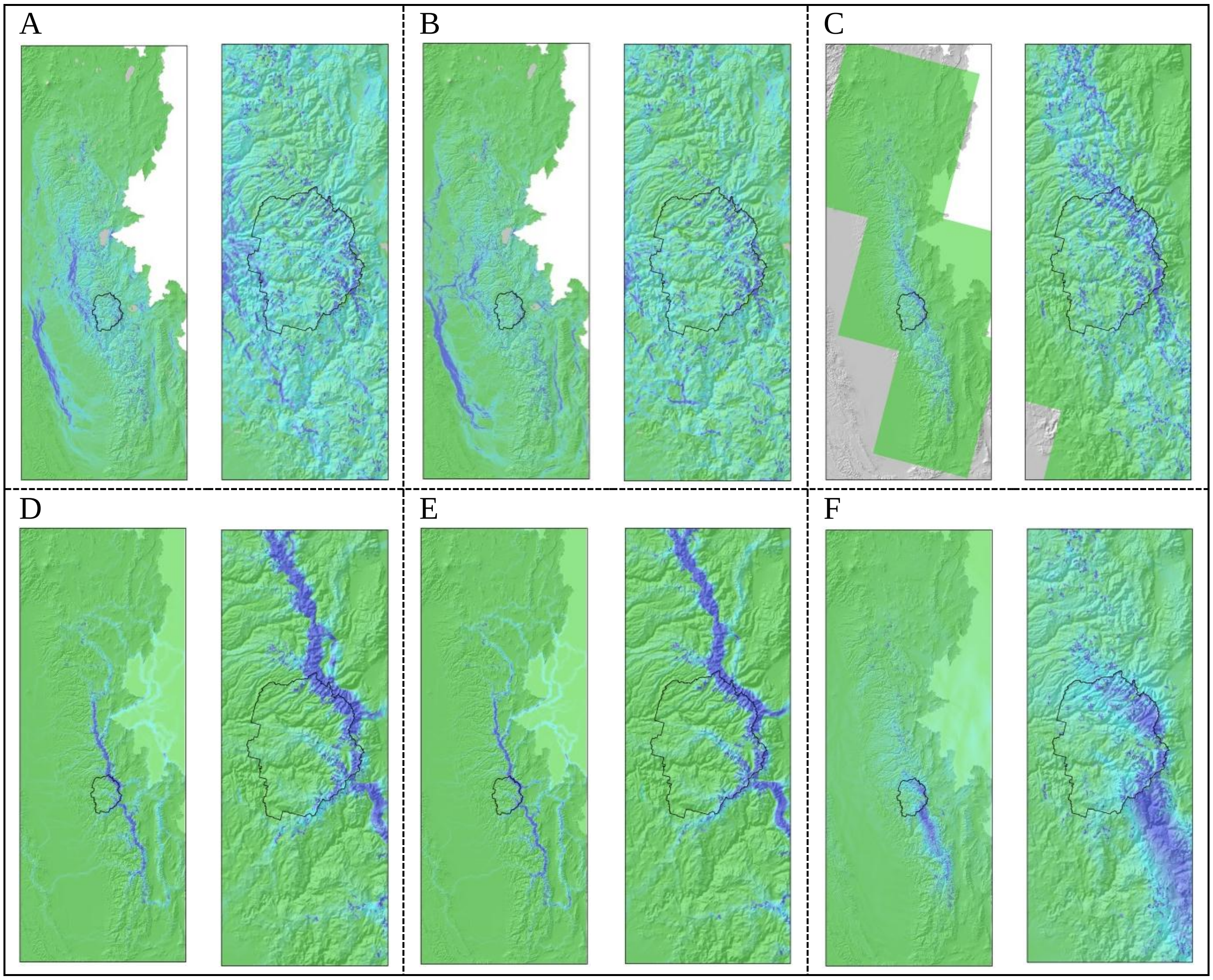

Figure 5: Patterns in connectivity based on six friction surfaces. The friction surfaces represent a subset of hypotheses of isolation of the "meadow systems": environmental heterogeneity (measured from spatial variability in climatic water deficit in Historical (A) and Modern (B) periods); elevationally weighted distance (C); Presence of watercourses (D); distance from watercourses (E); and distance from roads (F). We present each summary map over a hillshade surface to highlight the potential relationships between connectivity and topography, as well as a zoomed view of the Central Sierra. Each hypothesis resulted in distinct general patterns: the mottled but well-connected pattern with environmental heterogeneity; the patchiness resulting from roads; and spaghetti pattern following crests based on distance from watercourses and elevation. We include the outline of Yosemite National Park for reference.

whereas watercourses and topography had more contiguous areas of high values associated with higher elevations. Isolation by roads had a mixture of these patterns, with a relatively contiguous pattern in the southern Sierra Nevada and more patchily-distributed areas of high connectivity in the north. Meadows with high connectivity values tended to be larger and occurred at higher elevations than less-connected meadows (Figure 6). The geographic pattern of well-connected and relatively well-connected meadows shows a broad distribution within the Sierra Nevada, with clustering in parts of the central and southern regions.

The geographic positions of surveys were well spread throughout Yosemite (Figure 2011 Surveys), and sites were at least 2km apart. These data supported the hypothesized connectivity maps; measures of connectivity were higher for occupied sites than unoccupied sites from the 2011 Belding's ground squirrel surveys ($t_{24.952} = 3.1705$, $P = 0.002$). Furthermore, several potential refugial measures showed differences between the occupied and unoccupied sites (Table 1).

Meadows that were well-connected and refugial were more isolated. Projected future changes suggest many meadows will change beyond our refugial constraints. The magnitude and extent of refugial meadows depended upon the scenario; the less severe B2 scenarios projected some stable sites throughout the next century, whereas the A1 scenarios projected the absence of refugial meadows (Table 3). However, the elevational distribution of the meadows, along with the naïve hypothesis that species will move upward in elevation to deal with warming temperatures, suggests that some meadow specialists may have dispersal routes to reach suitable habitats. Furthermore, some of the refugial variables show well-connected refugia may occur in the southern Sierra Nevada by the end of the next century (Figures 7 & 8, Appendix).

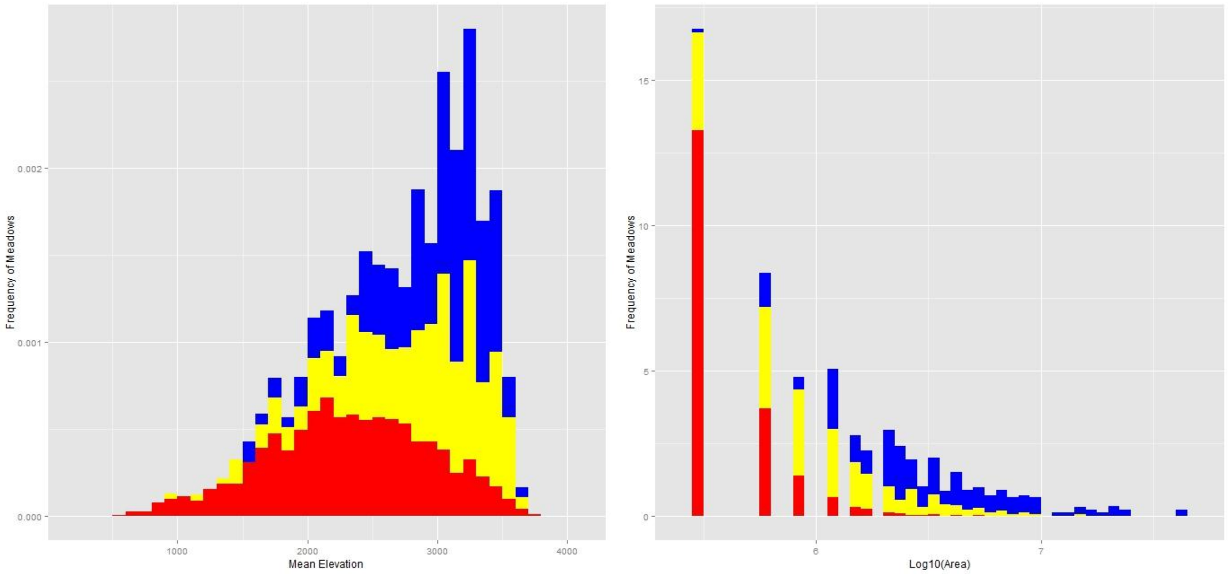

Figure 6. Frequency of connectivity with elevation and size. The stacked histograms shows meadows that have high connectivity values in each of four non-climate related resistance surfaces occur at high elevations and, in general, are of larger size. Blue bars represent meadows occurring in the 90th quantile of each connectivity surface; yellow bars are meadows within the 75th quantile, but not the 90th quantile; red bars are the remaining meadows.

Table 3. Number of Refugial Meadows Relative to Associated Connectivity. The count of meadows in which variables did not exceed the refugial climate threshold based on change from historical observations. Meadows were classified as well-connected and relatively well-connected (WC and RWC, see text for details), and we present those unclassified under the Rest heading. Estimates are presented for two circulation models (GFDLA and PCM) under two emission scenarios (A2 and B1) for 30 year periods.

Variable (Threshold Value)	**Period**	**GFDLA**						**PCM**					
		A2			**B1**			**A2**			**B1**		
		WC	**RWC**	**Rest**	**WC**	**RWC**	**Rest**	**WC**	**RWC**	**Rest**	**WC**	**RWC**	**Rest**
Annual Temp (1° C)	2010–2039	137	461	550	148	520	710	134	462	603	132	433	557
	2040–2069	79	225	68	89	282	129	79	232	73	93	292	143
	2070–2099	0	0	0	76	211	65	3	15	0	72	196	62
Max Temp of the Warmest Month (1° C)	2010–2039	127	633	1119	154	748	1390	204	978	1685	238	1186	2133
	2040–2069	69	176	33	101	365	401	108	354	305	126	465	680
	2070–2099	0	0	0	72	200	89	48	116	15	114	385	400
Min Temp of the Coldest Month (1° C)	2010–2039	55	221	500	8	50	309	69	276	568	25	120	495
	2040–2069	0	3	89	8	31	285	8	40	290	61	247	447
	2070–2099	0	0	4	1	9	124	0	0	35	1	11	151
Mean Temp of the Coldest Quarter (1° C)	2010–2039	221	899	1353	162	579	756	124	404	508	83	264	182
	2040–2069	81	240	90	82	272	150	61	178	66	93	295	275
	2070–2099	0	0	2	69	195	55	0	0	0	11	37	20
Annual Precipitation (10%)	2010–2039	337	1526	1482	236	956	906	222	845	608	2	28	14
	2040–2069	296	1229	1104	301	1207	1062	165	605	374	315	1372	1426
	2070–2099	197	1101	2010	317	1537	2162	111	388	284	61	247	221
Climatic Water Deficit (10%)	2010–2039	14	72	439	30	106	466	44	139	694	37	154	754
	2040–2069	0	7	61	3	38	304	16	64	336	16	74	428
	2070–2099	0	4	10	0	13	161	0	8	105	20	83	358
1 April Snowpack (10%)	2010–2039	221	941	973	226	1075	1046	272	922	816	20	270	440
	2040–2069	256	865	736	225	732	627	232	651	476	290	967	885
	2070–2099	78	282	283	88	321	334	182	433	376	184	616	565
Extreme Max Temp (30 Months)	2010–2039	98	267	121	99	285	161	117	395	387	100	292	303
	2040–2069	53	143	59	46	138	83	69	180	100	95	252	185
	2070–2099	0	0	0	45	136	54	5	33	34	52	153	91
Extreme Min Temp (30 Months)	2010–2039	115	413	372	131	496	586	123	479	479	110	423	369
	2040–2069	74	216	71	81	254	119	62	172	66	77	251	95
	2070–2099	0	0	0	67	192	61	6	19	0	60	181	60
Extreme Max Temp (60 Months)	2010–2039	143	451	341	154	529	507	190	685	966	168	595	798
	2040–2069	82	203	88	103	269	148	117	344	228	144	484	463
	2070–2099	2	15	3	82	199	101	47	131	59	102	267	195
Extreme Min Temp (60 Months)	2010–2039	217	966	1511	285	1212	1890	275	1162	1679	229	935	1356
	2040–2069	94	339	229	122	477	532	100	343	191	127	465	438
	2070–2099	5	30	0	92	323	189	42	116	31	96	335	180

