

Erosion of refugia in the Sierra Nevada meadows network with climate change

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Abstract. Climate refugia management has been proposed as a climate adaptation strategy in the face of global change. Key to this strategy is identification of these areas as well as an understanding of how they are connected on the landscape. Focusing on meadows of the Sierra Nevada in California, we examined multiple factors affecting connectivity using circuit theory, and determined how patches have been and are expected to be affected by climate change. Connectivity surfaces varied depending upon the underlying hypothesis, although meadow area and elevation were important features for higher connectivity. Climate refugia that would promote population persistence were identified from downscaled climate layers, based on locations with minimal climatic change from historical conditions. This approach was agnostic to specific species, yielding a broad perspective about changes and localized habitats. Connectivity was not a consistent predictor of refugial status in the 20th century, but expected future climate refugia tended to have higher connectivity than those that recently deviated from historical conditions. Climate change is projected to reduce the number of refugial meadows on a variety of climate axes, resulting in a sparser network of potential refugia across elevations. Our approach provides a straightforward method that can be used as a tool to prioritize places for climate adaptation.

Key words: Circuitscape; climate; connectivity; conservation; dispersal; meadows; refugia.

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INTRODUCTION

Managing climate refugia has been proposed as a climate adaptation option (Keppel et al. 2015, Morelli et al. 2016). Climate refugia have been characterized by various definitions, including patches that experience minimal environmental change through time, places where temperatures are cooler than the surrounding matrix, and areas with precipitation patterns that mollify warming conditions (Ashcroft 2010, Dobrowski 2011, Keppel

et al. 2012, 2015, Morelli et al. 2016). Climate refugia need not persist on the landscape for an extended period of time, and are not limited to fringe or trailing populations (Morelli et al. 2016). Accessibility may be a key attribute for these climate-buffered locations (Keppel et al. 2015), reflected by their connectivity (Epps et al. 2006, Isaak et al. 2015). Even if refugia merely act as holdouts in the face of climate change (Hannah et al. 2014), persistence of populations restricted to climate refugia likely will require dispersal

among patches to minimize the negative effects of inbreeding and stochastic disturbances (Opdam and Wascher 2004, Manel and Holderegger 2013, Hastings 2014). Nevertheless, connectivity can also increase the risk of invasion, spread, and persistence of pests and pathogens (Schreiber and Lloyd-Smith 2009, Maher et al. 2012), reducing the conservation value of connected patches (Hampe and Jump 2011, Mosblech et al. 2011, Ashcroft et al. 2012). Thus, mapping the occurrence of refugial patches and their connectivity within a habitat network is key to managing populations under future environmental change scenarios.

Connectivity of habitat patches within a landscape reflects the ability of individuals to move to new patches. It results from the permeability of the surrounding environmental matrix (Dunning et al. 1992, Damschen et al. 2006, Koen et al. 2012, Neuwald and Templeton 2013), and the spatial arrangement and size of habitat patches (Diffendorfer et al. 1995, With et al. 1997, Chisholm et al. 2011). Connectivity analysis has shed light onto patterns of dispersal corridors (Nuñez et al. 2013), invasion routes (Wilson et al. 2009), and how species may track climate change (Parmesan 2006). Further, quantifying potential connectivity between habitat patches provides hypothesis-driven metrics that can be tested using empirical datasets (Baguette and Dyck 2007, Maher et al. 2012, Berlow et al. 2013).

Here, we combine connectivity analyses (Urban and Swihart 2009, Zeller et al. 2012, Nuñez et al. 2013) with recent climate change and future projections to examine patterns of connectedness among climate change refugia for meadows in the Sierra Nevada. Montane meadows provide a useful system to evaluate the influence of climatic change on connectivity. In the Sierra Nevada of California, montane meadows are a discrete habitat network for a variety of flora and fauna (Hatfield and LeBuhn 2007, McIlroy and Allen-Diaz 2012, Roche et al. 2012, Berlow et al. 2013). These meadows occur within a matrix of mostly coniferous forests among a backdrop of dramatic topographic relief. Meadow quality and persistence is mediated by a mixture of geology, fire, climate, and water balance (Fites-Kaufman et al. 2007). In response to increasing temperatures and decreasing soil moisture, along with widespread fire suppression, conifers have expanded into Sierra

Nevada meadows over the 20th century (Millar et al. 2004). Moreover, anthropogenic climate change has contributed to heterogeneous shifts in elevation for a variety of taxa in the Sierra Nevada (Rapacciuolo et al. 2014, Rowe et al. 2015).

We compare patterns of connectivity based on four hypothesized factors that could affect isolation of meadows: distance, topography, watercourses, and roads. Next, we identify which meadows were climate refugia based on a suite of variables, including temperature, precipitation, and water balance. We use a simple approach to identify refugia that is agnostic to particular species by focusing on patches that have experienced and are expected to experience minimal deviations from recent past climate conditions. We provide mapped estimates of these refugia and examine patterns within different connectivity classes. Finally, we forecast the distribution of future climate refugia using projections of climate and make comparison of among categories of connectivity.

METHODS

Meadow distribution and size in the Sierra Nevada

We obtained a geodatabase representing montane meadows throughout the Sierra Nevada from the Information Center for the Environment (Fryjoff-Hung and Viers 2012). The dataset contained 17,039 individually designated meadows collated from various sources, representing the most complete enumeration of meadows across the Sierra Nevada and surrounding regions (Appendix S1: Fig. S1). We compared this dataset with another well-curated representation of meadows that was limited to Yosemite, Sequoia, and Kings Canyon National Parks (E. Berlow, *personal communication*) and found the data concordant, and assume that the representations outside these parks are equally concordant with the actual distribution of meadows. As the size of small meadows precludes their inclusion in the analysis, we first added a 150-m buffer around each meadow polygon and then used the dissolve tool to merge overlapping polygons using ArcGIS 10 (Environmental Systems Research Institute 2012), resulting in 7969 polygons, which we refer to as “meadows” for simplicity (Appendix S1: Fig. S1). This buffer accounted for potential errors in

delineation and position of meadows, reduced computational time, and provided a simpler and more conservative landscape from which we could generate connectivity estimates. The buffer and dissolve shifted the range of area from 0.004–18.658 km² to 0.111–42.076 km². We made the simplifying assumptions that (1) currently existing meadows have always been meadows, representing fixed nodes in a connected network; (2) the majority of nodes have experienced little change in size or shape since the early part of the 20th century; and (3) node characteristics will remain consistent through the 21st century. This third assumption likely represents a best-case scenario because drought, habitat transformation, and changes in fire frequencies will likely alter the extent of individual meadows.

