

Effects of changing climate on aquatic habitat and connectivity for remnant populations of a wide-ranging frog species in an arid landscape

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Abstract

Amphibian species persisting in isolated streams and wetlands in desert environments can be susceptible to low connectivity, genetic isolation, and climate changes. We evaluated the past (1900–1930), recent (1981–2010), and future (2071–2100) climate suitability of the arid Great Basin (USA) for the Columbia spotted frog (*Rana luteiventris*) and assessed whether changes in surface water may affect connectivity for remaining populations. We developed a predictive model of current climate suitability and used it to predict the historic and future distribution of suitable climates. We then modeled changes in surface water availability at each time period. Finally, we quantified connectivity among existing populations on the basis of hydrology and correlated it with interpopulation genetic distance. We found that the area of the Great Basin with suitable climate conditions has declined by approximately 49% over the last century and will likely continue to decline under future climate scenarios. Climate conditions at currently occupied locations have been relatively stable over the last century, which may explain persistence at these sites. However, future climates at these currently occupied locations are predicted to become warmer throughout the year and drier during the frog's activity period (May – September). Fall and winter precipitation may increase, but as rain instead of snow. Earlier runoff and lower summer base flows may reduce connectivity between neighboring populations, which is already limited. Many of these changes could have negative effects on remaining populations over the next 50–80 years, but milder winters, longer growing seasons, and wetter falls might positively affect survival and dispersal. Collectively, however, seasonal shifts in temperature, precipitation, and stream flow patterns could reduce habitat suitability and connectivity for frogs and possibly other aquatic species inhabiting streams in this arid region.

Introduction

Ongoing and impending changes to Earth's climate have important implications for suitability and connectivity within species' current ranges (Walther et al. 2002). Aquatic species living in arid and semiarid regions of the world may experience earlier and more severe consequences of changes in precipitation and temperature because these areas are already water limited and may

approach thermal tolerances for some species (Arismendi et al. 2013). Although many arid regions are predicted to have warmer temperatures in the near future, predictions for more variability in the amount and timing of precipitation could also be problematic for aquatic species (Hamlet et al. 2005; Cayan et al. 2010; Walls et al. 2013). Such variability is likely to lead to altered stream hydrology and wetland hydroperiods causing connectivity among populations in arid landscapes to decrease during

extended drought or possibly increase during periods of deluge. Hence, an understanding of how climate change may affect aquatic species in arid environments is a high priority for conservation of aquatic biodiversity in many parts of the world.

Amphibian species have relatively narrow climate niches (Bonetti and Wiens 2014), and changes in temperature and precipitation patterns may influence the life history, and possibly persistence, of some species (Corn 2005; Araújo *et al.* 2006; Lowe 2012; McCaffery *et al.* 2012; Walls *et al.* 2013). Amphibians depend on sustained moisture (*i.e.*, usually surface water) and optimal temperatures in their environment for successful reproduction and survival. A species' response to climate change likely depends on the specificity of these habitat relationships, as well as adaptive genetic variation within populations (Carey and Alexander 2003; Cahill *et al.* 2013; Gerick *et al.* 2014). Species living in desert habitats, for example, are adapted to hot, arid conditions, but some desert environments may become too hot or dry in the near future to allow the species to persist (Gerick *et al.* 2014).

The ability of amphibians to persist under rapidly changing climate conditions may depend on their ability to disperse to suitable locations. Amphibians are able to exploit both aquatic and terrestrial resources for food, shelter, and travel, and many species move considerable distances (*e.g.*, >1 km) to reach distant habitats (Smith and Green 2005). Interpopulation movements facilitate genetic diversity and metapopulation dynamics (Sjögren 1991). Exceptionally hot, cold, or dry conditions can preclude the use of certain habitats or limit the use to brief periods when favorable conditions exist (Lemckert *et al.* 2012).

The goal of this study was to understand past and predict future responses of an aquatic-obligate species to changes in climate suitability and aquatic connectivity in a vast, arid landscape. To this end, we examined the climate relationships and interpopulation connectivity of the Columbia spotted frog (*Rana luteiventris*) across the Great Basin, the largest (>400,000 km²) desert in North America. The objectives of this study were to (1) quantify the past, recent, and future climate suitability and surface water availability for Columbia spotted frogs at currently occupied locations and across the Great Basin and (2) quantify interpopulation connectivity, based on hydrology and genetic data, as a means to examine potential consequences of changes in the amount and timing of available surface water. If this species' disjunct distribution and observed population declines in the Great Basin are related to climate changes, we expected to find that climate suitability

and surface water availability have declined at currently occupied sites and across the Great Basin over the past 100 years. We also expected interpopulation connectivity and gene flow to be (1) related to surface water availability, (2) low between neighboring sites, (3) greater between sites on stream networks than between ponds or between ponds and nearby streams, (4) lower between sites in more distant regions of the Great Basin, and (5) higher through private, rather than federal or state land given that most private lands in the Great Basin occur along valley bottoms where water is available for agriculture. Support for these hypotheses does not necessarily imply a causal link between climate change and the current status of the Columbia spotted frog in the Great Basin, but combining information on climate suitability, surface water availability, and landscape connectivity could provide an important means of examining potential climate change effects on some of the most potentially vulnerable species: amphibians or other aquatic organisms living in arid and semiarid regions of the world.

Methods

Study species

The Columbia spotted frog is a widely distributed species that once occupied large portions of the Intermountain West, from central Nevada to Alaska. The success of the species may be related to its ability to breed in a variety of freshwater habitats and climates, ranging in elevation from 500 to 3036 m (Reaser and Pilliod 2005). In spite of these broad environmental tolerances, in the southern portion of the species' range (*i.e.*, the Great Basin), Columbia spotted frogs now only persist in disjunct populations. Phylogenetic analyses suggest little gene flow among these isolated remnant populations in the Great Basin, apparently because the intervening habitats have become unsuitable (*i.e.*, warmer, drier, and occupied by nonnative predators) during the present interglacial period (Green *et al.* 1996; Bos and Sites 2001; Funk *et al.* 2008). Further, the availability of habitat patches (*e.g.*, water bodies) and corridors connecting them may have declined sharply with widespread trapping of beaver in the 1800s and the diversion of streams and draining of wetlands for agricultural development (Engilis and Reid 1996; Gibson and Olden 2014). These changes have fragmented suitable habitat for Columbia spotted frogs across the Great Basin and likely led to increased isolation of populations as movement of individuals between sites became less frequent, similar to isolating mechanisms observed in the northern part of the

species' range (Funk *et al.* 2005a; Goldberg and Waits 2010). Columbia spotted frogs in the Great Basin are now considered to be a genetically distinct population segment (DPS), isolated from populations in the northern part of the species' range (Funk *et al.* 2008). The Great Basin DPS is of conservation concern due to the apparent isolation of remnant populations and various threats to their habitats; these conservation issues are not unique to spotted frogs and represent broader issues for aquatic species in the Great Basin and other arid regions of the world (Sada and Vinyard 2002).