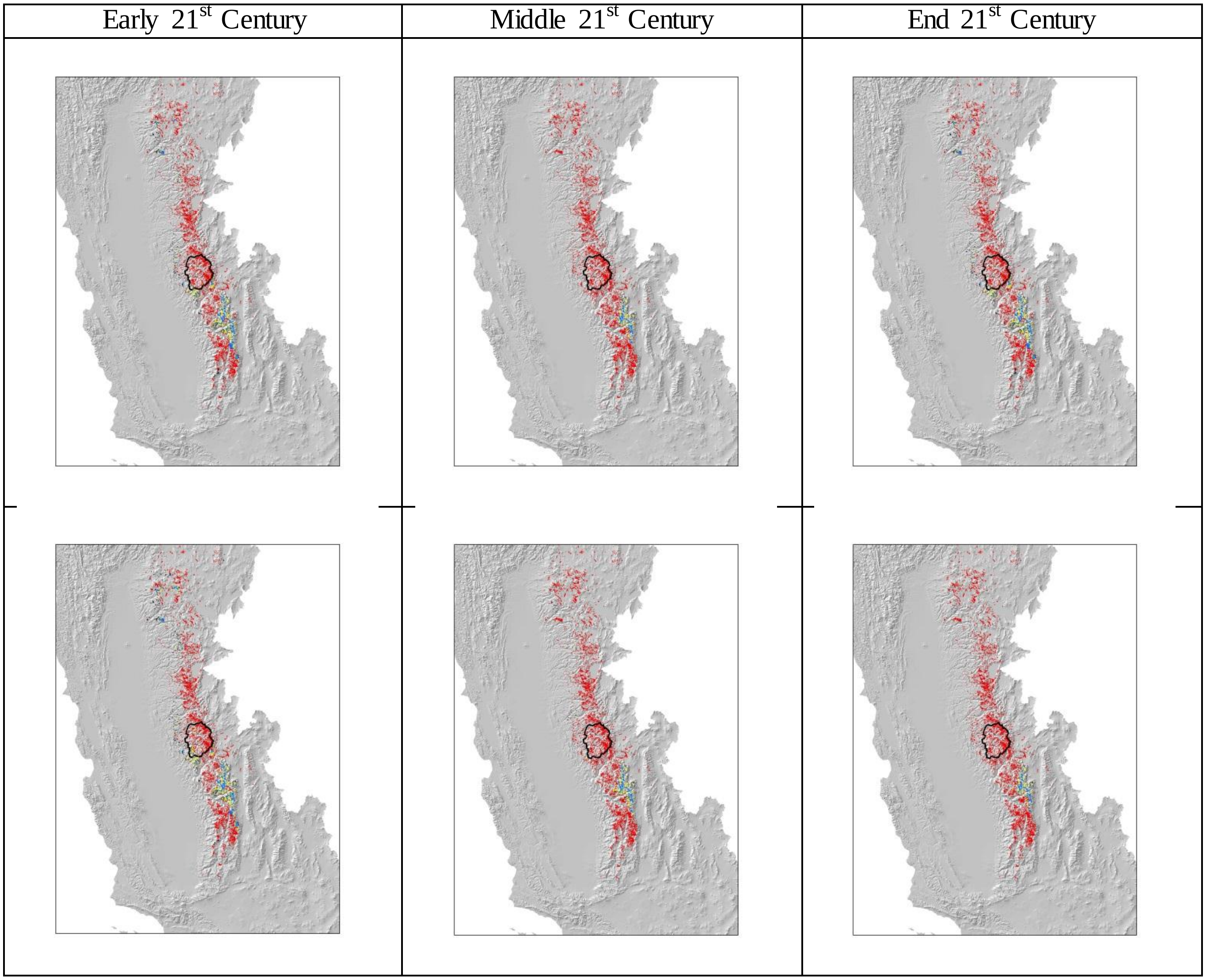

Figure 7. Expectation of well-connected, potential refugial meadows using GFDLA circulation models. Maps show well-connected meadows that are within in 1°C in annual temperature in blue, and those relatively well-connected in yellow under A2 (top row) and B1 (bottom row) scenarios. Change is the difference in expected annual temperature from the historic period (see text). Overall, it is expected that most well-connected meadows will change beyond the historical conditions, expect those in the southern Sierra Nevada.

Patterns of Genetic Diversity as Validation of Meadow Refugia and Connectivity

Initial geographic partitioning by the STRUCTURE analysis split state-wide samples into four genetic regions (indicated by circles in Figure 2): Northern California (red), Yosemite area (blue), Mono Lake County Park (orange) and the southern Sierra (green). Subsequent partitioning further split these areas into 9 populations, as can be seen in Figure 1 and its subset. F_{ST} values supported this differentiation, with especially high values among the four genetic regions and lowest values within population areas. Three of the nine groups occur in the northern extent of our sampling, four around and within Yosemite National Park, and two more in the Southern Sierra Nevada. Based on these 9 subdivisions, we compared Fst values, which measure gene flow between populations, to the hypothesized connectivity between these locations. When comparing matrices for 9 populations we found parsimonious support for Hypothesis 3, watercourses as barriers, ($\beta_{river\_con} = -0.011$, $\beta_{river\_bin} = 133.78$, $F = 35.78$, $P = 0.001$, $R^2 = 0.684$). A more parameter-rich model supporting multiple hypotheses was found ($\beta_{modcwd} = -1.16e-06$, $\beta_{pathdist} = -1.04e-05$, $\beta_{river\_con} = 20.76$, $\beta_{river\_bin} = -0.027$, $F = 61.69$, $P =$

0.001, $R^2 = 0.89$), but the extra coefficients, while significant, were very close to unity. When treating the Central Sierra Nevada sites as populations, again there was support for Hypothesis 3 ($\beta_{river\_con} = 54.99$, $F = 53.32$, $P = 0.001$, $R^2 = 0.34$), although less of the variation was explained.

Next, we characterized patterns of allelic richness across the nine populations and with the restricted Central Sierra Nevada set. We found no support that refugial sites had higher allelic richness across the Sierra Nevada using the 9 populations. However, refugial sites in the Central Sierra Nevada did have higher values of allelic richness that were associated with modern values of the mean temperature of the coldest quarter ($\beta = -0.60$, $t_9 = -4.47$, $R^2_{adj} = 0.68$, $P = 0.002$). Higher connectivity values were also associated with increased allelic richness ($\beta = 0.48$, $t_9 = 2.92$, $R^2_{adj} = 0.43$, $P = 0.017$), but a multiple regression suggested that climate was the more contributing factor ($\beta_{Bio11} = -0.28$, $t_7 = -4.83$, $P = 0.0016$, $\beta_{Conn} = 2.29\text{e-}06$, $t_7 = 1.518$, $P = 0.17$, $\beta_{Int} = 3.98\text{e-}07$, $t_7 = 1.615$; $R^2_{adj} = 0.82$, $F_{3,7}; = 10.39$, $P = 0.006$).

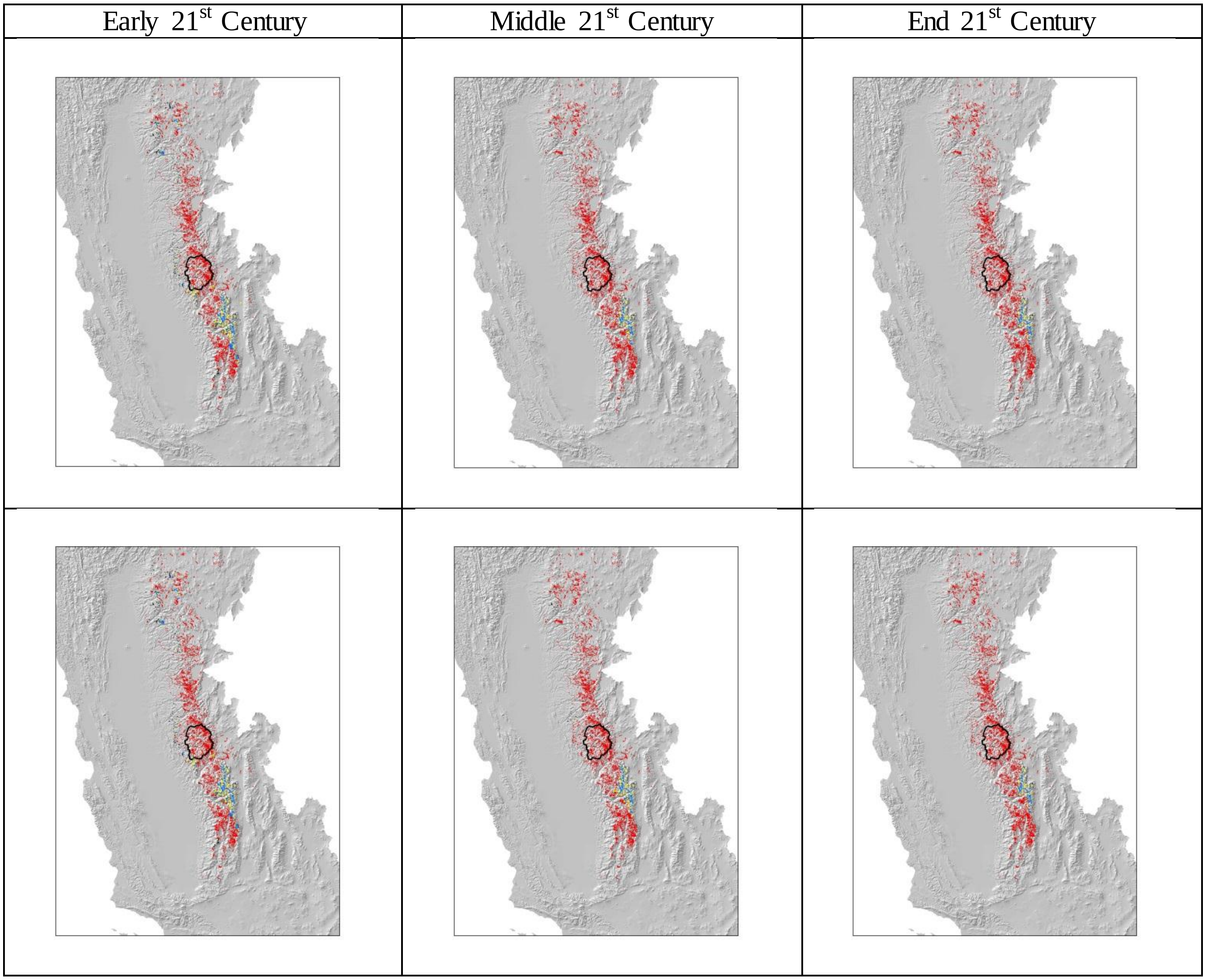

Figure 8. Expectation of well-connected, potential refugial meadows using PCM circulation models. Maps show well-connected meadows that are within in 1°C change in annual temperature in blue, and those relatively well-connected in yellow under A2 (top row) and B1 (bottom row) scenarios. Change is the difference in expected annual temperature from the historic period (see text). Overall, most well-connected meadows are projected to change beyond the historical conditions, except those in the southern Sierra Nevada.

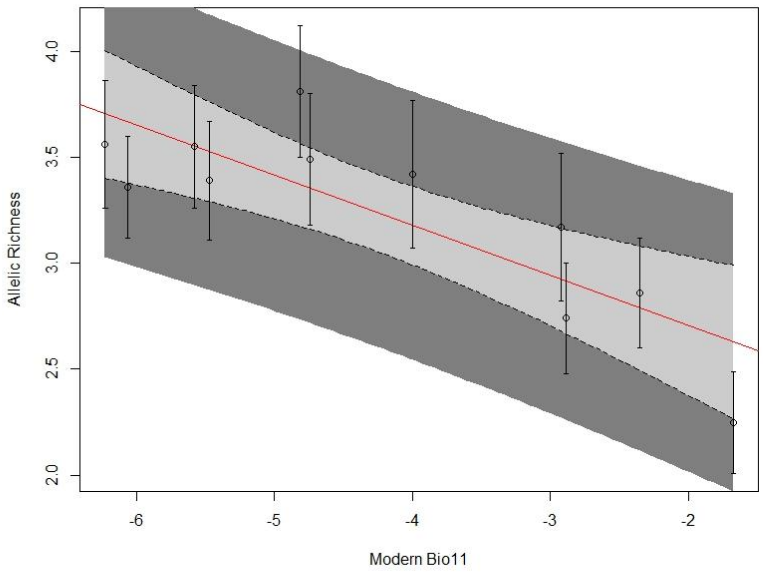

Figure 9. Linear regression of mean temperature of the coldest quarter predicting allelic richness for sites in the Central Sierra Nevada. The best-fit line is shown in red; confidence intervals are shown in light gray; predictions intervals are shown in dark grey. Each of the sample sites is plotted with error bars representing ±1 SE.

When interpolating patterns of allelic richness across the Sierra Nevada using values from individual sites, error rates were high given the magnitude of expected values (Table 4) and spatial methods performed better than the linear model. Patterns of allelic richness based on spatial interpolation showed a relatively even expectation across the species' range in the Sierra Nevada, whereas the linear model provided more variability and a striking decrease in the north (Figure 9). There was also disagreement between the classes of maps in the southern extent, as the spatial methods found a reduced expectation and the linear model predicted higher values of allelic richness. The number of underestimated sites was not different than expected by chance for any of the methods ($P > 0.05$ in all cases).

Table 4. Accuracy assessments of interpolation of Allelic Richness.

Interpolation Method	RMSE	Locations Underestimated
IDW	0.486	9
Kriging	0.361	9
Co-Kriging	0.361	9
LinearModel	0.746	7

Analysis of Individual Species Responses to Climate Change

To understand how results generalized across taxa, we modeled changes in occupancy for 17 small mammal species across the Sierra Nevada. Thirteen species showed signals of climate change on extinction (Table 5), while the null model was the top models for the 4 species (*T. alpinus*, *P. truei*, *M. longicaudus*, and *Dipodomys heermanni*). 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*. For many taxa, too few observations were available to make a reasonable estimate of extinction probability, and even those presented here represent a liberal interpretation of parameters.