Estimation of connectivity

We hypothesized four factors could influence the isolation of individual patches: distance, topography, watercourses, and roads. For each hypothesis, we developed friction surfaces to represent the difficulty or ease of movement between meadows. These layers were then used with our meadows layer in Circuitscape (Shah and McRae 2008). Circuitscape applies concepts from circuit theory to better address potential movement across a landscape. It uses a random walk approach that does not assume perfect knowledge of the landscape, which other cost-distance approaches require. Briefly, the friction surface is converted to a graph in which each cell is considered a node and edge weights are defined by the raster value. Habitat patches (e.g., meadows) are then associated with the collection of nodes that are geographically coincident; current is allowed to flow between patches to represent movement along the landscape. In our executions, we used the following settings: all-to-one-mode for focal nodes (i.e., meadow raster layer), eight neighbors to connect cells, and friction surfaces set to either resistance (barriers) or conductance (vectors) based on the expected effect on dispersal. The all-to-one setting is suggested for corridor analysis and movement between multiple patches (McRae et al. 2013). All friction surfaces were rasters with a cell size of 540 m because of computation restrictions. Thus, after converting the meadow layer from polygon to raster, the number of meadows was further reduced to 5894, which varied in area from 0.111

to 42.076 km². We used the cumulative summary map to visually compare corridors of movement and extract mean connectivity values for each meadow using the zonal statistic operation in ArcGIS. With meadows as nodes within a network, the connectivity value represents the frequency of movement through the patch given the factor. Thus, high connectivity values represent patches that are frequently traversed within the network and thus are less isolated.

Our simplest assumption was isolation by distance, for which we used a uniform friction surface. For isolation by topography, we incorporated the difficulty of moving over steep slopes by weighting movement using the PathDistance tool in ArcGIS Spatial Analysis. To first represent elevation, we used a 90-m digital elevation model that was resampled to 540 m using bilinear interpolation. We estimated the cost of moving across slopes using the symmetric inverse linear function under default settings (i.e., increased weight of movement with increased or decreased slope), and did not permit movement if the slope was greater than 45°. Upslope and downslope movements were equally weighted, assuming a dispersing individual was likely to avoid steep areas, regardless of direction. As larger values represent increasing distances between points, this layer was used as a resistance surface.

To estimate isolation by watercourses, we obtained a polyline layer representing watercourses (i.e., rivers and streams) throughout the contiguous United States (Lehner et al. 2006). Friction surfaces were created to represent different aspects of how watercourses could act as either a vector or a barrier to dispersal. First, we created a raster layer in which watercourses were weighted heavily (value equals 100), whereas non-watercourses were weighted lightly (value equals 1). When used as a resistance surface, this layer reflects the presence of watercourses as a barrier to dispersal; when used as a conductance surface, the layer reflects the presence of watercourses as a vector of dispersal. Second, we generated a raster layer based on Euclidean distance from a watercourse. Used as a conductance layer, it suggests areas farther away from watercourses would facilitate movement; used as a resistance layer, it suggests areas closer to watercourses facilitate movement. We did not differentiate between stream orders in this analysis, as

datasets incorporating this information are not geographically complete for our study area. Moreover, weighting on stream order would require taxon-specific assumptions regarding dispersal ability and effect of the watercourse.

Isolation by roads was represented as the Euclidean distance from primary or secondary roads using a line shapefile dataset obtained from U.S. Census Bureau (2012). This surface also acted as a proxy for human activity and presences. This layer was used as a conductance layer and we assumed areas farther from roads would facilitate movement. We did not discriminate between road classifications; state, county, and interstate highways were considered equal impediments. Decomposing these effects further would have required generation of surfaces in relation to species-specific dispersal traits, which are not known for most species in the Sierra Nevada.

We compared log-transformed mean values of connectivity to scaled meadow attributes (area, elevation, and geographic position) using general linear models to assess the relative importance of these characteristics. To summarize patterns among surfaces, we first classified meadows that were in the upper quartile of connectivity in all surface measures as “well connected” (WC), using R ver. 3.0 (R Core Team 2013). Meadows that were in the upper quartile of at least one, but not all of the seven surfaces (watercourses \times 4, elevation, roads, and the uniform distribution), were classified as “more connected” (MC), and the remaining meadows were considered “least connected” (LC). We analyzed elevation and size of WC and MC meadows compared to LC meadows by plotting stacked histograms. If our classifications represent random draws of meadows in geographic space, we expected them to have similar size and elevational distributions.

Assessment of recent climate change

Climate data for all California hydrological units were estimated using 800-m PRISM data (Daly et al. 2008) downscaled to 270-m raster layers (Flint and Flint 2012). These data represented minimum temperature, maximum temperature, and precipitation of each month of each year during the 20th century and incorporate cold-air pooling (Lundquist et al. 2008). Application of the fine-scale hydrologic model, Basin Characterization Model (Flint et al. 2013), provided

monthly estimated values of snowpack (as snow-water-equivalent, SWE), runoff, and climatic water deficit (CWD, the difference between estimated actual and potential evapotranspiration, Stephenson 1990) based on empirically derived parameters. Climatic water deficit values for each water year (October–September) were summed to provide the annual estimates of water available to vegetation. Such fine-resolution data provide the necessary context for climate conditions in and around smaller habitat patches, particularly those in a topographically diverse landscape.

We defined climate refugia as areas on the landscape where the magnitude of change in climate and climate-derived measures was minimal, as measured from a baseline period of 1910–1939, which coincides with the time prior to measurable anthropogenic effects on climate (Hansen et al. 2010). We used a modern period, 1970–1999, which includes the period when anthropogenic climate change became observable (Hansen et al. 2010), to assess the observed climate refugia on the landscape. To represent temporally broad climate trends during each period, we used the R packages raster (Hijmans 2013) and dismo (Hijmans et al. 2013), particularly the function *biovars*, to generate summary variables that represent overall climate trends in each era. We were interested 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 based upon observed impacts on a suite of montane California species (e.g., Moritz et al. 2008, Morelli et al. 2012, Rubidge et al. 2012, Tingley et al. 2012, Rapacciuolo et al. 2014, Rowe et al. 2015). We also determined the mean of 1 April SWE and CWD for each period from output of the Basin Characteristic Model (BCM), as these measures also likely affect both fauna and flora (e.g., Lutz et al. 2010). 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. For variables representing differences in monthly or quarterly measures, the magnitude of values should be treated with caution because they may refer to different time periods in each dataset (e.g., minimum temperature of

the coldest quarter for a given pixel may have been December, January, and February in the historical period and January, February, and March 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 (see McCullough et al. 2015 for a similar approach). Extreme values in the historical record were identified as the 95th quantile (wetter and warmer) or the 5th quantile (drier) on a per-pixel, monthly basis. We totaled the number of modern months that exceeded the 95th quantile of minimum temperature, maximum temperature, and precipitation, respectively, and those that were less than the 5th quantile of precipitation. We determined the mean frequency that conditions were above or below the threshold for the 30-year modern period, such that low values represent stability and higher values designate pixels exhibiting a greater shift in climate regime.

Assessment of future climate change

To address the potential change in climate and estimate future refugia, we analyzed precipitation and air temperature reflecting two emissions scenarios (SRES A2 and B1, where A2 represents a business-as-usual scenario that assumes little mitigation, and B1 includes reduced future emissions) and two general circulation models (the NCAR Parallel Climate Model [PCM] and the NOAA Geophysical Fluids Dynamics Laboratory [GFDL]). These four future projections represent the range of projected climatic conditions in California (Cayan et al. 2008): warmer and wetter (PCM B1 and GFDL B1) and warmer and drier (PCM A2 and GFDL A2). We used these projections to calculate the same variables in the observed dataset, and incorporated cold-air pooling in the monthly minimum temperatures between December and May by imposing a 1.6°C temperature reduction to grid cells mapped as having cold-air pooling (Lundquist et al. 2008, Curtis et al. 2014). Further details regarding the development of these estimates can be found in Flint and Flint (2012). 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 that exceeded the variation in minimum temperature, maximum temperature, and precipitation from the historical era.