Study area

The Great Basin encompasses over 400,000 km² of the western United States and is delineated loosely by endorheic watersheds and phytogeographic provinces. We defined our study area using three Level III Ecoregions (Snake River Plain, Northern Basin and Range, and Central Basin and Range; http://www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm) that included parts of southeastern Oregon, southern Idaho, Nevada, western Utah, and eastern California (Fig. 1). The Great Basin is

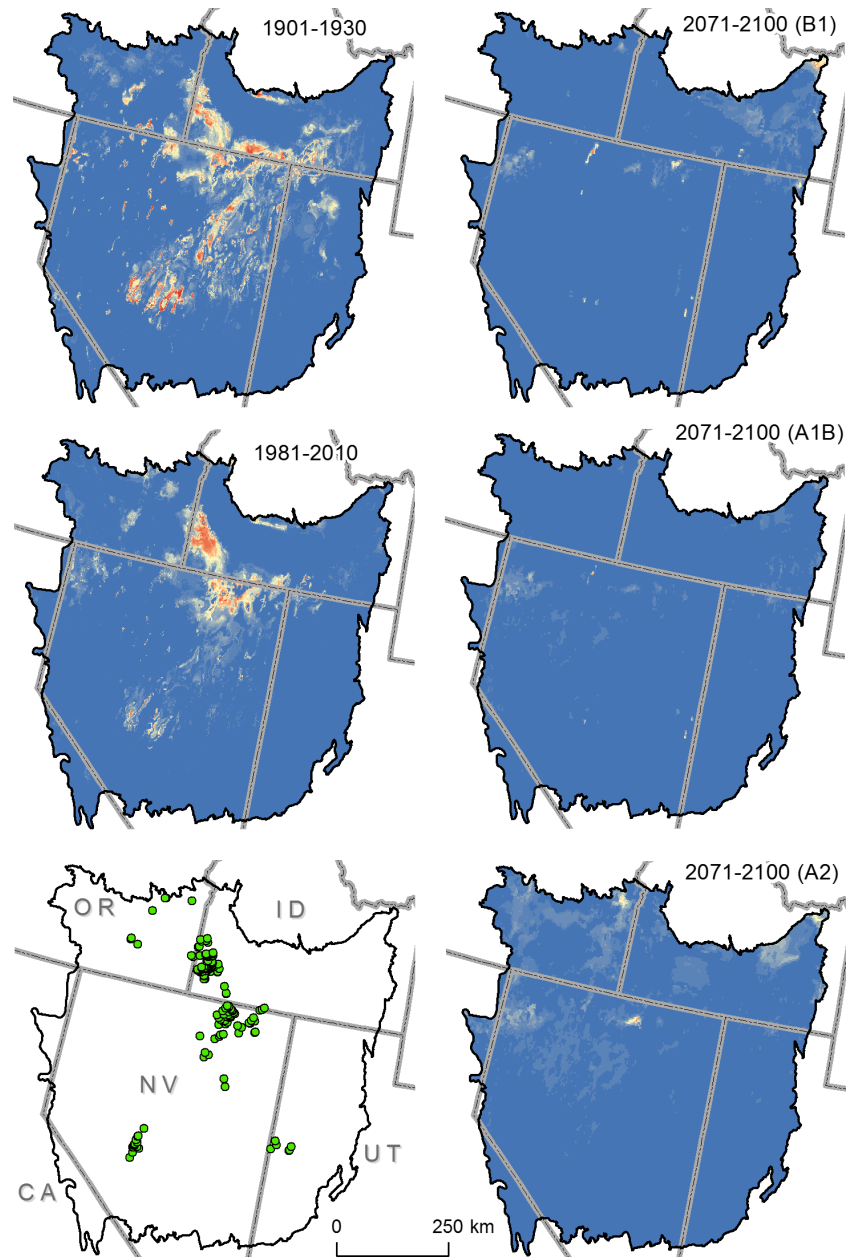


Figure 1. Geographic projections of past (1901–1930), recent (1981–2010), and future (2071–2100) climate suitability for Columbia spotted frogs in the Great Basin (black line). Projections were based on applying a model of breeding location climate to similar data from each time or carbon emission scenario (B1, A1B, and A2; ordered low to high carbon emissions). Each panel uses an equivalent color ramp, with cooler colors indicating lower probability of suitability and warmer colors indicating greater suitability (range = 0–0.97). Points shown in green are current breeding locations (points in Utah were not used in model development).

characterized by basin and range topography with elevations ranging from near sea level to >4,000 m. Low-elevation areas are dominated by arid and semi-arid grasslands and shrublands, which transition into piñon-juniper woodlands and pine-fir forests at higher elevations. Precipitation typically ranges from 12 to 35 cm, depending on elevation, and falls mainly as winter snow and early spring rain. Summers are hot and dry throughout the region, with average daily high temperatures from 29.8 to 33.8°C in July, also depending on elevation.

Climate suitability

We used field observations of Columbia spotted frog breeding (i.e., presence of eggs or larvae) combined with 30-year average monthly temperature and precipitation data for each breeding location to develop a spatially explicit predictive model of the distribution of suitable climates across the Great Basin. Frog observation data were compiled by the U.S. Fish and Wildlife Service (from federal, state, and university studies) for the years 1993 to 2012. To reduce effects of repeat observations made at particular locations (which would result in “spatial pseudo-replication” and subsequent over-fitting to areas with a high density of observations) and effects of potential location error associated with early global positioning systems (GPS, precise to within 10–100 m), we buffered each of these observations by 400 m, dissolved overlapping buffers into “breeding complexes” and calculated a centroid coordinate for each complex using ArcMap10.0 (ESRI, Redlands, CA). Buffer distances assume that Columbia spotted frogs can move up to 400–500 m across dry land and that adjacent breeding sites often exchange individuals and function as metapopulations (Engle 2001; Pilliod *et al.* 2002). We found no difference in mean annual temperature or precipitation conditions between centroid points and the original observation points that contributed to each centroid. The average area of breeding complexes was 69.3 ha (only 1.4% larger than the area encompassed by a single observation buffered by 400 m). This resulted in 151 breeding complex locations (hereafter “breeding locations”) within the Great Basin study area, with 145 in the Great Basin DPS (Great Basin clade) and six assigned to the Utah clade based on genetic analysis of mitochondrial DNA (Funk *et al.* 2008). Only breeding locations in the Great Basin DPS were used in analyses; however, we extended predictions from models to the entire study area, which included part of the Utah clade.

We used 30-year (1981–2010) average monthly temperature and precipitation data to derive recent climate variables (i.e., 30-year average temperature and precipita-

tion values for each month of the year resulting in 24 climate parameters) for each breeding location. We rescaled climate data from 800-m gridded PRISM data (Daly *et al.* 2002) to 270 m to match the spatial resolution of our other data, resulting in about 6.8 million 270-m pixels across the Great Basin study area (see Franklin *et al.* 2013 for discussion of the influence of spatial grain for climate analyses). Multivariate outlier analysis and nonmetric multidimensional scaling (NMS) ordination of recent climate data were conducted (as in Arkle *et al.* 2014) using PC-ORD 6.09 software (McCune and Mefford 2011) to identify breeding locations with average Sorenson distances greater than two standard deviations from the overall mean Sorenson distance between locations. Three breeding locations were identified as climatic outliers and were excluded from the input dataset because of potentially disproportionate influence on model outputs (Fig. A1), resulting in 142 breeding locations used in analyses.

We used the 24 climate parameters at the 142 breeding locations as input data for a maximum entropy model in MAXENT (version 3.3.3k), a presence-only modeling framework that is mathematically equivalent to Poisson regression and related to Poisson point process models (Renner and Warton 2013). We used this approach because we did not have reliable “absence” data or survey locations where Columbia spotted frog breeding was not observed. This modeling approach is sensitive to imperfect detection (Lahoz-Monfort *et al.* 2014) and sampling biases, particularly from nonrandom sampling (Royle *et al.* 2012). However, locations where repeat surveys were conducted yielded relatively high (0.89) detection probabilities for adults (Arkle and Pilliod *in press*) and nearly all breeding locations were obtained from surveys where catchments (and water bodies within them) were randomly selected for sampling rather than convenience sampling (e.g., Wentz *et al.* 2005). Temperature and precipitation data for each month were used, rather than totals or summary variables, because the timing of precipitation or temperature changes was hypothesized to be important for this species. The model was run using auto features and the default regularization scheme with 500 iterations and 10,142 background points. The resulting model output map reflects the probability that the climate in each 270-m pixel is suitable for Columbia spotted frog breeding based on 1981–2010 climate conditions at known breeding locations. We used Jackknife and permutation tests to measure the importance of each variable (monthly temperature or precipitation) for predicting climate suitability (Fig. A2).