For most species, models including a measure of isolation were not the best supported, but occasionally were within 2 AIC values. For instance, meadow isolation was strongly associated with extinctions in the western jumping mouse *Zapus princeps*, a species associated with grassy habitat and meadows, but not for other species associated with meadows, particularly voles. Many of the species we modeled in this framework prefer forests or are habitat generalists, which would limit the effect of connectivity on extinction because of limited metapopulation dynamics.

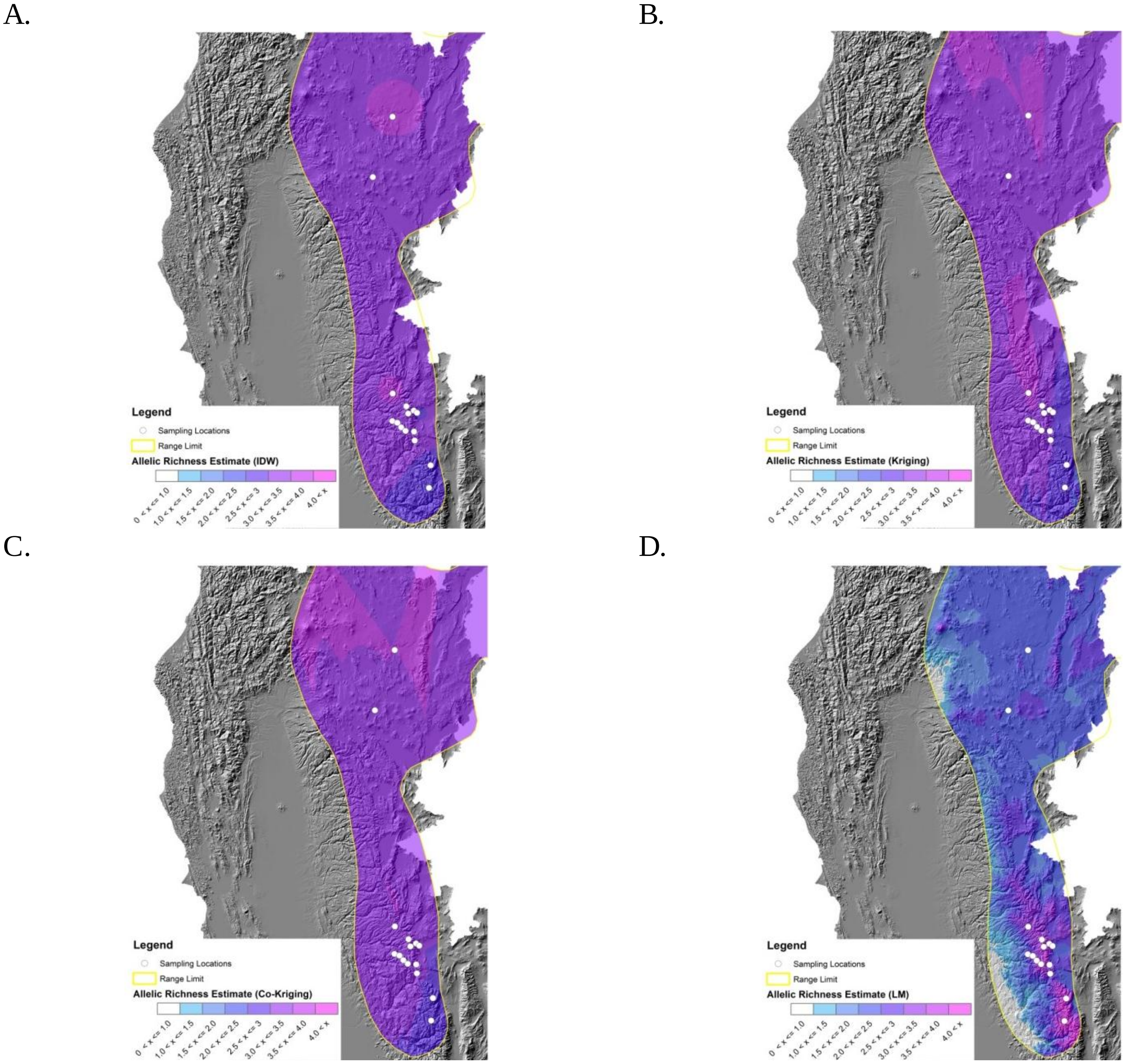

Figure 9. Patterns of allelic richness. Interpolated values of allelic richness. We present four estimates of patterns of AR of Belding's ground squirrel within the Sierra Nevada, overlaid on a hill-shade map (A. IDW, B. Kriging, C. Co-Kriging, D. Linear Model; see text for details). The species' range limit[35] is designated by the yellow line and sampling locations are shown as white dots. Higher values of expected AR are in bright purple, whereas lower values are in blue. Spatial methods suggest values ~3.5 throughout most of the range, whereas application of the linear model suggests much lower values in the northern extent.

Table 5. Summary of estimating the climate effects on extinction. Results are shown for species with support for climate as a possible mechanism for local extinction. Detection probabilities were fit as functions of trapping effort (T) and number of days at a site, whereas extinctions were fit as climate change variables or measures of isolation, defined as the distance to nearest observation of the species in the historic period.

Species	Extinction Covariates	Detection Covariates	AIC	ΔAIC
Callospermophilus lateralis	Extreme Min Temp + Extreme PPT (More)	logT + T100 + Time	621.084	0.000
	Extreme Min Temp	logT + T100 + Time	622.566	1.482
Microtus californicus	Extreme PPT (More)	logT + Time	338.261	0.000
	Extreme PPT (More)	logT + T100 + Time	339.276	1.015
	Extreme Max Temp+ Extreme PPT (More)	logT + Time	340.171	1.910
	Extreme Min Temp+ Extreme PPT (More)	logT + Time	340.236	1.975
Microtus montanus	Δ in Mean Precip + Δ in Mean Temp	logT + Time	572.021	0.000
	Δ in Mean Precip + Δ in Mean Temp	Time	572.569	0.548
	Δ in Mean Precip + Δ in Mean Temp	logT + T100 + Time	572.717	0.696
Neotoma cinerea	Δ in Mean Precip + Δ in Max Temp	Time	546.377	0.000
	Δ in Mean Precip + Δ in Mean Temp	Time	547.448	1.071
	Δ in Mean Precip + Δ in Min Temp	Time	547.735	1.357
Neotoma macrotis	Extreme Min Temp	T100 + Time	383.530	0.000
	Extreme Min Temp	Time	383.760	0.230
	Extreme Min Temp	logT + T100 + Time	383.897	0.366
	Extreme Min Temp+ Extreme PPT (Less)	T100 + Time	383.916	0.385
	Extreme Min Temp	logT + Time	384.290	0.759
	Extreme Min Temp+ Extreme PPT (Less)	Time	385.418	1.888
	Extreme Min Temp+ Extreme PPT (More)	T100 + Time	385.436	1.905
	Extreme Min Temp+ Extreme PPT (Less)	logT + T100 + Time	385.497	1.967
Peromyscus boylii	Δ in Snowpack	logT + Time	677.339	0.000
	Δ in Snowpack	logT + T100 + Time	677.968	0.629
Peromyscus maniculatus	Extreme PPT (Less)	logT + T100 + Time	1014.858	0.000
	Extreme Max Temp+ Extreme PPT (Less)	logT + T100 + Time	1016.488	1.630
Reithrodontomys megalotis	Δ in CWD + Δ in Max Temp	logT + T100 + Time	406.804	0.000
	Extreme Max Temp	logT + T100 + Time	407.154	0.350
	Extreme Max Temp + Extreme Snowpack (Less)	logT + T100 + Time	407.238	0.434
	Extreme Max Temp + Extreme PPT (More)	logT + T100 + Time	407.864	1.060
	Δ in CWD + Δ in Max Temp	T100 + Time	408.256	1.452
	Extreme Max Temp + Extreme Snowpack (More)	logT + T100 + Time	408.422	1.618
	Extreme Max Temp	T100 + Time	408.708	1.903
	Extreme Max Temp + Extreme Snowpack (Less)	T100 + Time	408.753	1.949
	Δ in CWD + Δ in Mean Temp	logT + T100 + Time	408.788	1.984
Sorex palustris	Δ in Mean Precip + Δ in Mean Temp	Time	348.582	0.000
	Δ in Mean Precip + Δ in Mean Temp	T100 + Time	349.373	0.791
	Extreme Snowpack (More)	Time	349.428	0.846
	Isolated + Isolated (Up or Down)	Time	349.451	0.869
	Δ in Mean Precip + Δ in Min Temp	Time	349.528	0.946
	Isolated + Isolated (Up or Down)	T100 + Time	349.661	1.078
	Extreme Snowpack (More)	T100 + Time	349.681	1.099

	Δ in Mean Precip + Δ in Mean Temp	logT + T100 + Time	350.014	1.432
	Δ in Mean Precip + Δ in Mean Temp	logT + Time	350.228	1.646
	Δ in Mean Precip + Δ in Mean Temp	1	350.234	1.652
	Δ in Mean Precip + Δ in Min Temp	T100 + Time	350.311	1.729
	Isolated + Isolated (Up or Down)	logT + T100 + Time	350.367	1.785
	Extreme Snowpack (More)	logT + T100 + Time	350.461	1.879
Sorex trowbridgii	Δ in CWD + Δ in Max Temp	Time	282.169	0.000
	Δ in CWD + Δ in Max Temp	T100 + Time	283.516	1.347
	Δ in Min Temp + Δ in Max Temp	Time	283.569	1.400
	Δ in Max Temp	Time	283.728	1.560
	Δ in Min Temp + Δ in Max Temp	T100 + Time	284.004	1.835
	Δ in CWD + Δ in Max Temp	logT + Time	284.019	1.850
	Δ in Mean Precip + Δ in Mean Temp	Time	284.093	1.924
Tamias speciosus	Extreme Min Temp+ Extreme PPT (More)	logT + T100 + Time	637.782	0.000
	Extreme Max Temp+ Extreme PPT (More)	logT + T100 + Time	638.069	0.288
Zapus princeps	Isolation + Δ in Min Temp + Δ in Max Temp	logT + Time	466.943	0.000
	Isolation + Δ in Min Temp + Δ in Max Temp	T100 + Time	467.289	0.347

DISCUSSION

Our project used a multi-faceted approach to understand small mammal responses to changing climate and the role of connectivity in persistence. We measured climate and environmental change during the 20th century, generated a map of the connectivity of meadows across the Sierra Nevada, highlighted hypothesized refugial meadows, and validated hypotheses of refugia and connectivity using genetic and survey data from a meadow specialist. Our results provide empirical insight into the expectation of forthcoming change, particularly identifying sensitive regions in the Central Sierra Nevada.

A primary scientific 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 a focus, as suggested by resource managers and federal researchers, because it is likely that connectivity between these important and sensitive habitats will be consistent for a variety of mammal taxa. Furthermore, we expect that other taxonomic groups, such as amphibians and reptiles, likely are impacted by similar changes in the landscape and their populations could be influenced by isolation in a manner similar to non-volant small mammals. The ability of species to move in response to climate change[36] may be influenced by the ease that they can move through the matrix of habitat and non-habitat. Identifying putative barriers, such as watercourses, can inform management decisions regarding facilitated movement and distinguishing sensitive and isolated habitats.

Our results showed a heterogeneous geography of climate change, particularly that aspects of seasonal dynamics will be in flux. Well-connected habitats should maintain a metapopulation structure, particularly for vagile species that are able to move through a changing matrix. Our results suggest that Belding's ground squirrels are isolated by watercourses, suggesting that dispersal across such barriers is limited or that individuals use alternative routes around these features. If meadow systems change due to decreases in moisture or encroaching trees, we expect that populations will become increasingly fragmented.

Analysis of the genetic diversity also demonstrated a link to recent environmental conditions. Habitats that were warmer had reduced allelic richness, suggesting they may represent areas of frequent re-colonization after local extinction events, possibly due to environmental stress. The frequency of population extirpations before recolonization is not yet clear, although both recent and long-term trends in the environment can predict Belding's ground squirrel occupancy[8].

Occupancy modeling results suggested that local extinction events were related to changing environmental conditions, especially changes in precipitation and temperature. Changes in precipitation have been dramatic, particularly in the northern Sierra Nevada; increased precipitation likely had an indirect effect 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 are 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. Future work by Sean Maher and Steve Beissinger will focus on using information from multiple species to provide more robust estimates of local extinction with respect to 20th century climate change.

Logistically, the full activities of the project were delayed due to the departure of the primary postdoctoral researcher for a position with the US Forest Service; her replacement did not begin work for another five months. Thus we are grateful to the LCC for allowing us to extend the project for several months past the original timeline, allowing us to meet all of the original project objectives.