Identification of climate refugia

We overlaid the meadows layer on the climate-related raster layers and extracted values. Meadows were then classified as “refugial” or “non-refugial” based on the differences in values of the BCM output. For simplicity, we first assessed whether a meadow was refugial based on a single environmental axis (e.g., change in mean annual temperature or frequency of extreme minimum temperature). We used the following three thresholds to define minimal change in climate conditions: (1) temperature changes within 1°C; (2) relative precipitation, snowpack, and CWD changes within 10%; and (3) no more than 1 or 2 months/yr on average exceeding the extreme historical temperature and precipitation variation, respectively. These values were chosen to represent deviations that would likely impact persistence in a variety of species; a species-specific approach could use more precise thresholds. We added additional complexity by classifying meadows as refugial if they also met threshold conditions for two environmental axes: (1) mean annual temperature and mean annual precipitation and (2) 1 April SWE and extreme monthly minimum temperature (1 month/yr threshold). While these criteria were not based on statistical models, they identified sites undergoing little change.

We tested whether meadows that were climate refugia in the past century had high connectivity and were at high elevation using logistic regression models. We then applied the climate refugia concept to future climate scenarios by extracting values from the future scenario change maps and used the same thresholds. This provided an opportunity to determine where climate refugia are expected to occur and the relative frequency of climate refugia expected during this century. We determined which meadows were expected to be refugial in sequence for each circulation model and scenario combination and compared the mean connectivity between those that were still considered refugia in an era and those that were no longer considered refugia in an era using *t* tests.

RESULTS

Estimation of connectivity

Each of the hypothesized factors that likely would impact connectivity across a variety of taxa (distance, watercourses, and roads) affected the geographic patterns and range of values of connectivity among Sierra Nevada meadows (Fig. 1; Appendix S1: Fig. S2). Distributions of connectivity values varied among hypotheses, although long tails of low connectivity were common (Appendix S1: Fig. S3). For all individual connectivity surfaces, meadows at higher elevations were more likely to have higher connectivity values than lower meadows (Appendix S1: Figs. S4, S5). Pairwise comparisons of connectivity suggested small to moderate differences between some connectivity surfaces; correlations for all surface pairs were significant ($P < 0.001$), but varied between 0.082 and 0.960 (Appendix S1: Table S1). The most predictive model (with the lowest Akaike's information criterion value) of connectivity explained 55.96% of the variation in log-transformed mean connectivity ($F_{15,5878} = 500.5$, $P < 0.001$). It included area, elevation, latitude, longitude, and interactions for all variables (Table 1; Appendix S1: Table S2). In this model, area and elevation accounted for much of variation explained in the model (38.5% and 42.2%, respectively), as did geographic position (latitude \times longitude; 15.3%).

We classified 329 of the 5894 meadows as WC (5.6%), 3091 as MC (52.4%), and 2474 as LC (42.0%). The amount of area represented by the WC meadows was large (30.6% of total), while MC meadows, despite being nearly five times as numerous, represented a similar proportion of the area (49.6%). Thus, the well-connected meadows tended to be larger than other meadows (Appendix S1: Figs. S4, S6). They also occurred at higher elevations (Appendix S1: Figs. S4, S5), although they were spread throughout the Sierra Nevada (Appendix S1: Fig. S7).

Recent climate refugia and connectivity

The proportion of meadows classified as climate refugia depended upon which climate variable was designated (mean = 0.556, range = 0.006–0.961; Table 2). Four variables yielded over 80% of the meadows as refugial, of which three reflected frequency of extreme events, whereas six variables

yielded less than half of the meadows as refugial (Table 2). Central tendency measures of temperature (annual mean = 0.878, maximum = 0.683, minimum = 0.287, mean temperature of the coldest quarter = 0.740) varied in assignment of refugial meadows. Few meadows were assigned as climate refugia under the two variable combinations we assessed (annual mean temperature and annual precipitation = 0.323; 1 April SWE and monthly minimum temperature extreme 0.051). Geographically, regions of meadows that were refugial varied among variables tested, such that meadows were not consistently classified between similar climate variables (Fig. 2); there were definite contrasts between minimum and maximum temperature climate refugia maps (Fig. 2B, C).

Logistic regression models of the relationship between logarithmically transformed mean connectivity and refugial status were significant for 14 of 15 variables tested ($P \leq 0.03$; Table 3). The sign of the coefficient was positive for 6 of 14 variables, although this proportion was not significantly different from random (binomial test, $P = 0.791$). Likewise, models of elevation and refugial status were significant ($P < 0.001$) in all variables, and eight coefficients were positive (Table 3).

Future climate refugia and connectivity

Scenarios for future climate conditions indicated a reduced proportion of meadows that were refugial (Fig. 3, Tables 4 and 5). For both circulation models, the A2 scenario yielded very few refugial meadows by the end of the 21st century based on projections of temperature changes (PCM mean = 1.6%, range = 0.0–8.3%; GFDL mean = 0.7%, range = 0.0–5.1%). Generally, the number of refugia designated by temperature measures decreased in each time step, regardless of connectivity and quantitative approach (Figs. 3, 4). The number of refugia classified on the basis of precipitation changed inconsistently through time, as there were differences between the measure of central tendency and the number of extreme months. Likewise, changes in refugia defined by 1 April SWE and CWD exhibited variations in their downward trends (Tables 4 and 5).

Regardless of circulation model and scenario, changes in logarithmically transformed mean connectivity between eras for climate refugia more often favored meadows with higher connectivity (Fig. 3, Tables 4 and 5). Accounting for only