We applied this recent climate model to historic (1901–1930) climate data (270-m downscaled from

800-m gridded PRISM data; Daly *et al.* 2002) to assess changes in the distribution of climate suitability within the Great Basin over the past 100 years. This “hindcasting” is based on the assumption that the climate-space requirements of Columbia spotted frogs in the region have not changed and that they currently have access to and occupy areas at or near climate optima for the species. We used the same approach to predict the distribution of future climate suitability in the Great Basin over the 30-year period 2071–2100. Future monthly temperature and precipitation data were derived from 16-model ensemble averages under three carbon emission scenarios: A2, A1B, and B1 (high, medium, and low emission scenarios, respectively; IPCC-TGICA 2007). Forecasting in this way assumes the species’ niche will be conserved across time and that predictions reflect the distribution of that niche (climate suitability) across the landscape under future conditions. These model outputs do not infer probability of occupancy, structural habitat suitability, or persistence.

To determine the location and extent of suitable climate in the Great Basin, we applied the final MaxEnt model to the whole study area for each of the five scenarios (i.e., time periods or carbon emission scenarios). We then generated kernel-smoothed probability density curves (based on all pixels) under each scenario using the “sm” package in R (Bowman and Azzalini 2014; R Development Team, 2014). Probability density curves allowed us to estimate the relative amount of suitable climate for the species across the landscape under each scenario. Results from the recent climate model showed that over 95% of breeding locations were contained in areas having a probability of climate suitability ≥ 0.20 . Consequently, we used 0.20 as a cutoff to define areas as “suitable” in subsequent analyses where a cutoff value was required. To evaluate changes in climate suitability at currently occupied locations only (i.e., not Great Basin-wide), we compared average monthly temperature and precipitation values under past, recent, and future scenarios only for pixels underlying current breeding locations ($n = 142$ pixels for each of the five scenarios).

Surface water availability

We used Variable Infiltration Capacity (VIC) data (Gao *et al.* 2010) to quantify surface water runoff in 6-km pixels across the entire Great Basin for similar time periods as described above. VIC is a spatially explicit, coarse-scale, surface water hydrologic model that combines gridded land surface modeling approaches with meteorological data. While we recognize the importance of ground water for the hydrology of streams and wetlands, VIC runoff data allowed us to assess at least the relative changes in

surface water contributions to streams and wetlands under different scenarios. As VIC data were not available for the exact time periods used for climate modeling, we selected the closest available corresponding year ranges: 1915–1930, 1981–2006, and 2080. Data provided for 2080 were derived from a 10-year model simulation approach, accounting for annual variability. Consequently, values from the 2080 dataset reflect projected climate conditions on a 10-year scale, centered around 2080. We calculated monthly average surface runoff values (depth per day, where 1 mm depth = 1 million L/km²) for each time period for all 6-km pixels in the Great Basin study area. We generated kernel-smoothed probability density curves for the months of May and September in each time period to quantify changes in the distribution of runoff values throughout the Great Basin. These 2 months were identified by our climate suitability model as the most important hydrologic (i.e., precipitation likely to fall as rain) predictors of spotted frog climate suitability (Fig. A3). To evaluate changes in monthly runoff at currently occupied locations only (i.e., not Great Basin-wide), we calculated the mean monthly runoff values for each time period at pixels underlying current breeding locations ($n = 142$ pixels for each of the three time periods).

Connectivity (landscape resistance models)

We quantified habitat connectivity between breeding locations using Circuitscape 4.0 (McRae *et al.* 2014), which employs circuit theory and random walk theory to predict movement across resistance surfaces. Resistance surfaces are developed from information on a species’ movement capabilities through a landscape of interest (McRae *et al.* 2008). We used the best available biological information on the species to create a resistance surface which assumes that Columbia spotted frogs move more easily or frequently through areas (i.e., pixels) nearer to permanent water, half as easily or frequently through areas near intermittent water, and least often through areas far from any water. For example, radio-telemetry studies in a variety of landscapes have found that Columbia spotted frogs will travel 5–6 km along water courses, but only about 500 m over land depending on habitat moisture and weather conditions (Reaser 1996; Bull and Hayes 2001; Engle 2001; Pilliod *et al.* 2002; Funk *et al.* 2005b).

We extracted all permanent water bodies in the NHDPlus database (<http://nhd.usgs.gov/>) and calculated the distance from each 270-m pixel in the Great Basin to the nearest permanent water. We repeated this process, calculating the distance from each pixel to the nearest intermittent water source and multiplying by 2 to double the resistance under the assumption that intermittent water

bodies would be available for use half of the time. We only included intermittent water sources within areas having climate suitability ≥ 0.20 to avoid over-predicting movement through unsuitable areas. For each pixel, we took the minimum of those two distance values such that our resulting resistance surface was composed of 270-m pixels, with the value of each pixel based on the minimum of (1) its distance to the nearest perennial water or (2) twice its distance to the nearest intermittent water.

We first modeled connectivity for all 151 breeding locations in the Great Basin using a “one-to-all” method where one amp of electrical current is injected into each breeding location iteratively with all others tied to ground. This analysis depends on the particular sites included for analysis because current flows from a single site to (potentially) all 150 other sites in each iteration. Current values were recorded for each pixel in each iteration, and cumulative current flow was mapped across the landscape. We included six sites in the Utah genetic group for reference.

Connectivity and gene flow (validation models)

To examine how the relationship between landscape resistance (\hat{R}) and genetic distance differed across the region, we needed to delineate the distinct genetic groups within the Great Basin. We estimated the number of genetic clusters (K) using the program STRUCTURE 2.3.3 (Pritchard *et al.*, 2000). STRUCTURE implements a Bayesian clustering algorithm to compute the likelihood $L(K)$ for assignment to each cluster based on Hardy-Weinberg (HW) and linkage disequilibrium (LD) characteristics (model conditions: burn-in 100,000 iterations; 3,000,000 iterations post burn-in; admixture model; correlated allele frequencies; $K = 1-15$; 10 replicates for each K). We selected K based on the ΔK method (Evanno *et al.*, 2005) and the posterior probability of K given the data (Pritchard *et al.*, 2000). To detect the presence of substructure within each cluster, we iteratively reran clusters until $K = 1$ (Murphy *et al.*, 2010a). The clustering method implemented in STRUCTURE confirmed that Columbia spotted frogs used in this analysis were partitioned into three genetic groups in the Great Basin: Owyhee Uplands in southwestern Idaho, Steens Mountains and other sites in southeastern Oregon, and Jarbidge Mountains in Northern Nevada. Two other groups (Toiyabe Mountain and Ruby Mountain, both in Nevada) are likely, but as genetic data were not available, these were not included in our validation Circuitscape model or in our gene flow comparisons. They were, however,

included in range wide landscape resistance models of connectivity between all known breeding locations.