There are multiple management implications for this study. In the context of anthropogenic climate change, natural resource managers need to make decisions about where to focus restoration, resilience, and other adaptation strategies[37,38]. To help guide limited resources, tools such as the maps produced through this study can aid identification of areas of particularly high value or high vulnerability. Thus the connectivity maps can be used to locate putative areas of exceptionally low or high connectedness and respond accordingly. Moreover, the climate change refugia indicated through this study could be assessed for potential management intervention and considered in the context of the connectivity measures in order to optimize management efforts (Table 6).

Table 6. We provided Yosemite National Park with data regarding meadows classified by connectivity and whether they were refugial or not. Below is a sample of columns and rows from the attribute table.

Longitude	Latitude	Area	WC	RWC	CWD	Ann Temp	Ann Precip	Max Temp Warmest Month	Min Temp Coldest Month	Mean Temp Coldest Quarter	Extreme Min Temp
-119.6204190	37.4055448	583200	0	0	1	1	1	1	0	1	0
-119.5757525	37.4117922	291600	0	1	1	1	1	0	0	1	0
-119.5664543	37.4093164	874800	0	1	1	1	1	0	0	1	0
-119.6188484	37.4187746	291600	0	0	1	1	1	0	0	1	0
-119.6015762	37.4178841	291600	0	0	1	1	1	0	0	1	0
-119.7212831	37.4210378	1166400	0	0	1	1	1	0	0	1	0
-119.5983124	37.4240151	291600	0	0	1	1	1	0	0	1	0
-119.5795628	37.4224767	291600	0	1	1	1	1	0	0	1	0
-119.6697471	37.4353329	291600	0	0	1	1	1	0	0	1	0
-119.6966551	37.4344543	583200	0	0	1	1	1	0	0	1	0
-119.5571795	37.4248557	2332800	0	1	1	1	1	0	0	1	0
-119.7379657	37.4357625	291600	0	0	1	1	1	0	0	1	0
-119.4963547	37.4390637	291600	0	0	1	1	1	0	0	1	0
-119.6792205	37.4403955	291600	0	0	1	1	1	0	0	1	0
-119.6705769	37.4399391	291600	0	0	1	1	1	0	0	1	0
-119.5440574	37.4407233	291600	0	1	1	1	1	0	0	1	0
-119.7460678	37.4434937	291600	0	0	1	1	1	0	0	1	0
-119.4982991	37.4440201	291600	0	0	1	1	1	0	0	1	0
-119.5053684	37.4460604	291600	0	0	1	1	1	0	0	1	0
-119.4252083	37.4447862	291600	0	0	1	1	1	0	0	1	0
-119.4805953	37.4391952	1166400	1	0	1	1	1	0	0	1	0
-119.4571539	37.4461686	583200	0	1	1	1	1	0	0	1	0
-119.5612078	37.4504282	291600	0	1	1	1	1	0	0	1	0
-119.4732491	37.4498806	291600	0	0	1	1	1	0	0	1	0
-119.7312258	37.4516607	291600	0	0	1	1	1	0	0	1	0
-119.4363310	37.4496594	291600	0	1	1	1	1	0	0	1	0
-119.6371465	37.4522861	291600	0	0	1	1	1	0	0	1	0
-119.7456780	37.4516790	583200	0	0	1	1	1	0	0	1	0
-119.4634141	37.4524467	291600	0	1	1	1	1	0	0	1	0

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Determining Landscape Connectivity and Climate Change Refugia Across the Sierra Nevada

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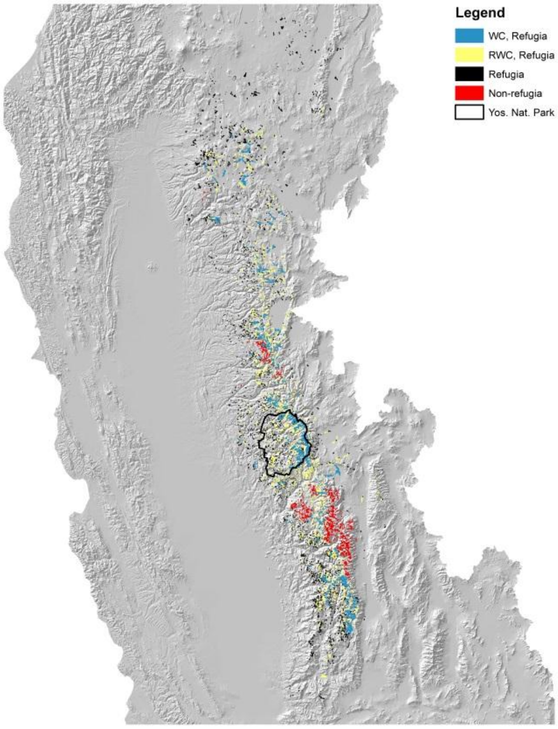
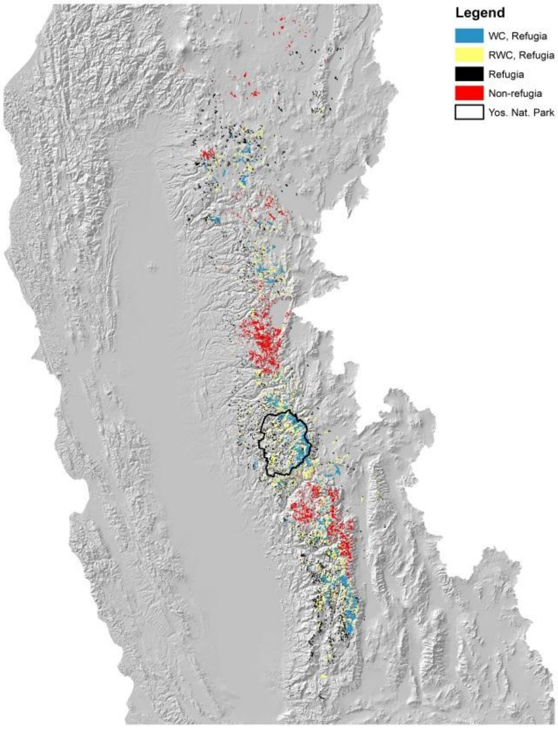
Appendix – Refugia Maps

On the following pages, we present results of estimating connectivity between meadows and classification of these as well-connected (WC), relatively well-connected (RWC), or neither. Furthermore we classify meadows as refugia and non-refugia based on observed or expected changes in the environmental variable.

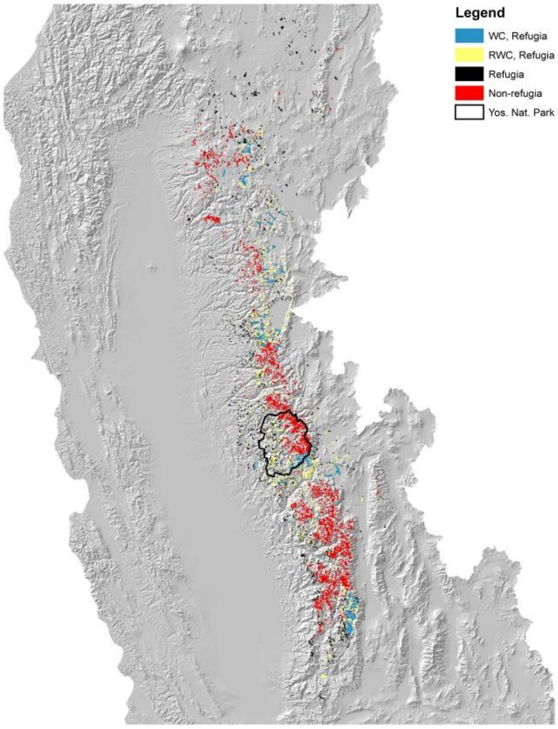
20th Century Annual Temperature



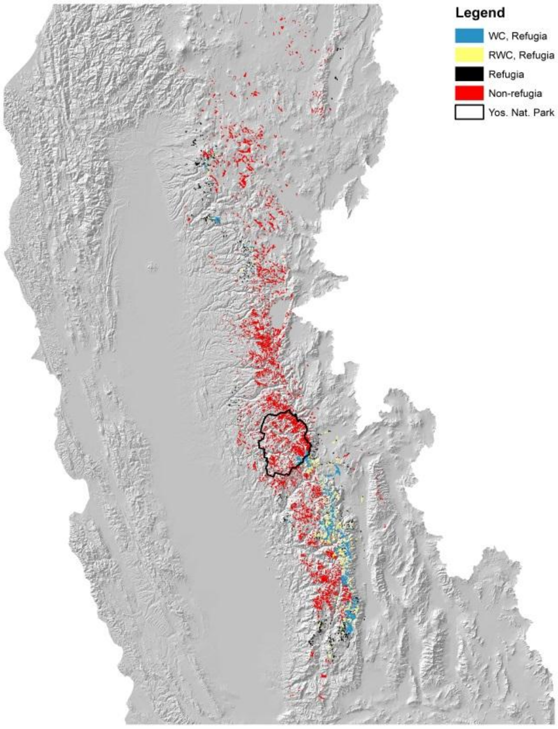
20th Century Mean Temp of Coldest Quarter