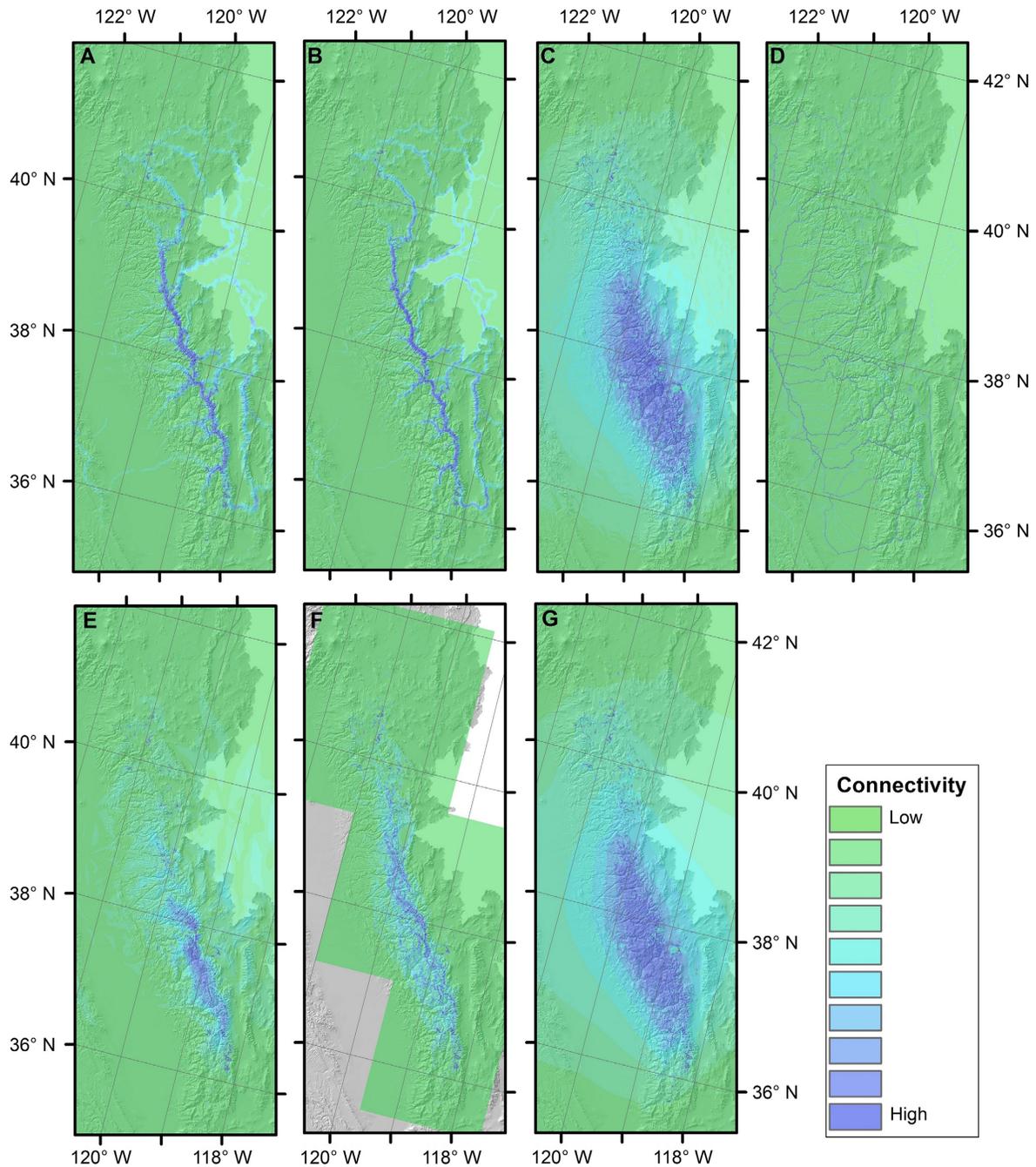


Fig. 1. Patterns in connectivity based on four hypotheses of isolation. Each hypothesis was represented by at least one friction surface: presence (as barrier, A; as vector, C) and distance from watercourses (as barrier, B; as vector, D); distance from roads (E); elevationally weighted distance (F); and uniform (G). We present each summary map over a hillshade surface to highlight the potential relationships between connectivity and topography (darker blue is higher connectivity). For watercourses as barriers, the general patterns of connectivity were consistent regardless of implementation (presence or distance), whereas the watercourses as vectors yielded different patterns and the presence surface resulted in patterns similar to the uniform surface. The remaining friction surfaces show patchiness along the Sierra Nevada, with clusters of high connectivity either in southern (distance from roads) or in the middle (topographically weighted distance) parts of the range.

Table 1. Model comparison of log-transformed mean connectivity values as a function of attributes and position.

Model	AIC	Δ AIC	R^2_{adj}
Area \times elevation \times latitude \times longitude	451.9703	0	0.5597
Area \times latitude \times longitude	2062.5341	1610.5638	0.4206
Elevation \times latitude \times longitude	2637.5677	2185.5974	0.3612
Area \times elevation	2699.4849	2247.5146	0.3540
Latitude \times longitude	3935.4826	3483.5123	0.2033
Elevation	3963.2523	3511.2820	0.1993
Area	4183.7295	3731.7592	0.1688
Longitude	5000.9067	4548.9364	0.0452
Latitude	5053.3096	4601.3393	0.0366

Note: AIC, Akaike's information criterion.

significant changes in connectivity and scenarios under the GFDL model, continued refugial meadows had higher connectivity in all cases (A2: 8 of 11 between 2010–2039 and 1970–1999, 9 of 11 between 2040–2069 and 2010–2039, 1 of 3 between 2070–2099 and 2040–2069; B1: 6 of 11 between 2010–2039 and 1970–1999, 8 of 11 between 2040–2069 and 2010–2039, and 4 of 5 between 2070–2099 and 2040–2069). Likewise, accounting for only significant changes in connectivity and scenarios under the PCM, continued refugial meadows had higher connectivity in all cases (A2: 7 of 9 between 2010–2039 and 1970–1999, 9 of 10 between 2040–2069 and 2010–2039, 3 of 3 between 2070–2099 and 2040–2069; B1: 6 of 11 between

2010–2039 and 1970–1999, 8 of 9 between 2040–2069 and 2010–2039, and 6 of 8 between 2070–2099 and 2040–2069).

Climate refugia, when they occurred in future scenarios, tended to be in higher elevations, although the general loss depended upon the climate variable in question (Fig. 4; Appendix S1: Fig. S8). In several cases, deviations from historical conditions occurred dramatically in a given era (Fig. 4, Tables 4 and 5). Mapping meadows as future climate refugia and WC, MC, and LC status showed regional patterns of occurrence, particularly in the southern and eastern Sierra Nevada, regardless of connectivity classification (Appendix S1: Figs. S9, S10).

Table 2. Proportion of meadows that were designated as refugia during the 20th century based on limited change in different environmental variables and classified by their connectivity value.

Variables	Measure (threshold)	All	WC	MC	LC
CWD	Central tendency (10%)	0.545	0.313	0.512	0.618
1 April SWE	Central tendency (10%)	0.367	0.410	0.424	0.291
Annual temp.	Central tendency (1°C)	0.878	0.787	0.845	0.930
Annual precip.	Central tendency (10%)	0.379	0.471	0.434	0.299
Max. temp.	Central tendency (1°C)	0.683	0.623	0.664	0.715
Min. temp.	Central tendency (1°C)	0.287	0.347	0.266	0.306
Mean. temp. of coldest quarter	Central tendency (1°C)	0.740	0.666	0.696	0.805
Monthly min. temp.	Extreme warming (1 month/yr)	0.227	0.337	0.229	0.211
Monthly min. temp.	Extreme warming (2 months/yr)	0.502	0.556	0.493	0.506
Monthly max. temp.	Extreme warming (1 month/yr)	0.696	0.672	0.674	0.727
Monthly max. temp.	Extreme warming (2 months/yr)	0.961	0.951	0.942	0.986
Monthly precip.	Extreme wet (1 month/yr)	0.006	0.024	0.007	0.003
Monthly precip.	Extreme wet (2 months/yr)	0.931	0.954	0.948	0.907
Monthly precip.	Extreme dry (1 month/yr)	0.254	0.198	0.235	0.287
Monthly precip.	Extreme dry (2 months/yr)	0.936	1.000	0.997	0.988
Annual temp. and annual precip.	Central tendencies	0.323	0.334	0.361	0.288
SWE and monthly min. temp	Central tendency and extreme (1 month/yr)	0.051	0.091	0.064	0.029

Note: WC, well connected; MC, more connected; LC, least connected; CWD, climatic water deficit; SWE, snow-water-equivalent.