Genetic dissimilarity (hereafter, genetic distance) was determined from F_{ST} values. F_{ST} values were obtained from a subset of our breeding locations, including 34 sampling sites and 591 individuals, with an average of 17 individuals sampled per site (median = 18; range = 6–33; Robertson *et al.*, unpublished data). Polymerase chain reaction (PCR) was used to amplify eight microsatellite loci in two multiplex reactions for each individual (Murphy *et al.*, 2010b), and genotypes were binned and checked using GeneMarker (SoftGenetics 2010). All loci were tested for possible null alleles, HW proportions, and LD (van Oosterhout *et al.*, 2006). The study estimated pairwise F_{ST} between all sites within and among regions and assessed significance in Arlequin suite ver 3.5 (Excoffier and Lischer 2010).

We evaluated our connectivity model by running a validation Circuitscape model using “pair wise” connections between the 25 Great Basin sites with genetic data and calculating pairwise resistance distance (\hat{R}) between them. \hat{R} , when calculated in a pairwise fashion, represents connectivity between two locations and differs from least-cost path metrics in that it incorporates both

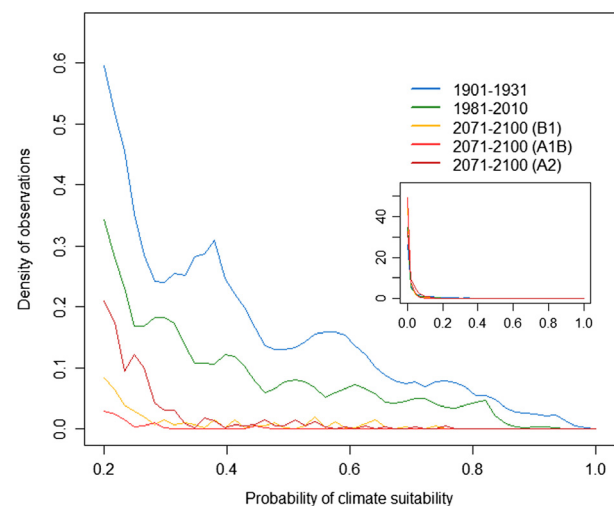


Figure 2. Kernel-smoothed probability density of climate suitability values for all 270-m pixels in the Great Basin by time or carbon emission scenario. Values were derived by modeling recent (1981–2010) breeding location climate conditions and projecting to climate data for all pixels, under each scenario. Underlying future climate data derived from 16-model ensemble averages under B1 (low), A1B (medium), and A2 (high) carbon emission scenarios. Inset shows the full range of the x-axis, whereas the main figure shows the density of observations only in x-axis values ≥ 0.20 to better illustrate differences in the area of suitable climate among the time periods and carbon emission scenarios.

movement cost and route redundancy (i.e., the availability of alternative routes between locations; Spear et al. 2010). We tested whether pairwise \hat{R} values explained a significant amount of the variation in F_{ST} for 600 site pairs (i.e., 25 sites with genetic data) by fitting a nonparametric multiplicative regression model (NPMR; McCune 2009) and assessing model fit through the average cross-validated R^2 (xR^2) derived from 100 bootstrap runs. Using \hat{R} and FOCALSITE (a categorical variable representing each site's pairings with each other site) as predictor variables allowed for different functions to be fit for each of the 25 sites. Consequently, the connectivity of each focal site could be compared to all other sites and to the mean of all focal sites. Finally, we calculated mean \hat{R} and F_{ST} values for all site pairs within and between each isolated genetic group (defined by STRUCTURE).

We also evaluated connectivity by habitat type and land ownership. For sites in the Owyhee group, the group with the highest density of sites with genetic data, we calculated mean \hat{R} and F_{ST} values for each of the following: pairs of pond sites, pairs of sites on stream networks (but not necessarily on the same stream network), and pond–stream site pairs. This allowed us to assess whether dry land surrounding ponds reduced connectivity and gene flow relative to sites where it is possible to travel along streams or riparian corridors. We assessed the importance of lands managed by different owners to Columbia spotted frog connectivity (through areas of suitable climate only) by generating kernel-smoothed probability density curves by land owner for all pixels with a probability of climate suitability ≥ 0.20 .

Results

Climate suitability

The climate suitability model fit observed breeding location climate data well (full data set AUC = 0.98) without overfitting to training data (10-fold test AUC average \pm SE = 0.95 ± 0.006). May, September, and December precipitation and September temperature were the most important predictors of breeding location climate suitability in the full model, whereas the best single variable predictors were May, June, September, and December temperature (Fig. A3). Predicted suitability was highest in areas with intermediate temperatures during these months and in areas with high May precipitation, and intermediate to high September and December precipitation (Fig. A3). Temperature and precipitation values during other months were not particularly useful for differentiating breeding locations from random locations in the study area.

Only 5.4% of the Great Basin had suitable climate conditions for Columbia spotted frog breeding during the 1981–2010 time period (Figs 1 and 2 inset). The area of suitable climate (i.e., ≥ 0.20) has declined by 49% since the period 1901–1930 on the basis of relationships derived from the current climate model projected into the past (Fig. 2). The model also predicts a further decline of 77–97% (depending on carbon emission scenario) of the area with suitable climate in the period 2071–2100 relative to the 1981–2010 time period (Figs 1 and 2). A greater proportion of the Great Basin is expected to have moderately suitable (i.e., 0.20–0.30) climate conditions under the high (A2) emission scenario than under the medium (A1B) and low (B1)

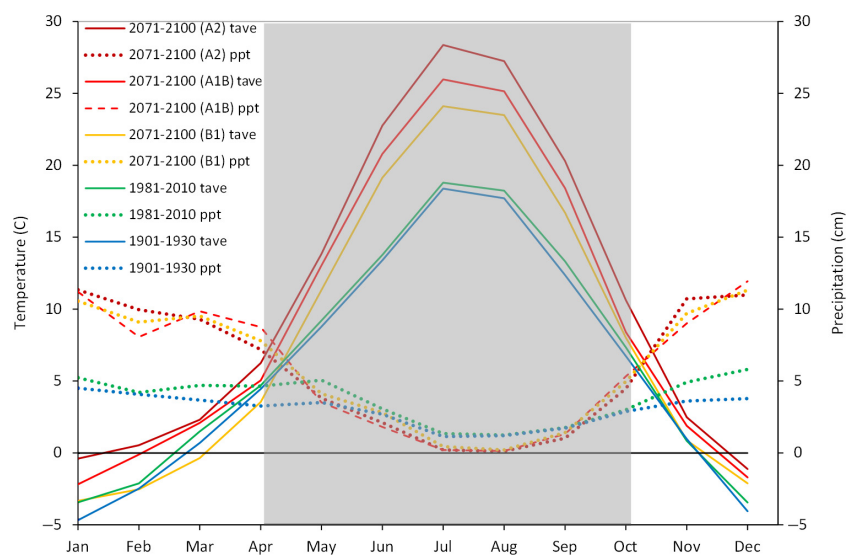


Figure 3. Average monthly mean temperature (tave, solid lines) and average monthly total precipitation (ppt, dashed lines) for 30-year periods under past, recent, and three future climate scenarios at 142 spotted frog breeding locations. Black line indicates freezing or zero precipitation. Gray shading represents spotted frog annual active period.