20th Century Climatic Water Deficit

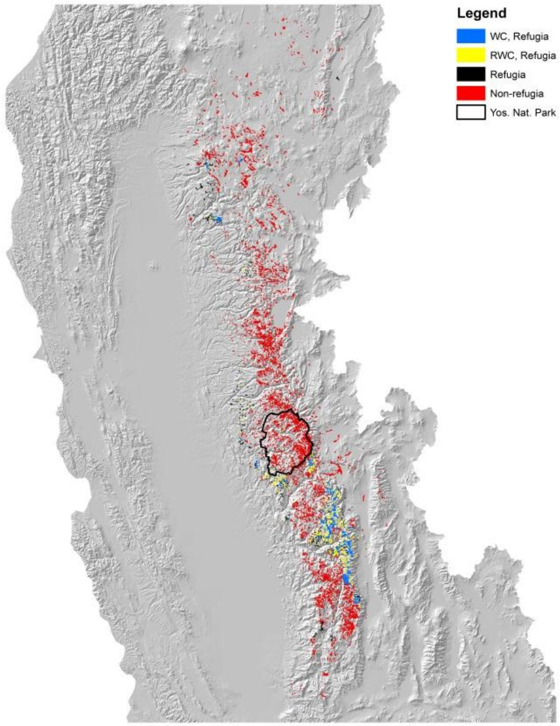


20th Century Extreme Minimum Temperature

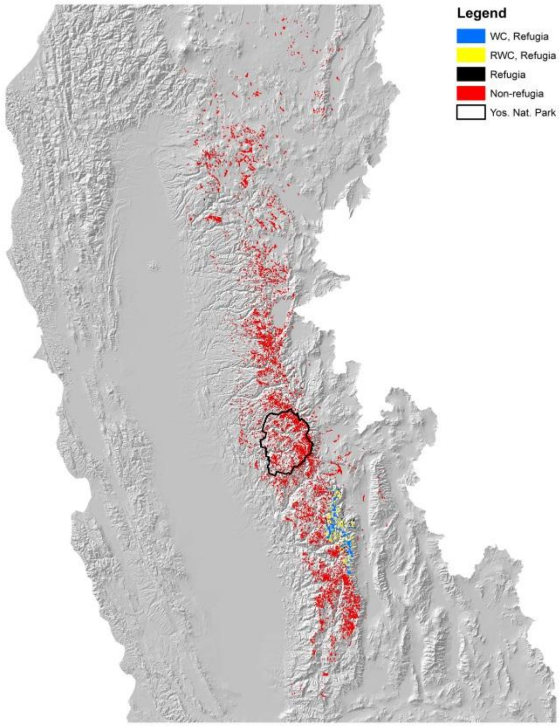


GFDL A2 Annual Temperature

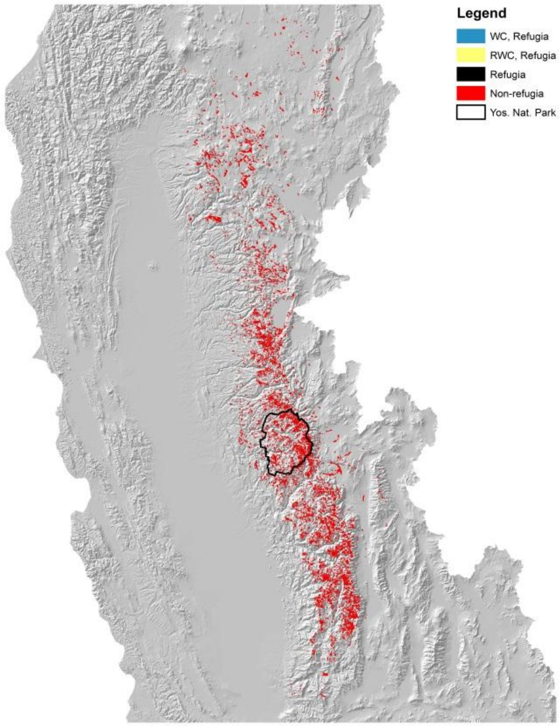
2010–2039

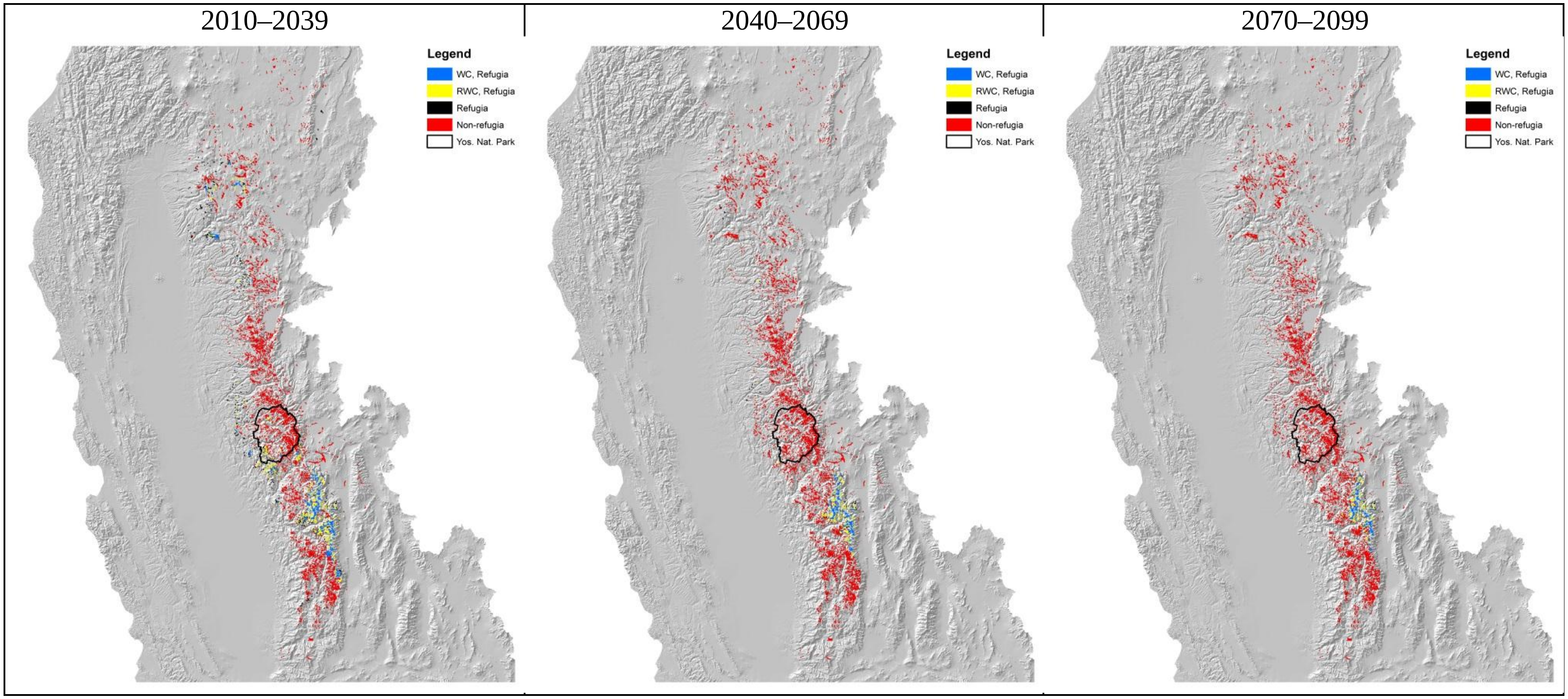


2040–2069



2070–2099





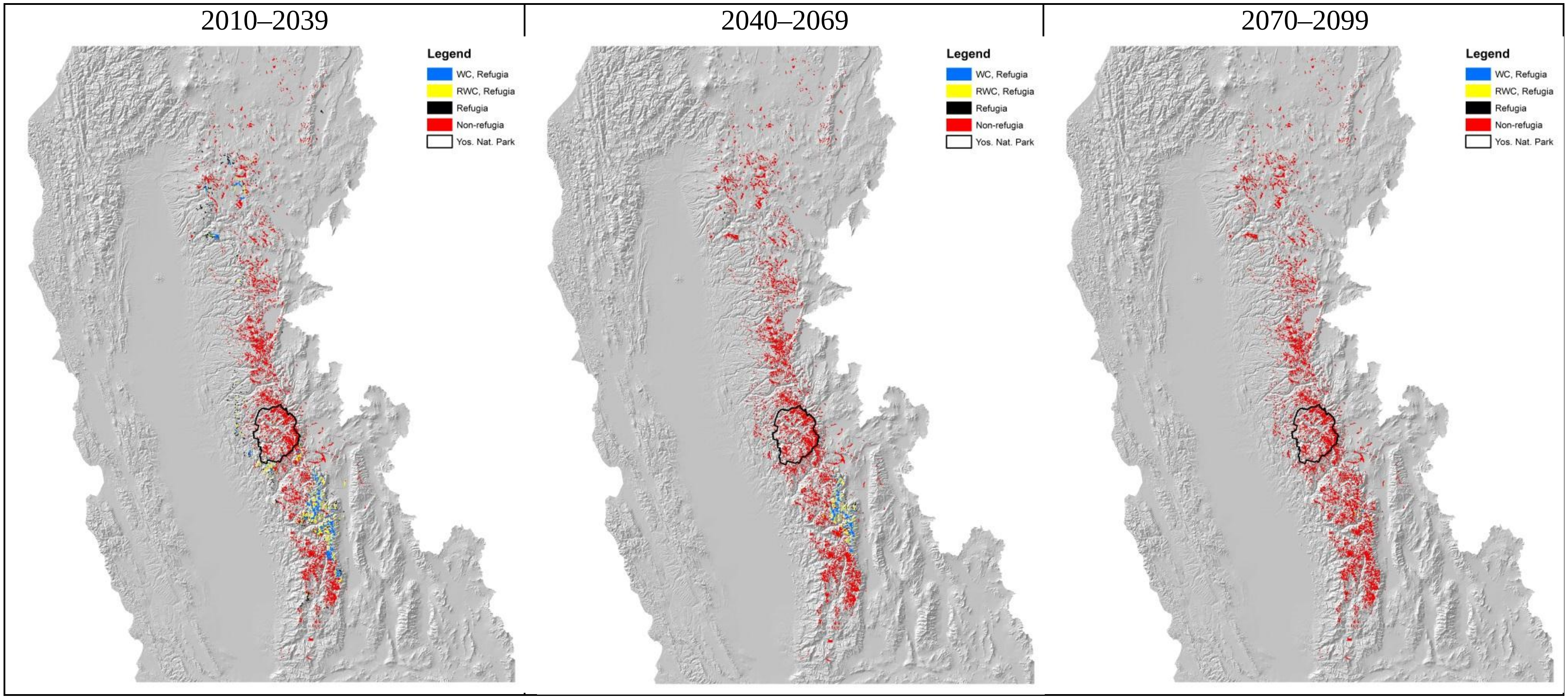
GFDL B1 Annual Temperature

2010–2039

2040–2069

2070–2099

PCM A2 Annual Temperature

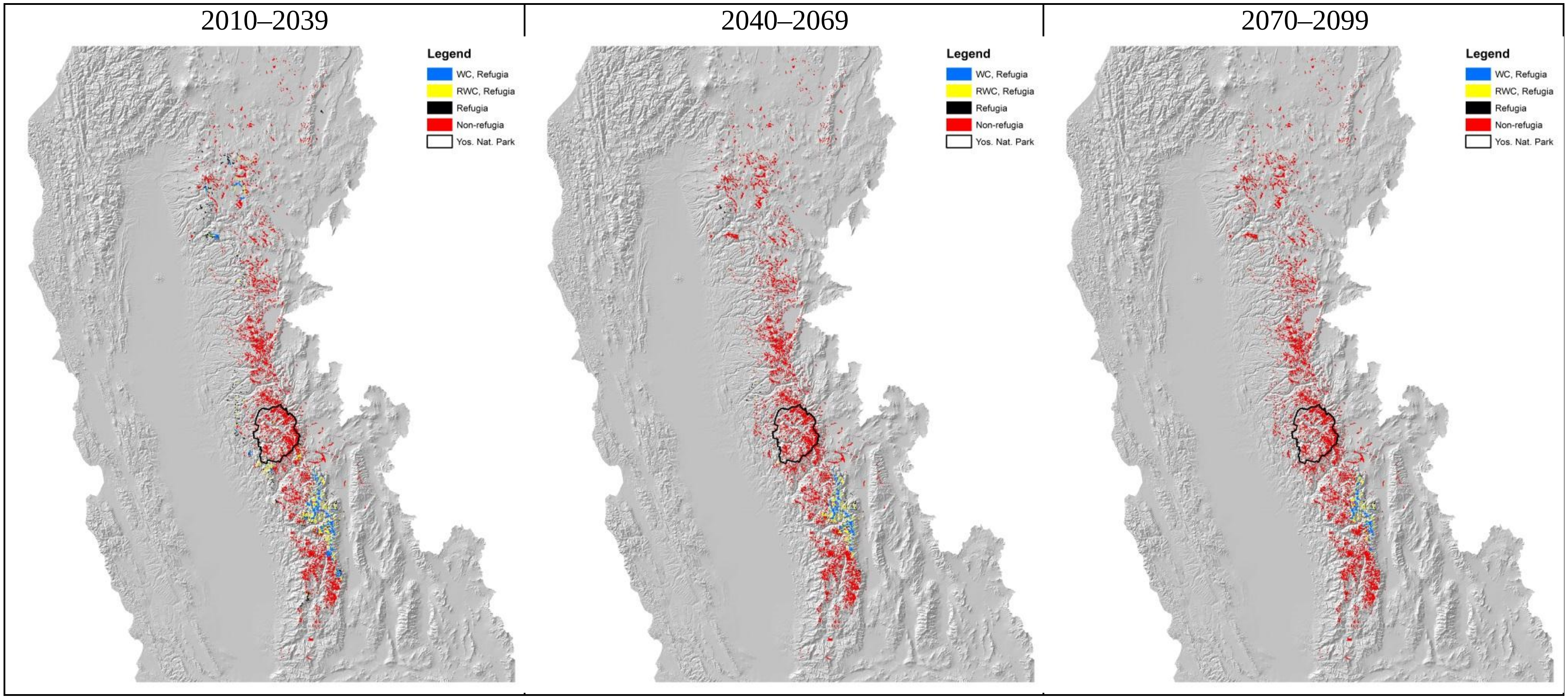


2010–2039

2040–2069

2070–2099