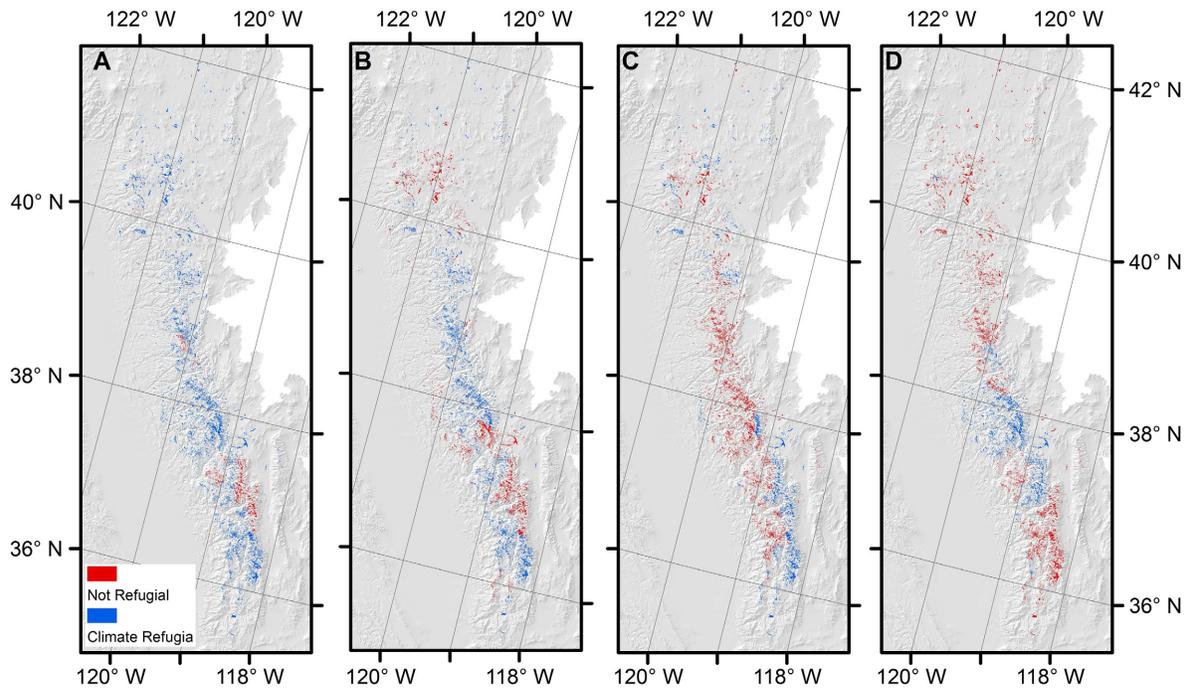


Fig. 2. Distribution of meadows that are climate refugia (blue) and those that are not (red) depending upon variable under consideration (annual temperature, A; maximum temperature, B; minimum temperature, C; annual precipitation, D; see Table 3).

Table 3. Results of logistic regression models of climate refugia and log10 mean connectivity and elevation, in which predictor variables were scaled.

Variables	Measure (threshold)	Mean connectivity			Mean elevation		
		β	Z	P-value	β	Z	P-value
CWD	Central tendency (10%)	-0.424	-15.129	<0.001	-1.184	-32.578	<0.001
1 April SWE	Central tendency (10%)	0.419	14.784	<0.001	0.265	9.544	<0.001
Annual temp.	Central tendency (1°C)	-0.512	-13.368	<0.001	-1.314	-23.255	<0.001
Annual precip.	Central tendency (10%)	0.520	17.821	<0.001	0.424	14.857	<0.001
Max. temp.	Central tendency (1°C)	-	-	-	-0.103	-3.659	<0.001
Min. temp.	Central tendency (1°C)	-0.317	-10.302	<0.001	0.165	5.657	<0.001
Mean. temp. of coldest quarter	Central tendency (1°C)	-0.314	-10.577	<0.001	-0.108	-3.612	<0.001
Monthly min. temp.	Extreme warming (1 month/yr)	0.092	3.005	0.003	0.623	17.779	<0.001
Monthly min. temp.	Extreme warming (2 months/yr)	-0.111	-3.932	<0.001	-0.549	-17.572	<0.001
Monthly max. temp.	Extreme warming (1 month/yr)	-0.123	-4.670	<0.001	0.470	16.893	<0.001
Monthly max. temp.	Extreme warming (2 months/yr)	-0.366	-5.932	<0.001	-0.778	-9.892	<0.001
Monthly precip.	Extreme wet (1 month/yr)	0.697	5.109	<0.001	1.802	6.698	<0.001
Monthly precip.	Extreme wet (2 months/yr)	-0.364	-11.230	<0.001	-0.888	-25.250	<0.001
Monthly precip.	Extreme dry (1 month/yr)	0.753	12.578	<0.001	1.012	17.696	<0.001
Monthly precip.	Extreme dry (2 months/yr)	1.447	8.095	<0.001	1.435	7.735	<0.001

Note: CWD, climatic water deficit; SWE, snow-water-equivalent.