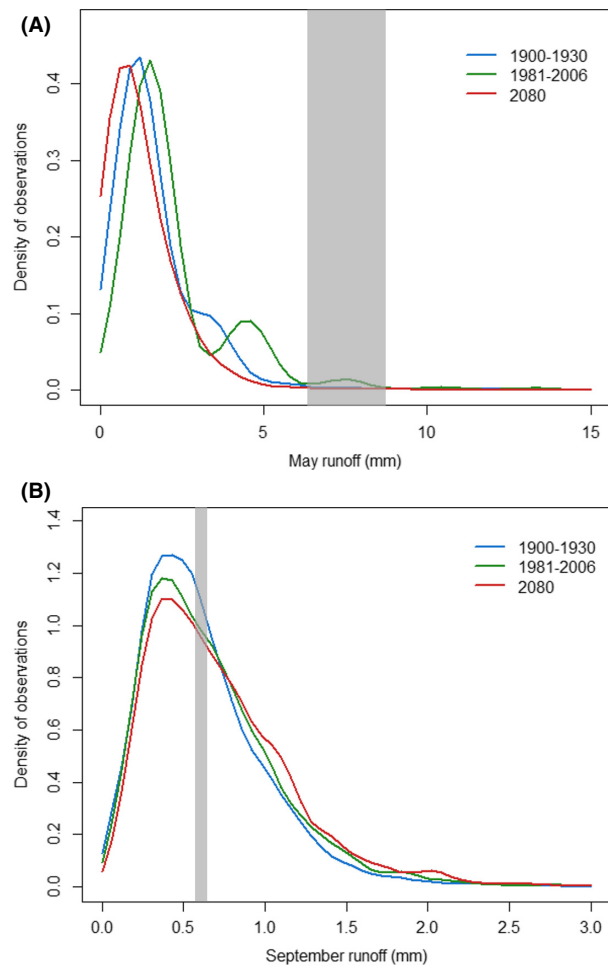


Figure 4. Kernel-smoothed probability density of surface water runoff values for all 6-km pixels in the Great Basin by time period. Runoff values were derived from variable infiltration capacity (VIC) data averaged within each time period for the months of May (A) and September (B). Gray shading represents average ± 1 SE runoff at known breeding locations.

emission scenarios (Fig. 2). Figure A4 provides values expressed as percent of the study area rather than density of observations.

Despite the greater availability of moderately suitable future conditions predicted throughout the Great Basin under the high (A2) scenario (relative to the medium [A1B] and low [B1] scenarios), all three carbon emission ensemble models predicted that known breeding locations will be much warmer and somewhat drier during the frog's current active season (April–November) in 2071–2100 compared to recent conditions (Fig. 3). Precipitation is expected to decrease during the driest summer months (June–August), but increase during the fall and winter months (Fig. 3). Given the warmer winter temperatures, this precipitation is likely to fall as rain instead of

snow. Climate conditions did not change substantially at these breeding locations between 1901–1930 and 1981–2010 (Fig. 3).

Surface water availability

Surface runoff was higher, in general, during 1981–2006 period compared to the 1915–1930 and 2080 time periods. According to the VIC model, the area of the Great Basin with May surface runoff values of 4–8 mm (relatively high values that correspond to values at currently occupied breeding locations) increased between the 1915–1930 and 1981–2006 time periods (Fig. 4A). However, May surface runoff is expected to be substantially lower throughout the Great Basin during the 2080 time period than was observed for 1915–1930 or 1981–2006 time periods (Fig. 4A). The area of the Great Basin with relatively high (i.e., >0.70 mm) September surface runoff also increased between 1915–1930 and 1981–2006 (Fig. 4B). However, in contrast to May, September runoff is expected to increase in much of the Great Basin between the 1981–2006 and 2080 time periods.

Monthly surface runoff values at breeding locations indicate that, on average, runoff has been higher recently (i.e., 1981–2006) than at the same locations from 1915 to 1930 during several months of the year (particularly during spring and winter months; Fig. 5). Surface runoff is expected to be lower from March–July (i.e., during much of the period when eggs are deposited and tadpoles are developing) during the 2080 time period than during the other time periods. The dry months of August and September are not predicted to change substantially, whereas October–February runoff is expected to be greater in 2080 than during the other time periods (Fig. 5).

Connectivity and gene flow

Landscape connectivity as measured by resistance distance (\hat{R}) among the 151 Columbia spotted frog breeding locations varied by geographical location (Table 1, Fig. 6, Fig. A5). Groups (and thus breeding locations) in the northern part of the study area tended to have higher connectivity to other breeding locations than groups in the southern part of the Great Basin, with a few exceptions (Table 1, Fig. A5). Some populations in southeastern Oregon (Other Oregon) were especially isolated, but still less isolated than the West Desert, Utah populations, which were included for comparison.

The validation connectivity model produced \hat{R} values that were well correlated with F_{ST} values for 600 site pairs spanning the northern Great Basin (mean \pm SE $\times R^2$ for 100 bootstrap runs = 0.68 ± 0.004). FOCALSITE was an

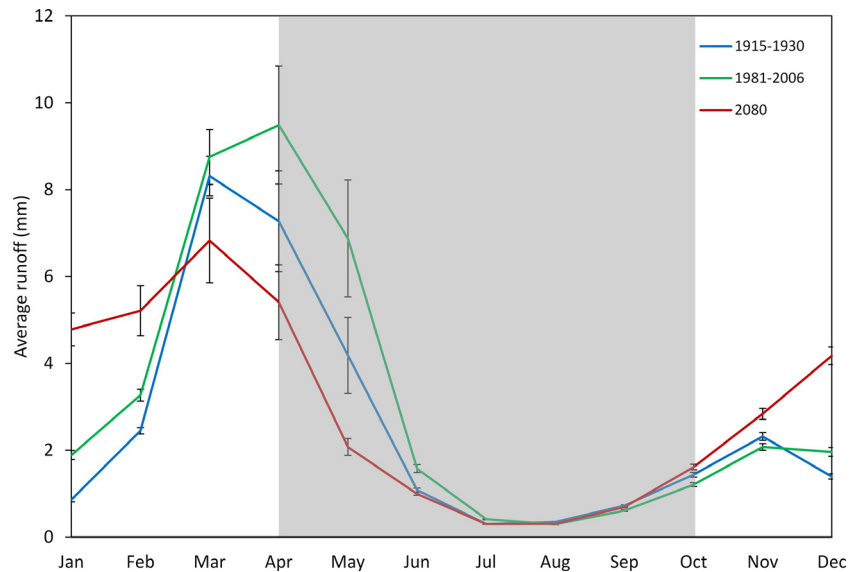


Figure 5. Average \pm 1 SE monthly runoff at recent spotted frog breeding locations ($n = 142$) for three different time periods. Runoff values were derived from variable infiltration capacity (VIC) data averaged within each time period. Gray shading represents spotted frog annual active period.

Table 1. Average \pm SE connectivity (\hat{R}) for 151 Columbia spotted frog breeding locations by genetic group (defined by Funk et al. 2008 and this study). Groups are organized north to south in the Great Basin.

| Columbia spotted frog group | N sites | Ave \hat{R} (one-to-all) |
|---------------------------------|-----------|----------------------------|
| Southeast Oregon (Steens) | 4 | 89.9 ± 36 |
| Southeast Oregon (Other Oregon) | 3 | 1052.7 ± 474.5 |
| Southwest Idaho (Owyhee) | 74 | 84 ± 4.5 |
| Northern Nevada (Jarbidge) | 49 | 119.3 ± 6.6 |
| Central Nevada (Ruby) | 2 | 309.9 ± 29.8 |
| Southern Nevada (Toiyabe) | 13 | 167.8 ± 34.9 |
| Utah (West Desert) | 6 | 4406.6 ± 1014.9 |

important predictor, indicating that the relationship between \hat{R} and F_{ST} was not identical for all sites (i.e., based on F_{ST} values, some sites were consistently more isolated than others for a given range of \hat{R} ; Fig. 7). F_{ST} increased rapidly to about 0.70 as \hat{R} approached 800 and then leveled off. Once \hat{R} exceeded approximately 800 (Fig. 7), a value that corresponded to an average Euclidian distance of approximately 200 km, genetic distance between sites ceased increasing. \hat{R} explained more variability in F_{ST} than did Euclidian distance (mean \pm SE $\times R^2$ for 100 bootstrap runs = 0.61 ± 0.007), despite a strong correlation between \hat{R} and Euclidian distance ($R^2 = 0.90$).