PCM B1 Annual Temperature

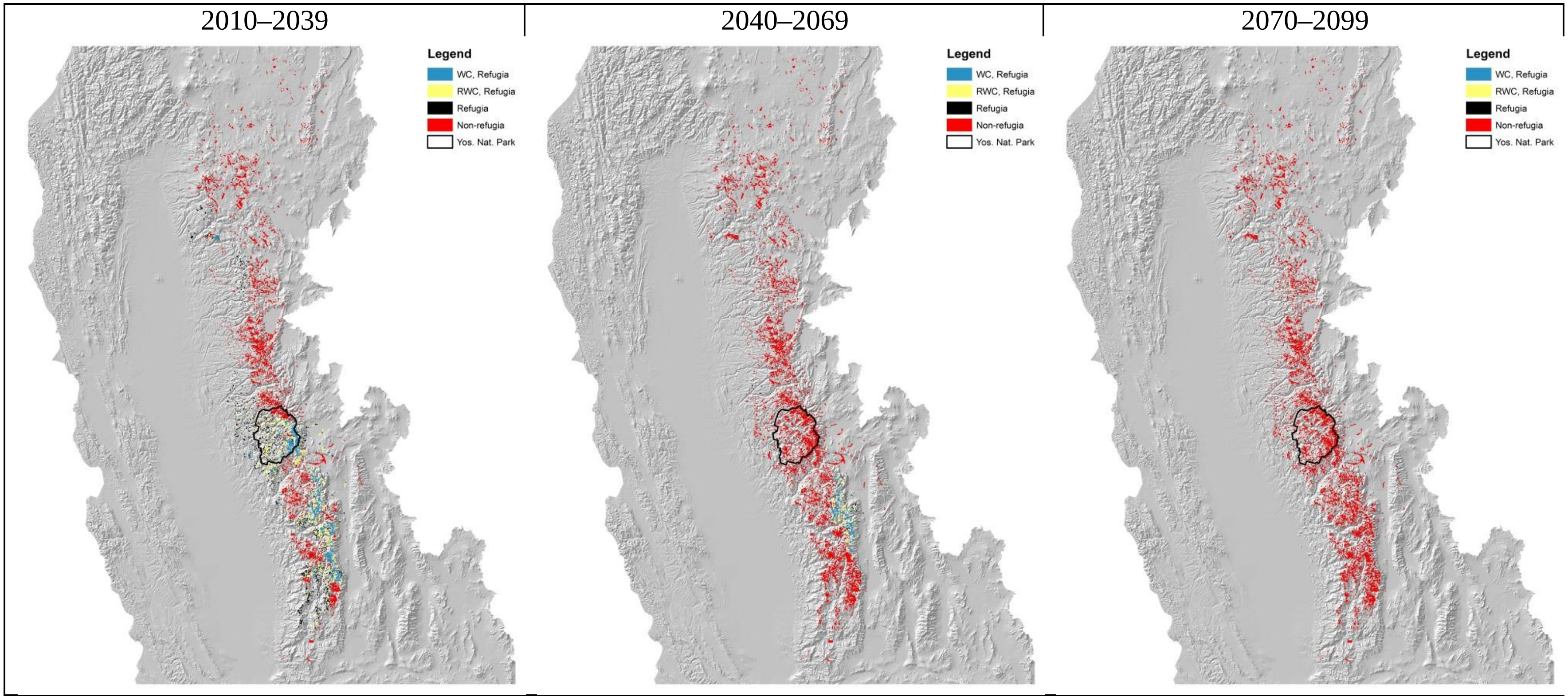


2010–2039

2040–2069

2070–2099

GFDL A2 Mean Temperature of the Coldest Quarter

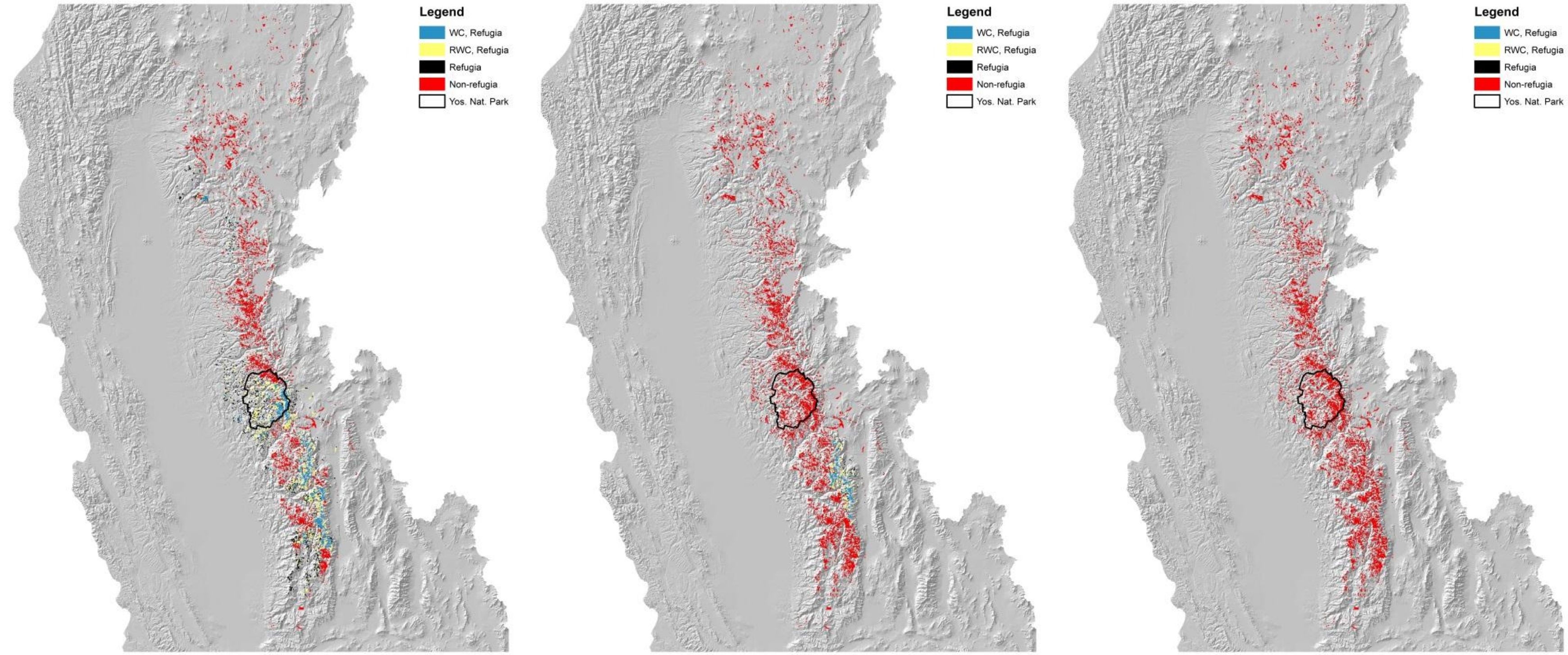


2010–2039

2040–2069

2070–2099

GFDL B1 Mean Temperature of the Coldest Quarter

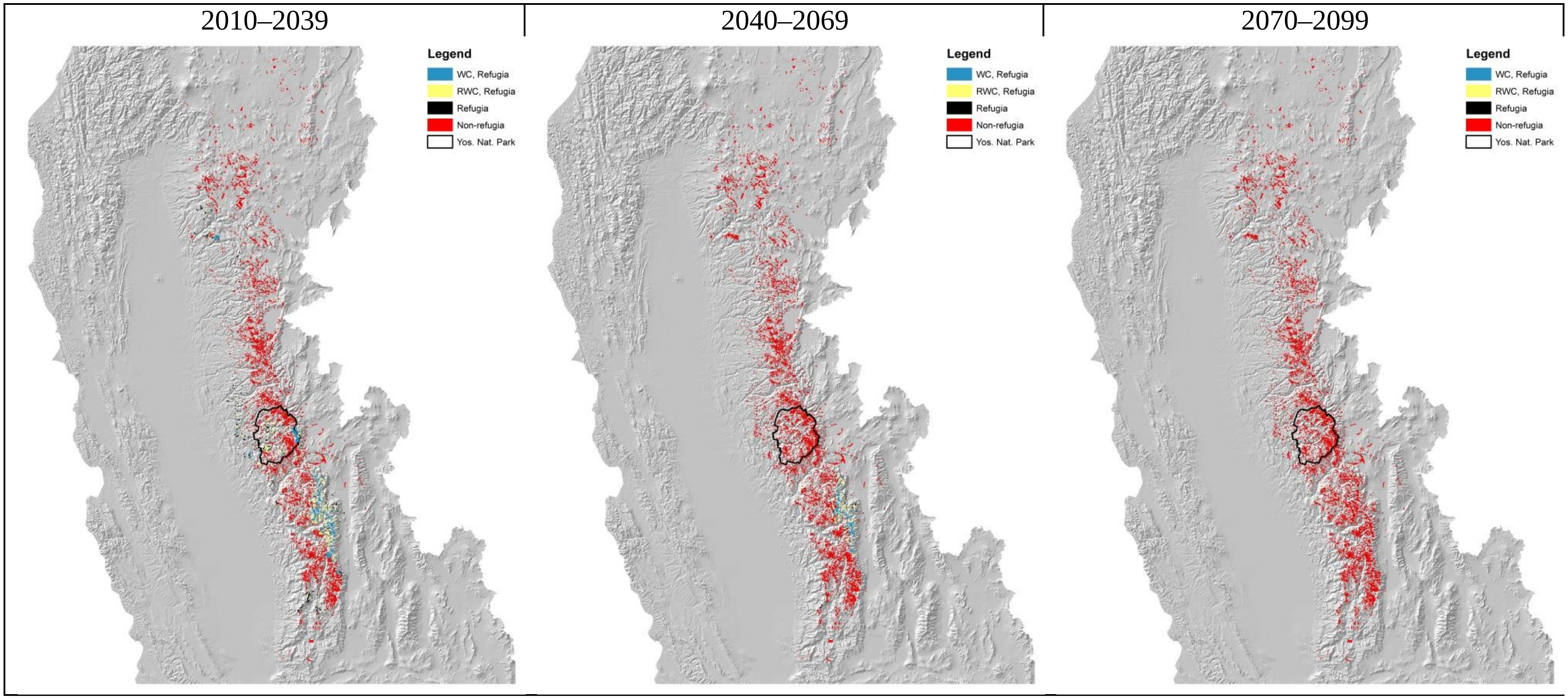


2010–2039

2040–2069

2070–2099

PCM A2 Mean Temperature of the Coldest Quarter

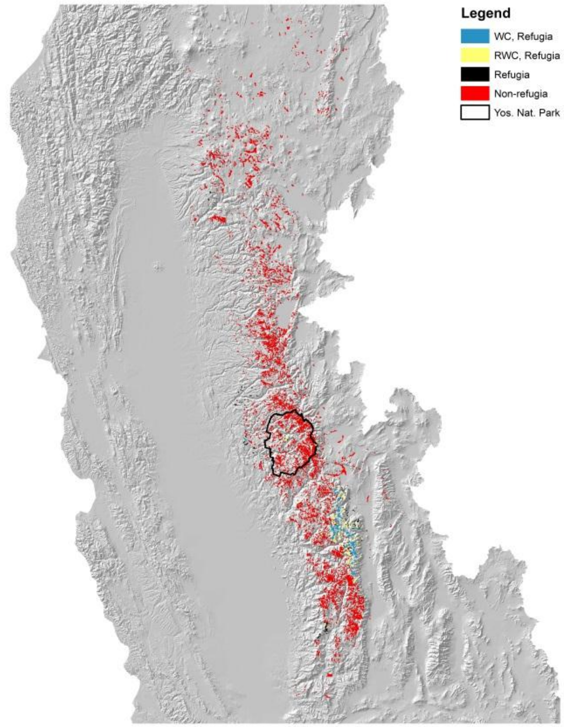
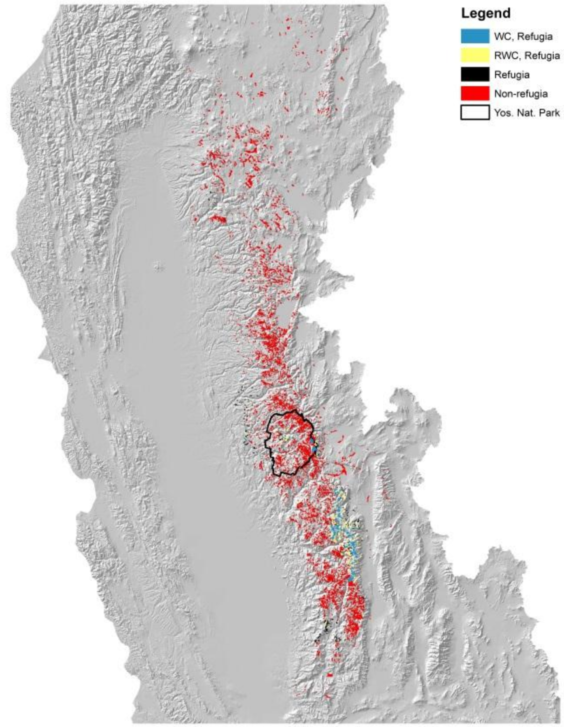
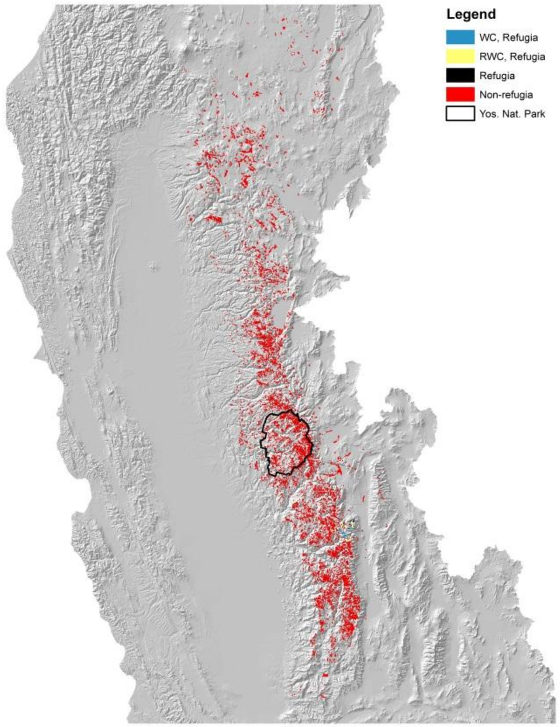