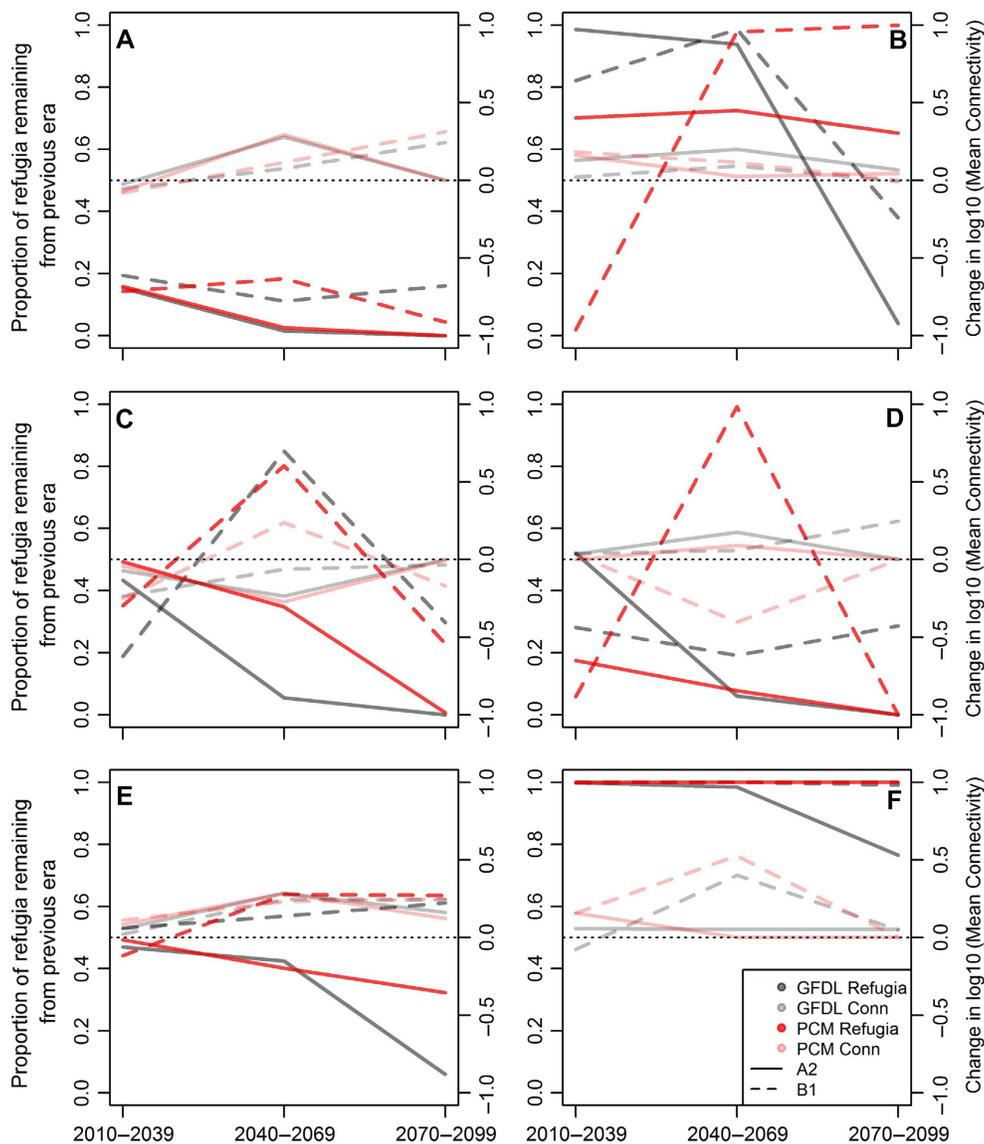


Fig. 3. Trends of change in expected number of refugia and mean connectivity of the network through time depending upon the climate variable (mean annual temperature A; mean annual precipitation B; minimum temperature C; mean temperature of the coldest quarter D; extreme minimum temperature at 2 months/yr E; extremely low precipitation at months/yr F). Gray lines represent the GFDL circulation model, and red lines represent the PCM circulation model; darker lines are the proportion of refugia remaining from the previous era (left y-axis) and the lighter lines are the change in connectivity from the previous era (right y-axis). Solid lines are the A2 climate scenario, and dashed lines are the B1 climate scenario. GFDL, Geophysical Fluids Dynamics Laboratory; PCM, Parallel Climate Model.

DISCUSSION

Connectivity and climate refugia

We found a positive relationship with connectivity and elevation and meadow size (Appendix S1:

Figs. S4–S6). These relationships were impacted by interactions and geographic position, as identified in our preferred linear model (Table 1; Appendix S1: Table S2). In fact, the interaction coefficient combining latitude and longitude

Table 4. Change in meadow network under GFDL circulation model and various climate variables.

Variable	Measure	Scenario	2010–2039			2040–2069			2070–2099		
			Proportion remaining refugia from		Δ mean conn.	Proportion remaining refugia from		Δ mean conn.	Proportion remaining refugia from		Δ mean conn.
			1910–1939	1970–1999		1910–1939	2010–2039		1910–1939	2040–2069	
CWD	Central tendency (10%)	A2	0.062	0.114	–0.185***	0.010	0.164	–0.145**	0.002	0.233	0.120
		B1	0.047	0.086	–0.217***	0.043	0.913	0.014	0.025	0.578	–0.057
1 April SWE	Central tendency (10%)	A2	0.141	0.385	0.087***	0.123	0.868	0.138***	0.013	0.108	–0.534***
		B1	0.249	0.677	0.183***	0.096	0.387	0.146**	0.009	0.092	–0.650***
Annual temp.	Central tendency (1°C)	A2	0.134	0.153	–0.022	0.002	0.015	0.278**	0.000	0.000	–
		B1	0.170	0.194	–0.053***	0.019	0.112	0.076**	0.003	0.161	0.245**
Annual precip.	Central tendency (10%)	A2	0.374	0.986	0.130*	0.351	0.938	0.200***	0.014	0.040	0.068
		B1	0.311	0.821	0.022	0.307	0.986	0.093	0.116	0.379	–0.007
Max. temp.	Central tendency (1°C)	A2	0.094	0.138	–0.083***	0.000	0.000	–	0.000	0.000	–
		B1	0.145	0.212	–0.050***	0.006	0.040	–0.016***	0.000	0.000	–
Min. temp.	Central tendency (1°C)	A2	0.124	0.433	–0.071***	0.007	0.055	–0.236***	0.000	0.000	–
		B1	0.054	0.188	–0.236***	0.046	0.849	–0.064*	0.014	0.296	–0.034
Mean. temp. of coldest quarter	Central tendency (1°C)	A2	0.385	0.521	0.035**	0.023	0.061	0.175***	0.000	0.000	–
		B1	0.208	0.281	0.036**	0.040	0.191	0.058*	0.011	0.286	0.246***
Monthly min. temp.	Extreme warming (1 month/yr)	A2	0.095	0.419	0.328***	0.060	0.629	0.116***	0.000	0.000	–
		B1	0.100	0.438	0.307***	0.069	0.697	0.138***	0.053	0.763	0.083*
Monthly min. temp.	Extreme warming (2 months/yr)	A2	0.236	0.470	0.055***	0.100	0.424	0.286**	0.006	0.059	0.162***
		B1	0.266	0.530	0.022	0.152	0.569	0.245***	0.093	0.612	0.244***
Monthly max. temp.	Extreme warming (1 month/yr)	A2	0.074	0.106	0.299***	0.043	0.585	0.079***	0.000	0.000	–
		B1	0.077	0.111	0.269*	0.041	0.524	0.100**	0.036	0.900	0.105
Monthly max. temp.	Extreme warming (2 months/yr)	A2	0.142	0.147	0.158***	0.063	0.443	0.240***	0.051	0.808	0.023
		B1	0.180	0.187	0.081	0.083	0.465	0.286***	0.081	0.965	0.127
Monthly precip.	Extreme wet (1 month/yr)	A2	0.006	1.000	–	0.006	1.000	–	0.006	1.000	–
		B1	0.004	0.595	–0.160**	0.004	1.000	–	0.004	1.000	–
Monthly precip.	Extreme wet (2 months/yr)	A2	0.269	0.289	0.114***	0.218	0.809	0.185***	0.017	0.077	0.045
		B1	0.721	0.774	0.050**	0.637	0.884	–0.165***	0.338	0.530	0.006
Monthly precip.	Extreme dry (1 month/yr)	A2	0.254	1.000	–	0.254	1.000	–	0.254	1.000	–
		B1	0.251	0.987	0.273***	0.249	0.993	0.556***	0.249	1.000	–
Monthly precip.	Extreme dry (2 months/yr)	A2	0.992	0.998	0.058	0.977	0.985	0.051	0.747	0.765	0.054***
		B1	0.991	0.997	–0.076	0.990	1.000	0.402*	0.982	0.991	0.048

Note: GFDL, Geophysical Fluids Dynamics Laboratory; CWD, climatic water deficit; SWE, snow-water-equivalent.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

generally suggested increased connectivity moving north and east. However, interaction coefficients involving area frequently were negative, suggesting the effect of area is dampened when other variables were considered.