Connectivity between sites within nested groups was low relative to gene flow estimates reported for Columbia spotted frog populations in the northern part of their range (Funk et al. 2005a; Murphy et al. 2010b), and populations in different groups were effectively isolated (Table 2). Within the Owyhee group, connectivity (i.e., as estimated using both \hat{R} and F_{ST}) was lowest between pairs

of pond sites (which were not typically connected to perennial water), intermediate between stream–pond site pairs, and highest between pairs of sites on stream networks (regardless of whether the sites were on the same stream network; Table 3). However, two stream sites (in the Owyhee and Jarbidge groups) surrounded by lower-elevation stream segments with predatory redband trout (*Oncorhynchus mykiss newberrii*) had F_{ST} values 15–17% higher than expected for any given \hat{R} -value, indicating that these sites are relatively isolated compared to other sites.

Land ownership

The majority (56%) of the area of suitable climate in the Great Basin for the Columbia spotted frog occurred on lands managed by the Bureau of Land Management, whereas private, U.S. Forest Service, and state lands represented 21, 15, and 4%, respectively. In locations with suitable climate conditions areas with high connectivity (as measured by electrical current flow) tended to occur primarily on private, state, and U.S. Forest Service managed lands (Fig. A6). Bureau of Land Management lands had among the lowest connectivity, probably because these areas had little surface water.

Discussion

Our results suggest that the vast majority of the Great Basin is currently too dry to support Columbia spotted frog populations (mainly lower-elevation areas) and this relationship will hold under potential future climates. Areas that do receive sufficient precipitation are often at

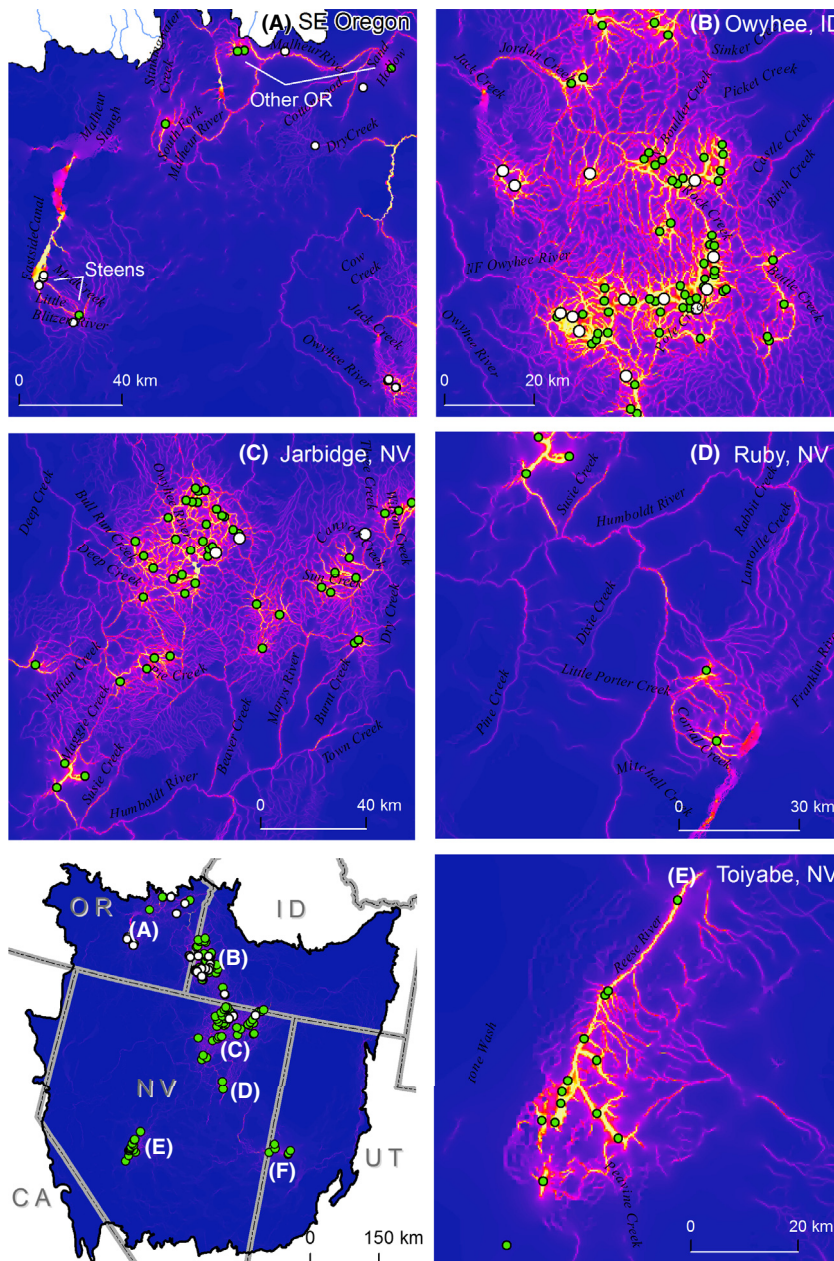


Figure 6. Connectivity analysis output for the entire Great Basin (lower left; also see Fig. A5), with 151 spotted frog breeding locations (green points; see Table 1) used for the full connectivity model, 25 breeding locations with genetic data (white points; see Table 2) used for validation connectivity model, and white letters corresponding to enlarged panels for each region. Individual regions are labeled in white text as Panels A - E, with stream and river names labeled in black. Panel F of the West Desert, Utah is not shown. Warmer colors indicate pixels (270 m) of higher electrical current flow and connectivity between breeding sites.

higher elevations and there is frequently an expectation that mobile species will shift their distributions upwards to these cooler, wetter areas. However, we did not observe an increase in future climate suitability at higher elevations. Milder winters with less snowpack will also influence wetland hydrology and permanence at higher elevations, which could reduce habitat availability or quality. Further, locations higher in watersheds have less drainage area contributing to ground and surface water accumulation and the steep topography in many Great Basin mountain ranges may limit the formation of

wetland habitat and thus the utility of these higher elevation areas as refugia under future climates.

We found that the climate at recently occupied locations has not changed much over the last century, which may explain why frogs persist in these locations. If this level of stability is rare in the region, our finding could explain why remaining populations in the Great Basin have become so isolated today. Climatic niche specialization within a fairly narrow range of temperature and precipitation is typical for amphibians globally (Bonetti and Wiens 2014). For example, common garden

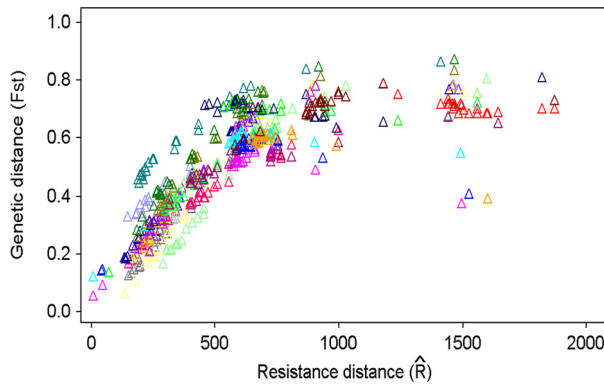


Figure 7. Resistance distance (\hat{R}) versus genetic distance (F_{ST}) for all pairwise combinations of 25 spotted frog populations in the northern Great Basin. Resistance distance values were derived from a Circuitscape model run in pairwise mode. Site pairs (open triangles; $n = 600$) are color-coded to show different functions for each site. Overall model fit was $xR^2 = 0.68$.

manipulations of temperature or hydroperiod have shown that amphibians are often adapted to conditions in their native ponds and lack plastic responses to induced environmental changes (Amburgey et al. 2012). Given a relatively narrow climatic niche requirement, these recently occupied locations may not be suitable into the future as the magnitude of temperature and precipitation change is expected to be substantially greater than the changes observed at these sites over the past 100 years. Our model projections from all three carbon emission scenarios suggest that the availability of locations with suitable climates may decrease. This may have negative consequences for population viability if hydroperiods of shallow wetlands and intermittent streams become too short to support successful frog reproduction (Hossack et al. 2013; Matthews et al. 2013; McCaffery et al. 2014), if conditions change too rapidly for populations to evolve (Urban et al.