2010–2039

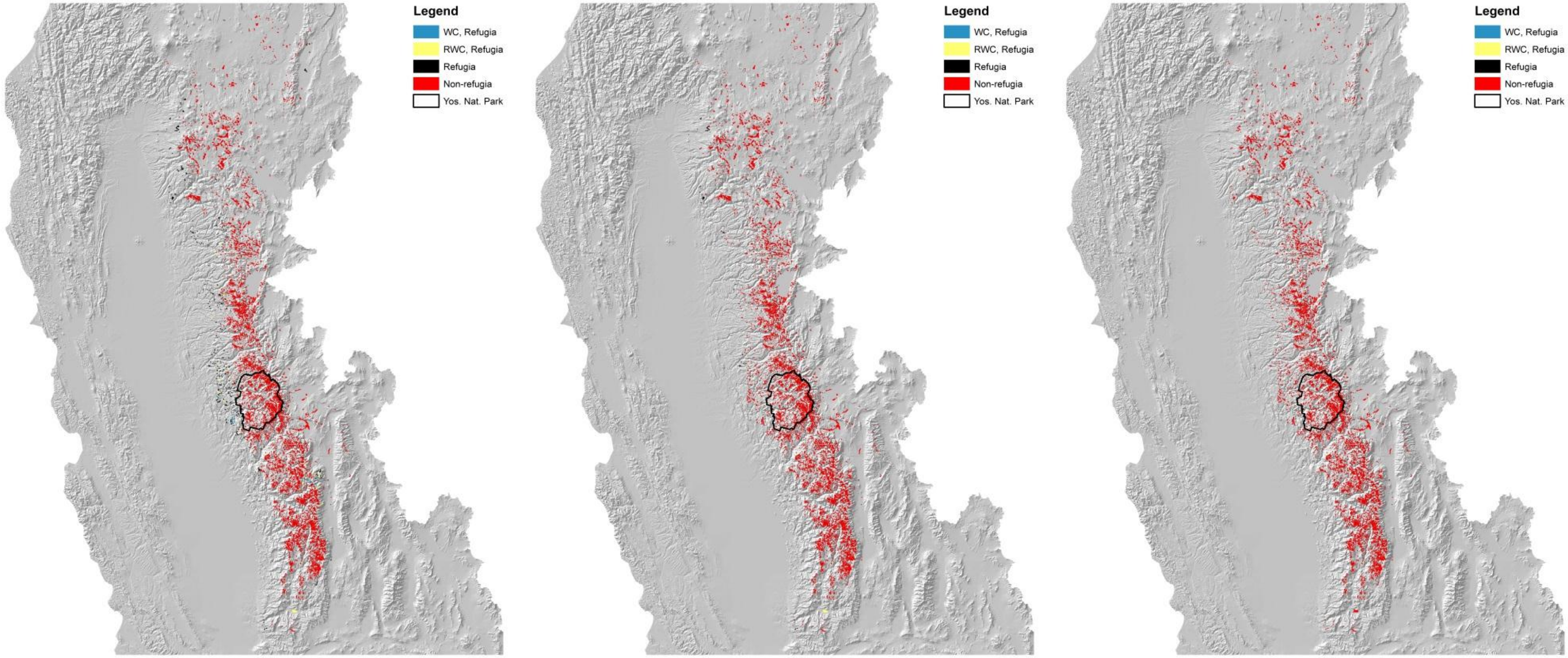
2040–2069

2070–2099

PCM B1 Mean Temperature of the Coldest Quarter

2010–2039	2040–2069	2070–2099
		

GFDL A2 Climatic Water Deficit

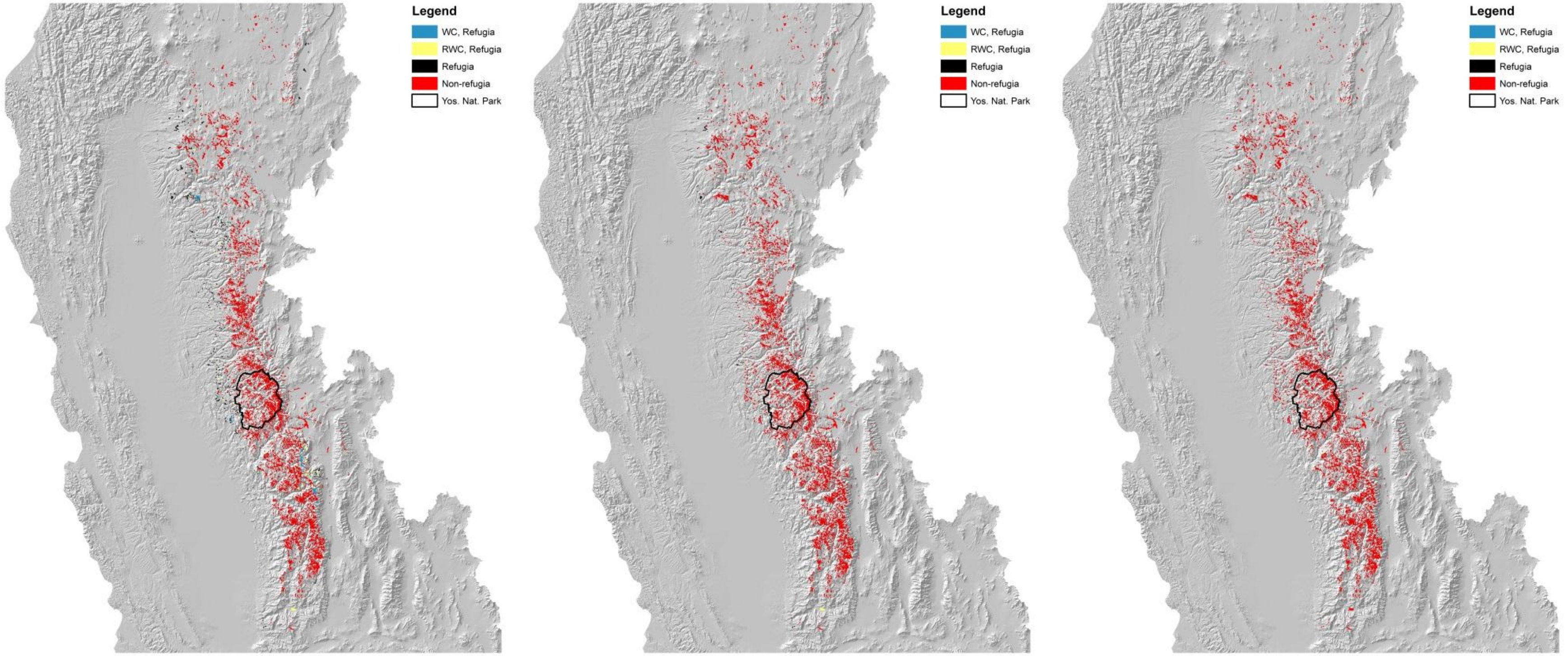


2010–2039

2040–2069

2070–2099

GFDL B1 Climatic Water Deficit



2010–2039

2040–2069

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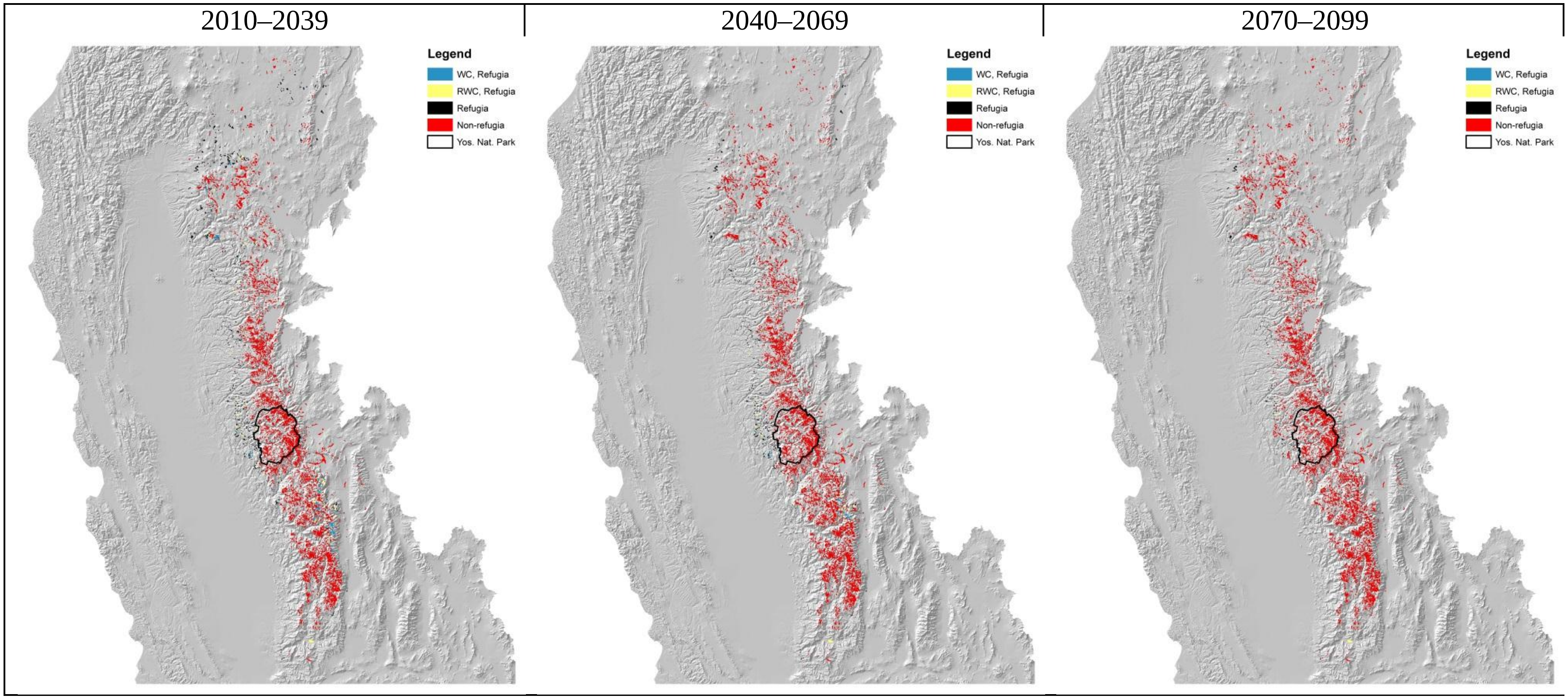
PCM A2 Climatic Water Deficit



2010–2039

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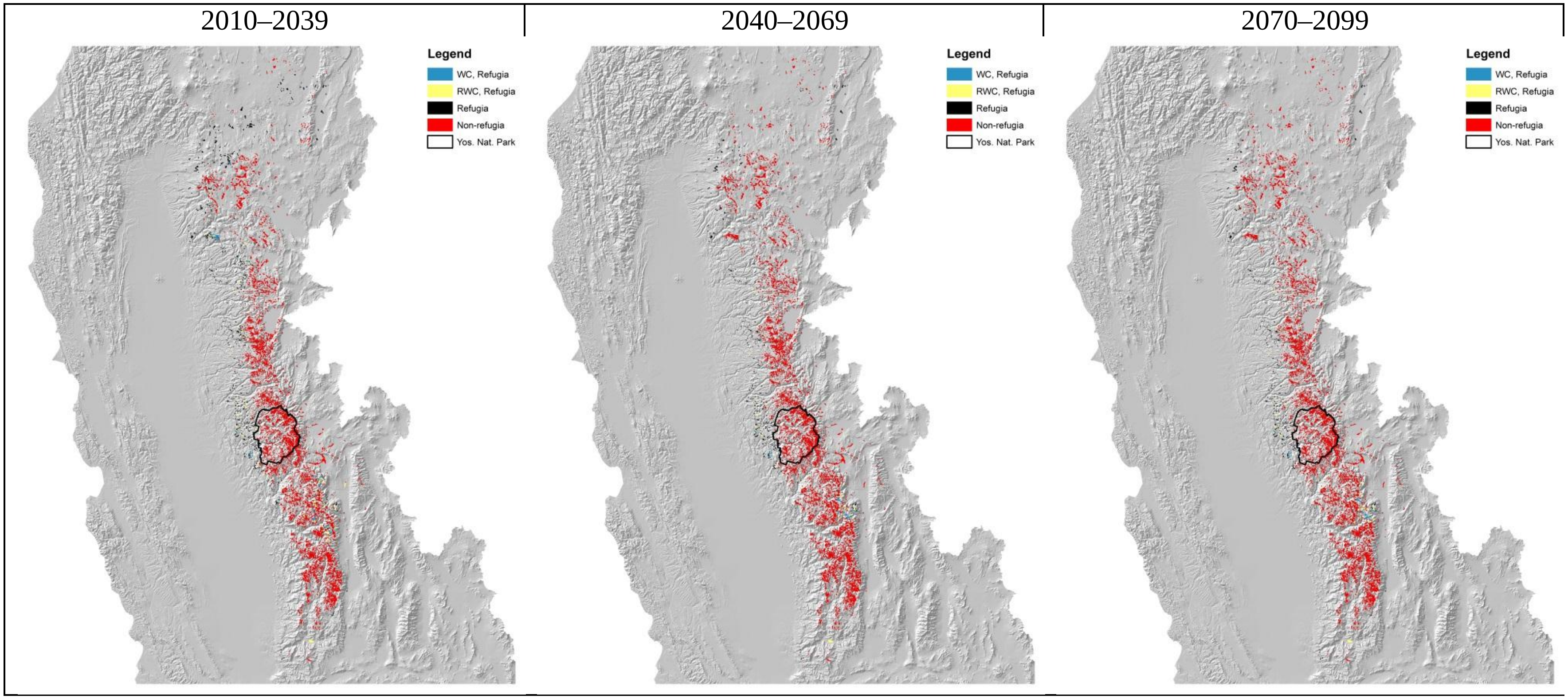
2070–2099