The proportion of meadows that were climate refugia varied greatly among variables and measures assessed. Refugia measured by mean annual temperature and annual precipitation diverged greatly in number (Table 2) and geographic position (Fig. 2), such that only 32.3% of meadows met our thresholds. Such broad changes across a

suite of climate patterns likely have impacted species within the Sierra Nevada meadow network. Meadows that have experienced dramatic shifts in CWD likely have altered hydrological conditions and species composition (e.g., Millar et al. 2004). Aspects of fire frequency (both current and future) will no doubt influence vegetation in the surrounding landscape (Moritz and Stephens 2008, Moritz et al. 2012), which will also impact meadows. Further, the sensitivity of the underlying geology to shifts in precipitation events and temperature may alter meadow persistence. Although

Table 5. Change in meadow network under PCM circulation model and various climate variables.

Variables	Measure	Scenario	2010–2039			2040–2069			2070–2099		
			Proportion remaining refugia from			Proportion remaining refugia from			Proportion remaining refugia from		
			1910–1939	1970–1999	Δ mean conn.	1910–1939	2010–2039	Δ mean conn.	1910–1939	2040–2069	Δ mean conn.
CWD	Central tendency (10%)	A2	0.088	0.161	–0.292***	0.048	0.549	0.128***	0.017	0.347	–0.055
		B1	0.091	0.167	–0.261***	0.061	0.667	0.029	0.049	0.802	0.177***
1 April SWE	Central tendency (10%)	A2	0.165	0.448	0.230***	0.115	0.699	0.101***	0.091	0.791	–0.070
		B1	0.070	0.190	–0.158***	0.013	0.187	–0.333*	0.013	1.000	–
Annual temp.	Central tendency (1°C)	A2	0.139	0.159	–0.068***	0.004	0.026	0.294***	0.000	0.000	–
		B1	0.125	0.142	–0.081***	0.023	0.183	0.116*	0.001	0.044	0.314*
Annual precip.	Central tendency (10%)	A2	0.266	0.701	0.162***	0.193	0.725	0.026	0.126	0.652	0.046*
		B1	0.007	0.020	0.183**	0.007	0.977	†	0.007	1.000	–
Max. temp.	Central tendency (1°C)	A2	0.283	0.415	0.054***	0.006	0.020	0.021	0.000	0.000	–
		B1	0.401	0.588	0.016	0.034	0.086	0.095*	0.013	0.389	–0.043
Min. temp.	Central tendency (1°C)	A2	0.141	0.493	–0.041	0.049	0.348	–0.272***	0.000	0.007	–0.003
		B1	0.101	0.352	–0.252***	0.081	0.802	0.237*	0.018	0.229	–0.171***
Mean. temp. of coldest quarter	Central tendency (1°C)	A2	0.129	0.175	–0.001	0.010	0.077	0.092	0.000	0.000	–
		B1	0.044	0.059	0.033	0.043	0.992	–0.403	0.000	0.000	–
Monthly min. temp.	Extreme warming (1 month/yr)	A2	0.097	0.426	0.316***	0.049	0.510	0.103***	0.004	0.086	0.198**
		B1	0.095	0.419	0.317***	0.068	0.710	0.144*	0.051	0.749	0.089
Monthly min. temp.	Extreme warming (2 months/yr)	A2	0.248	0.493	0.085***	0.099	0.401	0.285***	0.032	0.323	0.123***
		B1	0.222	0.441	0.111***	0.141	0.638	0.231*	0.090	0.635	0.249***
Monthly max. temp.	Extreme warming (1 month/yr)	A2	0.114	0.163	0.134***	0.054	0.479	0.314***	0.012	0.224	–0.230***
		B1	0.097	0.139	0.143***	0.076	0.781	0.400*	0.047	0.617	0.141***
Monthly max. temp.	Extreme warming (2 months/yr)	A2	0.287	0.298	–0.003	0.109	0.380	0.291***	0.083	0.760	0.068
		B1	0.243	0.253	0.001	0.167	0.689	0.261*	0.077	0.460	0.207***
Monthly precip.	Extreme wet (1 month/yr)	A2	0.006	0.946	0.459	0.004	0.743	–0.106	0.003	0.769	–0.101
		B1	0.001	0.216	–0.277*	0.001	1.000	–	0.001	1.000	–
Monthly precip.	Extreme wet (2 months/yr)	A2	0.869	0.933	0.060**	0.768	0.884	0.168***	0.767	0.999	0.100
		B1	0.832	0.893	0.195***	0.829	0.997	–0.048	0.800	0.965	–0.141***
Monthly precip.	Extreme dry (1 month/yr)	A2	0.243	0.957	0.049	0.236	0.968	0.544***	0.236	1.000	–
		B1	0.159	0.627	0.295***	0.159	1.000	–	0.159	0.997	0.475*
Monthly precip.	Extreme dry (2 months/yr)	A2	0.993	1.000	0.158	0.993	1.000	–	0.993	1.000	–
		B1	0.993	0.999	0.158	0.992	0.999	0.526*	0.992	1.000	–

Note: PCM, Parallel Climate Model; CWD, climatic water deficit; SWE, snow-water-equivalent.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

† Only one meadow changed classification.

we do not analyze the specific impacts of climate change on habitat patches, we expect that large deviations would have direct and indirect impacts on species that would alter physical and biological properties on which current biodiversity relies. Phenological patterns associated with climate could be disrupted and lead to a disconnection of annual cycles that result in negative (Dalsgaard et al. 2013) or positive feedbacks (Ozgul et al. 2010). Negative feedbacks could disrupt actual dispersal corridors for meadow species and lead

to population fragmentation, whereas positive feedbacks may result in an increase in dispersal because of local resource saturation.

Species responses to climate change

In California, species have responded variably to observed climate change, and climatic conditions have changed heterogeneously across the state (Rapacciuolo et al. 2014). Directional range shifts in elevation of diverse taxa along the Sierra Nevada have been mixed, and movements were