Table 2. Average ± 1 SE connectivity (\hat{R} ; derived from pairwise validation model) and genetic distance (F_{ST}) between pairs of Columbia spotted frog breeding locations (N) within and between each genetic group for 25 populations in the northern Great Basin. The number of populations within each group is given in parentheses. Lower values of \hat{R} and F_{ST} indicate higher connectivity.

| Comparison | N pairs | Ave \hat{R} | Ave Euclidian distance (km) | Ave F_{ST} | Ave migrants/generation ¹ |
|------------------------------------|-----------|------------------|-----------------------------|-----------------|--------------------------------------|
| Within groups | | | | | |
| Southwestern Idaho (Owyhee) | 105 (15) | 250.1 \pm 7 | 27.9 \pm 1.5 | 0.30 \pm 0.02 | 0.58 |
| Northern Nevada (Jarbidge) | 3 (3) | 389.6 \pm 77 | 38.6 \pm 14 | 0.37 \pm 0.16 | 0.43 |
| Southeastern Oregon (Steens) | 6 (4) | 128.2 \pm 61 | 11.9 \pm 6 | 0.17 \pm 0.05 | 1.22 |
| Southeastern Oregon (other Oregon) | 3 (3) | 1361.1 \pm 267 | 176.1 \pm 74 | 0.69 \pm 0.17 | 0.11 |
| Between groups | | | | | |
| Owyhee–Jarbidge | 45 | 510.6 \pm 15 | 141.8 \pm 3.4 | 0.56 \pm 0.02 | 0.20 |
| Owyhee–Steens | 60 | 634.4 \pm 7 | 167.8 \pm 2.5 | 0.62 \pm 0.01 | 0.15 |
| Owyhee–Other Oregon | 45 | 993.8 \pm 59 | 179.1 \pm 11 | 0.77 \pm 0.01 | 0.07 |
| Jarbidge–Other Oregon | 9 | 1196.5 \pm 134 | 305.2 \pm 19 | 0.70 \pm 0.02 | 0.11 |
| Jarbidge–Steens | 12 | 814.6 \pm 27 | 294.5 \pm 6.4 | 0.50 \pm 0.01 | 0.25 |
| Steens–Other Oregon | 12 | 846.6 \pm 77 | 125.7 \pm 2.7 | 0.51 \pm 0.02 | 0.24 |

¹Calculated as $F_{ST} = 1/(4Nm + 1)$, to provide an intuitive index of migration between sites. These values should not be interpreted literally (Whitlock and McCauley 1999).

Table 3. For 15 populations in the Owyhee group, average connectivity (\hat{R}) and genetic distance (F_{ST}) between pairs of Columbia spotted frog breeding locations (N) in stream–stream, stream–pond, and pond–pond site pairs. Stream–stream site pairs were not necessarily on the same stream network as one another. Twelve sites were in stream habitats and three were in pond habitats. Lower values of \hat{R} and F_{ST} indicate higher connectivity.

| Comparison | N pairs | Ave \hat{R} | Ave Euclidian distance (km) | Ave F_{ST} | Ave migrants/generation ¹ |
|---------------|-----------|-----------------|-----------------------------|-----------------|--------------------------------------|
| Stream–Stream | 66 | 213.5 \pm 5 | 23.6 \pm 1.4 | 0.19 \pm 0.01 | 1.1 |
| Stream–Pond | 25 | 311.2 \pm 6.1 | 24.9 \pm 2.1 | 0.24 \pm 0.03 | 0.79 |
| Pond–Pond | 6 | 342.1 \pm 59 | 30 \pm 9.1 | 0.38 \pm 0.13 | 0.41 |

¹Calculated as $F_{ST} = 1/(4Nm + 1)$, to provide an intuitive index of migration between sites. These values should not be interpreted literally (Whitlock and McCauley 1999).

2014), or if limited connectivity does not permit movement to more suitable locations.

As expected, extant Great Basin populations are relatively isolated and populations 100–200 km apart are unlikely to interbreed, even indirectly via “stepping stone” populations. Even neighboring populations within groups had little gene flow (F_{ST} values up to 0.30, which are high even for amphibians) and low connectivity (high \hat{R} values) despite being physically separated by distances <10 km. Our model shows that connectivity is influenced by available surface water in addition to distance. Although frogs bred in both ponds and streams, frog populations that bred in ponds were even more isolated than those that bred in streams (as measured by both F_{ST} and \hat{R} values). This finding is intuitive given that streams and their riparian vegetation are ribbons of green in an otherwise inhospitable, arid landscape. The importance of streams for frog movement has been documented in the northern portion of their range (Bull and Hayes 2001; Funk *et al.* 2005b). Streams that dry completely by early summer, lack vegetative cover, or have nonnative aquatic predators are less likely to be occupied and have lower functional connectivity (Murphy *et al.* 2010b; Arkle and Pilliod *in press*). For these reasons and because of our findings of relatively poor connectivity, we suspect that streams in the Great Basin play an even greater role in facilitating gene flow, connectivity, and dispersal than streams in the northern range of the species.

We are uncertain how connectivity will change under future climate scenarios because it is difficult to predict which perennial water bodies will become intermittent and which intermittent water bodies will become dry. Our analyses suggest that more of the Great Basin will experience higher runoff in September, a period when juveniles are dispersing and adults are migrating to overwintering habitats. This change could benefit frogs, except we found relatively small increases in September runoff at currently occupied breeding locations. The benefits of this small September increase in runoff may not outweigh the impacts of large decreases in spring runoff followed by normal dry summer conditions. Further, the consequences of higher winter runoff (*i.e.*, due to the transition from snow to rain dominated winter precipitation), in the mountains, may result in streams reaching base flows earlier in the year and for longer periods (Hamlet *et al.* 2007; Arismendi *et al.* 2013). Long-term or extreme changes in precipitation patterns (*e.g.*, drought; Cayan *et al.* 2010; Cook *et al.* 2015) may further isolate remaining populations.

In the Great Basin and in other parts of the world, biodiversity conservation is linked with land ownership (Kamal *et al.* 2014). Connectivity for frogs and other aquatic species in the Great Basin is largely driven by

available permanent water in streams, much of which originates at higher elevations but flows through valley bottoms, which are predominately private land. The U.S. Bureau of Land Management currently manages the areas with relatively high climate suitability (*i.e.*, >0.3), but these areas generally lack surface water. Private lands tend to have both suitable climate and surface water conditions, which has important implications for aquatic species conservation in light of predicted changes in climate. If these projections are realized, increased human intervention and cooperation of private, state, and federal landowners may be needed to facilitate aquatic habitat availability and connectivity for the long-term persistence of the Columbia spotted frog and other aquatic species in this arid region.

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Conflict of Interest

None declared.