PCM B1 Climatic Water Deficit



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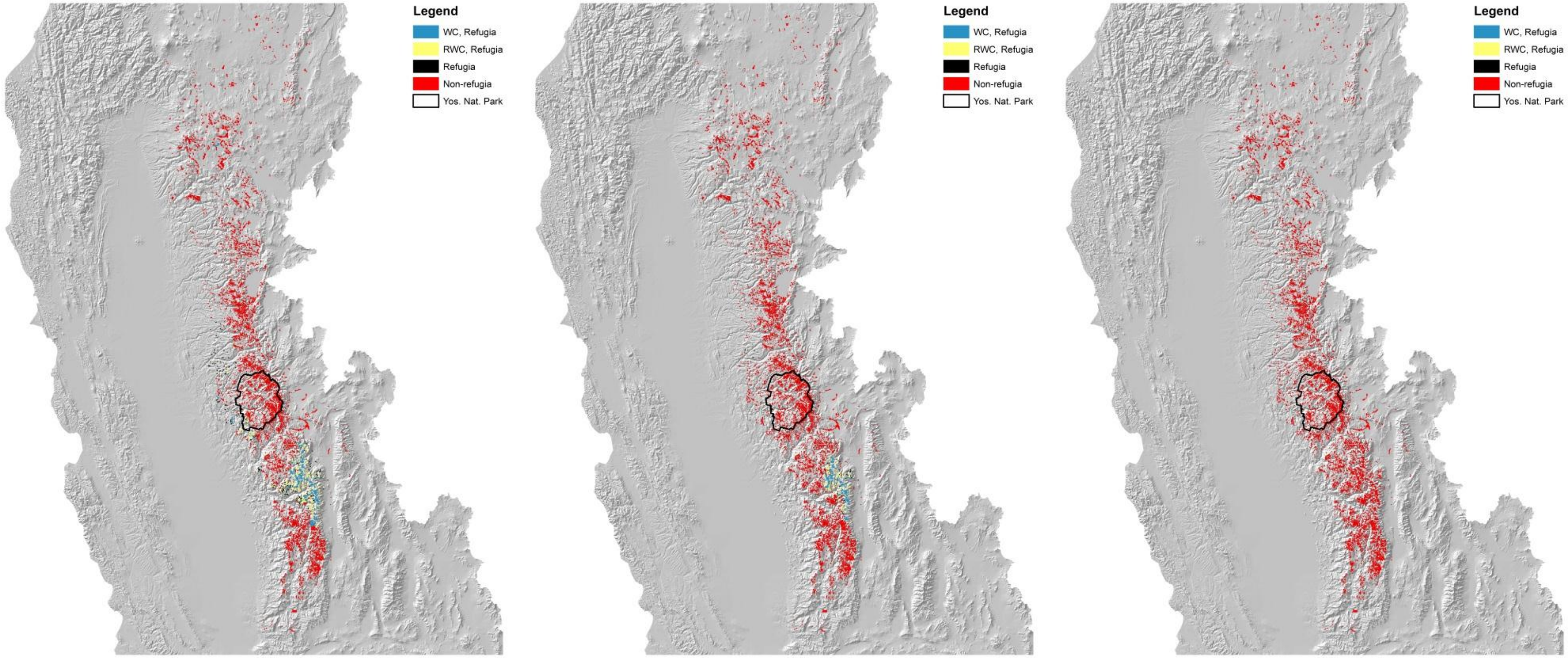
GFDL A2 Extreme Minimum Temperature (30 months)



2010–2039

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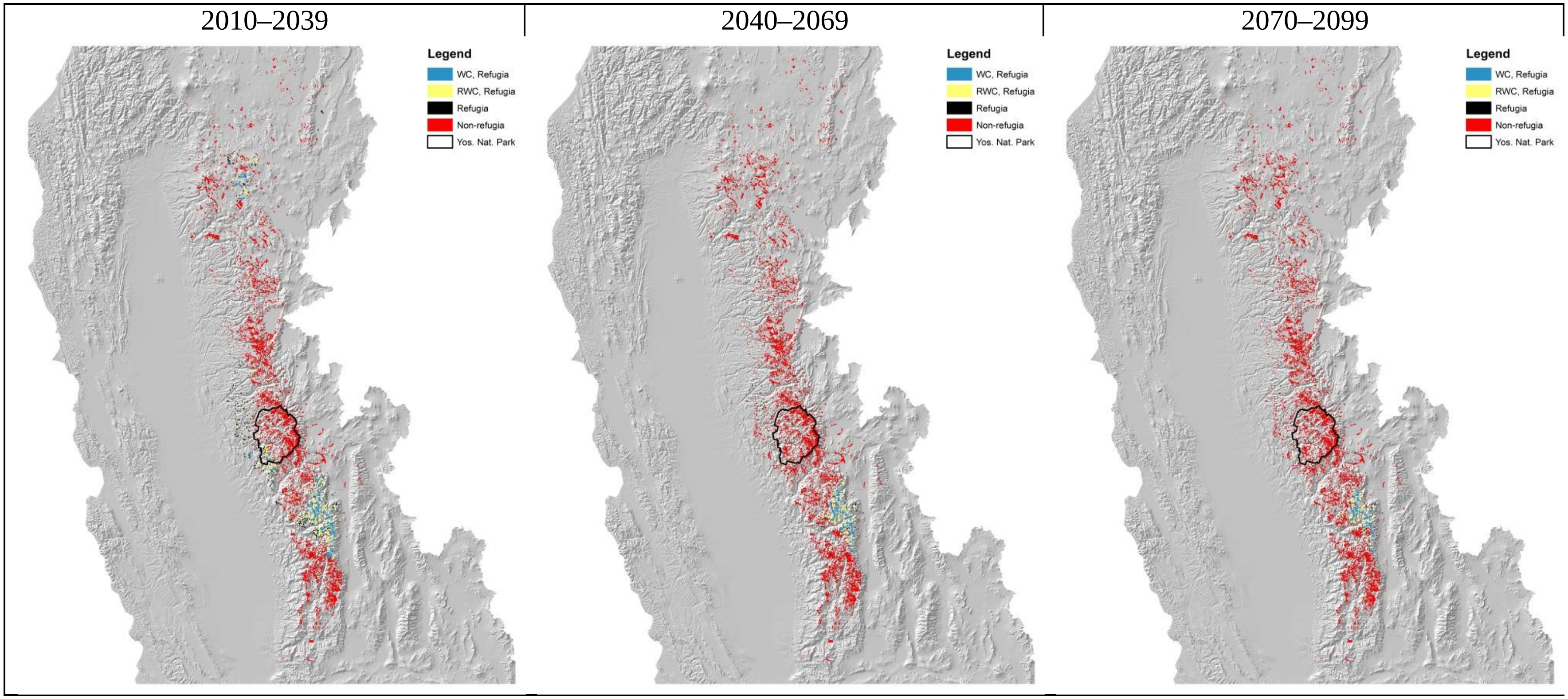
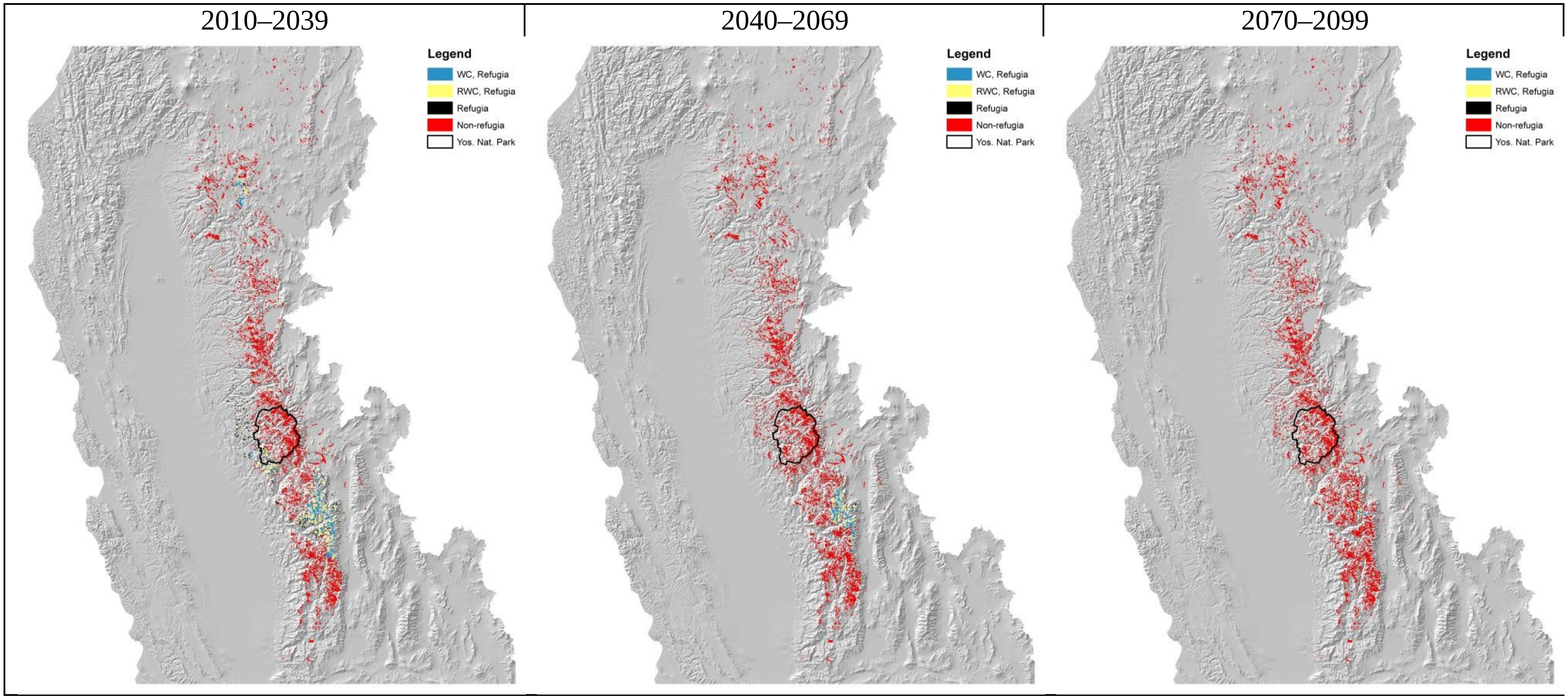
GFDL B1 Extreme Minimum Temperature (30 months)



PCM A2 Extreme Minimum Temperature (30 months)



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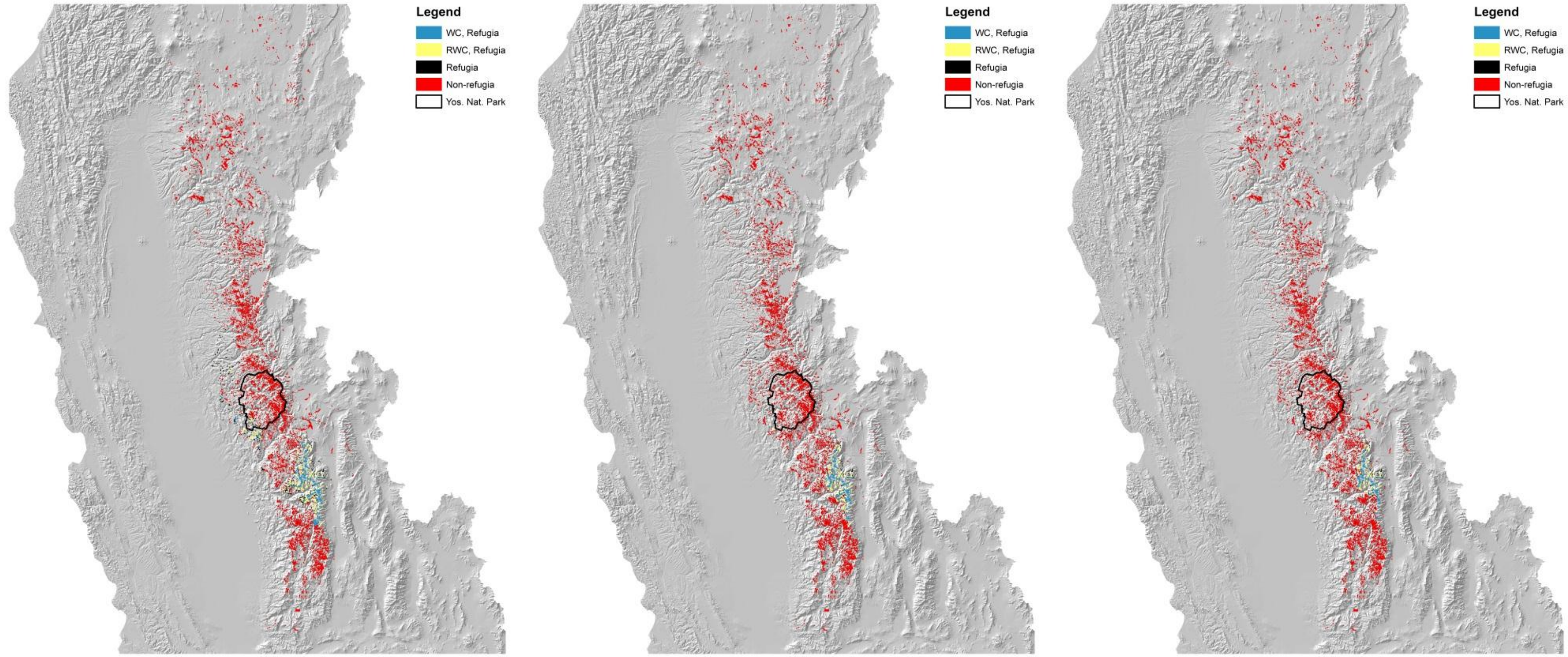
PCM B1 Extreme Minimum Temperature (30 months)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