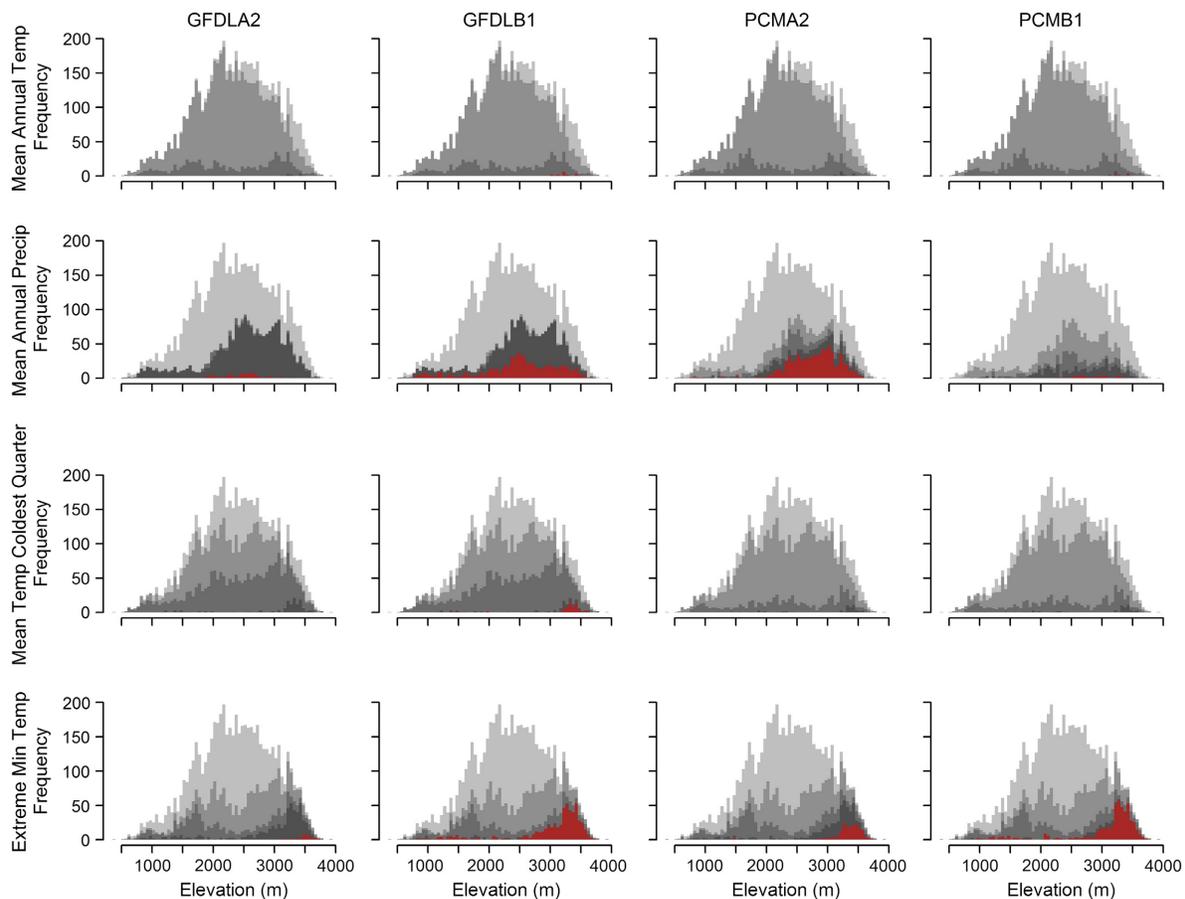


Fig. 4. Elevation distribution of climate refugial meadows under four future climate projections. In each window, lightest gray is the distribution of meadows, increased hue represents climate refugia for subsequent eras (end of the 20th century, 2010–2039; 2040–2069), and those in red represent expected climate refugia in 2070–2099. Each row represents a different climate change variable, and each column is a potential outcome based on circulation model and scenario. Thresholds for displayed climate refugia are 1°C for mean annual temperature and mean temperature of the coldest quarter, 10% mean annual precipitation, and 2 months/yr of extreme minimum temperature.

associated with temperature, precipitation, and water availability as potential drivers (e.g., Tingley et al. 2012, Rapacciuolo et al. 2014). Such range shifts could have been facilitated or impaired based upon the connectivity of habitats and the availability of corridors of movement. We did not find a consistent pattern with respect to mean connectivity and climate change refugia during the most recent century (Table 3). Furthermore, climate change refugia were not consistently found at high elevations, impacting naïve expectations of range shifts as meadow species might have limited access to habitats. Climate change refugia might have facilitated regionally persistence of

taxa (Morelli et al. 2012). Furthermore, climate refugia with high connectivity might yield negative outcomes for meadows by facilitating range shifts of invasive species or pathogenic organisms.

Under potential future climate scenarios, very often climate refugia will occur in meadows that have relatively higher connectivity, given the available network of refugial meadows from the previous era (Fig. 3, Tables 4 and 5). Perhaps this will facilitate movement and genetic exchange within stable habitats in the near future; management of these areas also could be key to minimize negative effects of connectivity on populations. However, many of the meadows will deviate strongly from

historical conditions and few will continue to experience similar climate patterns through this century (Fig. 4). In many respects, there will be restricted geographic availability of meadows that will be climate refugia, and these were often clustered in the southern and eastern Sierra Nevada in our maps. The overall meadow network will become reduced regardless of climate change scenario, which would further fragment meadow-dependent metapopulations. Populations buffered from negative impacts of invaders or pathogens through isolation may still become extirpated because of the shifting climate. If species can adapt to new climates, population shifts in distribution may be prevented, but not if suitable dispersal corridors that link climate refugia also disappear from the landscape. The consequent increasing isolation of populations could lead to genetic bottlenecks and influence viability of metapopulations supported by meadow networks (Orrock 2005).

Estimating impacts of climate change on species can require detailed species-specific information (Kearney and Porter 2004, Sinervo et al. 2010), but can inform conservation directions. Alternatively, identifying whether areas may act as a climate refugia could be more impactful for resource managers (Keppel et al. 2015, Morelli et al. 2016). The approach herein would be applicable where there is a diverse suite of species and limited information on physiological constraints of each. Integration of connectivity into such management decisions will also be key to potentially prepare for range shifts, invasions, and persistence with climate change (Rudnick et al. 2012, Gillson et al. 2013).

Assumptions and caveats

Our analysis made several assumptions regarding the history and designation of the meadows we compared. For instance, we do not know the size and status of these meadows prior to anthropogenic climate change, nor do we consider how meadow size will change under future conditions. There is already evidence of expansion of conifers into meadows during the 20th century (Millar et al. 2004), and further changes in groundwater may alter these ecosystems. However, it is likely that existing meadows have been meadows for periods longer than the last 100 years, so our beginning network represents a

best-case scenario for the future extent. Because of the complex processes that result in meadows, it is unlikely that new meadows will naturally form in the time-frame under consideration.

Our estimates of the influences of climate change on meadow connectivity should be robust to the diverse topographic landscape of the Sierra Nevada. Both the observed climate and future climate scenarios account for cold-air pooling (Curtis et al. 2014), which is an important characteristic for this region. However, our climate-related variables do not account for other heterogeneities in microclimates that may further create climate refugia (Ashcroft et al. 2012, Gillingham et al. 2012, Keppel et al. 2012, Millar et al. 2015). Nevertheless, the departure of the broader macroclimate variables expected in the future suggests that vegetation will be affected (Millar et al. 2004, Crimmins et al. 2011, Hijmans 2011, Stephenson and Das 2011) and patterns in the microclimate will change accordingly (D'Odorico et al. 2013).

By combining aspects of connectivity and climate refugia, we were able to examine where broader impacts of anthropogenic climate change have been and will be mediated in a meadow network. This approach provides a comprehensive examination of the impacts of climate change on a valuable habitat throughout the extent of the Sierra Nevada. Our approach helps to identify areas that, once evaluated using species-specific data, can then be prioritized for management action. We are confident that the patterns in potential connectivity we identified are likely to apply to a variety of organisms that disperse using various mechanisms and should represent restrictions for a number of taxa associated with meadows. How specific resistance surfaces explain dispersal constraints should be further evaluated using genetic data for species of concern.

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