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Appendix:

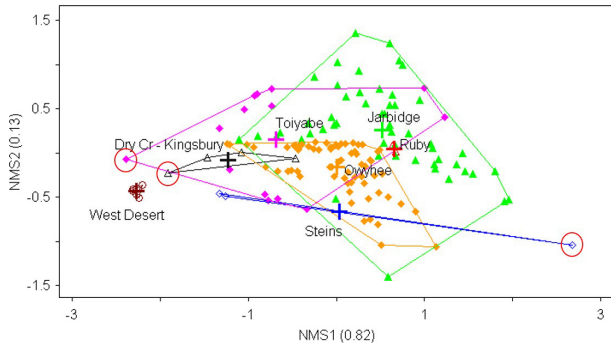


Figure A1. NMS ordination biplot of recent (1981–2010) PRISM climate data at 151 Columbia spotted frog breeding locations (complexes of sites, see methods) in the Great Basin study area.

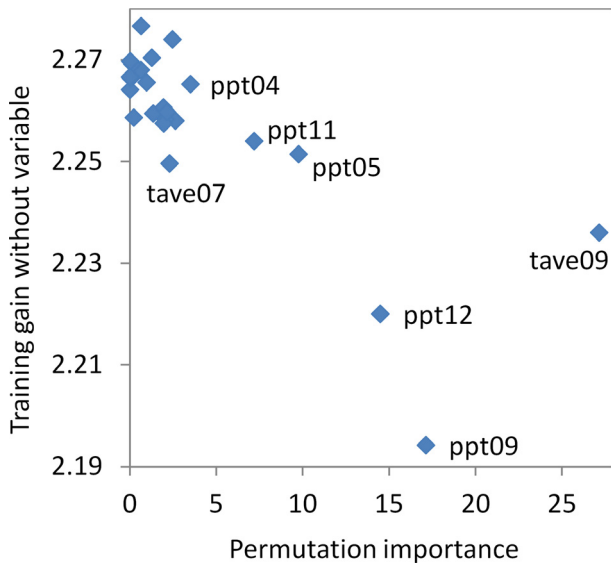


Figure A2. The relative importance of climate variables (points) for predicting breeding location climate suitability under current (1981–2010) climate conditions.

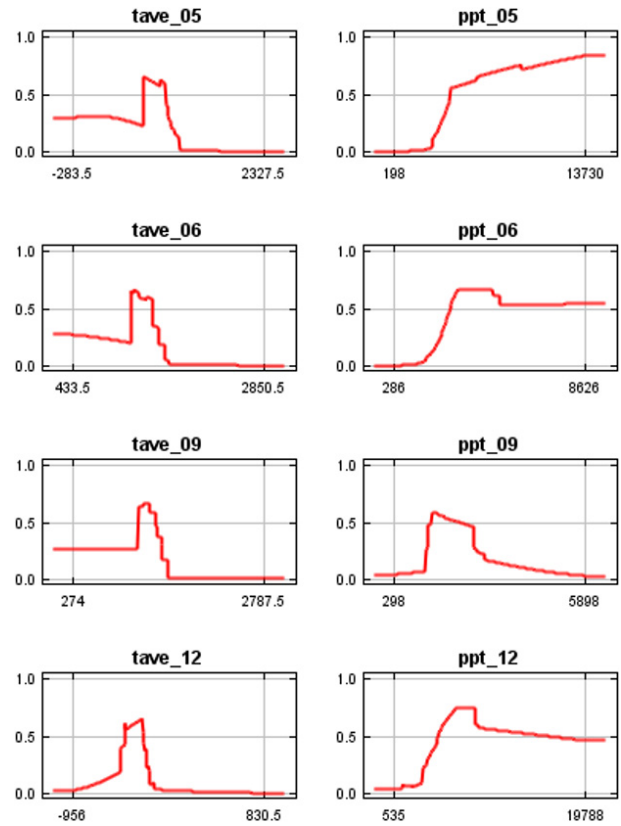


Figure A3. Partial dependence plots, each showing probability of suitability for Columbia spotted frogs (y-axes) as a function of a single-variable MaxEnt model, for eight important predictor variables.

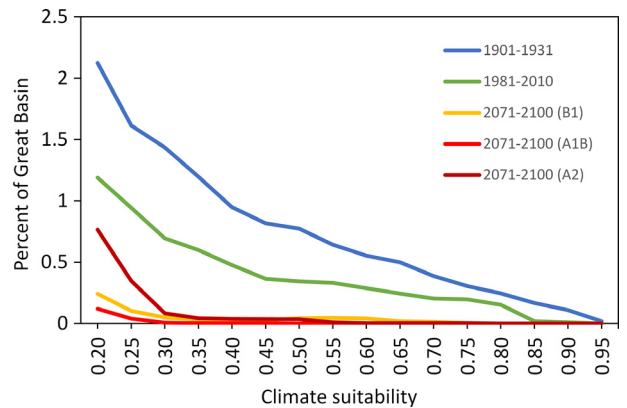


Figure A4. Percent of 270-m pixels in the Great Basin study area having climate suitability values greater than 0.20, by time or carbon emission scenario.

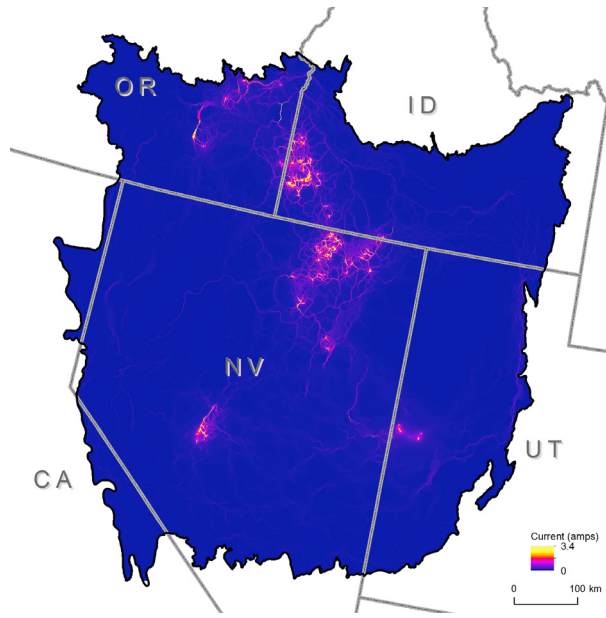


Figure A5. Connectivity as measured by electrical current flow between 151 spotted frog breeding locations in the Great Basin, including 6 locations in the Utah clade (*sensu* Funk *et al.* 2008).

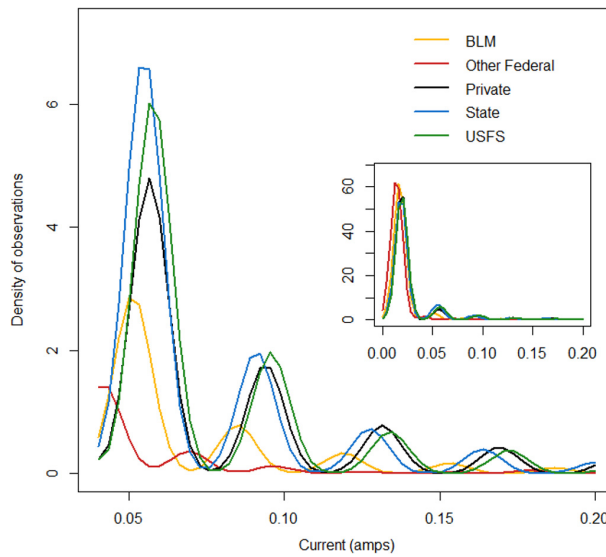


Figure A6. Kernel smoothed probability density of electrical current flow values, by land ownership, for all 270-m pixels ($n = 412,041$) in areas of the Great Basin with suitable climate conditions for spotted frog breeding.