

The Influence of Environmental Variables on High Priority Areas of Conservation for Amphibians

in North American Drylands

by

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ABSTRACT

Climate change is becoming an ever-increasing issue for conservation efforts, especially in dryland ecosystems where natural resources are already scarce for native species. This is increasingly true for native amphibians in the area, which are already experiencing threats to their range by human intervention, disease, and invasive species. The objectives of this study are to 1) identify how climate change impacts the distribution of native and non-native amphibian species and high priority conservation areas (HPCA) in the drylands of the Southwest United States and northern Mexico; 2) Describe the relationship between environmental variables and spatial configurations of HPCA; 3) Explore how amphibians distributions and HPCA may respond under climate change scenarios; 4) Investigate the projected change in drivers of climate change; 5) Investigate how climate change will impact the critical areas for conservation of native amphibians. Distribution maps were obtained for the 220 resident native and non-native amphibian species, and complementarity-based analysis was used to identify HPCA for amphibians. We used 34 predictor variables grouped into three categories, and ranked based on their influence in determining HPCA. Finally, Zonation, species richness, and rarity-weighted richness (RWR) were evaluated to identify complementarity to HPCA. Results show that water-related variables and -related variables such as temperature and solar radiation were the best indicators of amphibian conservation HPCA. Zonation also proved to be the best method for identifying these HPCA.

This study is the first to investigate the impact of climate change on site complementarity. The results from this study will open new inquiries for biogeography

and conservation biology and also have a functional use for natural resource managers in the United States and Mexico to monitor changes to these areas and plan for recovery if needed.

Keywords: Climate change, Zonation, Complementarity, High priority areas for conservation, Rarity-weighted richness

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INTRODUCTION

The decline in amphibian population and abundance has been staggering in the last decade, with 40.7% of amphibian species globally threatened (Lannoo 2005, Pounds 2001, Stuart et al. 2004, Luedtke et al. 2023). At the same time, science continues to investigate the driving causes. Many threats and concerns have been linked to amphibian population declines, including environmental pollution, invasive species, disease, and anthropogenic habitat alteration (Lannoo 2005, Blaustein et al. 2002, Beebee et al. 2005). Habitat alteration, which encompasses habitat loss and degradation, is among the most significant threats to amphibian diversity (Cushman 2006). Habitat alteration includes urbanization (e.g., housing and agricultural development), water withdrawals and stream diversions, pollution, and deforestation (Decena et al. 2020).

Modifications to the habitat often result in unsuitability for amphibians (Hamer and McDonnell 2008, Heinrichs et al. 2016). Habitat loss and fragmentation often reduce the number of suitable locations for amphibians, increase the isolation of populations, and increase the likelihood of extinction due to reduced genetic diversity within populations (Cushman 2006). Isolation and habitat alteration can be especially detrimental to dryland amphibian populations that utilize more limited environmental features to facilitate movement between water sources and migration to breeding sites (Hinderer et al. 2021). For example, the Chiricahua Leopard Frog (*Rana chiricahuensis*) is a native species to the drylands of central, southeastern Arizona, southwestern New Mexico, and northern Mexico (Platz and Mecham 1979, Stebbins 1985). This species has become threatened partially due to habitat alteration, which limits the available water sources and cattle

tanks the species utilizes (Hinderer et al. 2021, Team 2008). Recent studies have shown that climate will significantly modify the habitat suitability of desert areas, especially for amphibians (Albuquerque et al. 2024, Griffis-Kyle et al. 2018).

One way to mitigate the impacts of habitat alteration and avoid changes in habitat suitability is to map and highlight potential areas with high habitat suitability for conservation (Hereafter, high-priority conservation areas -HPCA). HPCA pinpoint crucial conservation locations for safeguarding species and thus necessitate urgent conservation efforts (Albuquerque and Beier 2015a). Therefore, identifying priority habitats is crucial for developing and implementing effective conservation and management plans (Epele et al. 2021).

The identification of HPCA, however, depends on knowledge about species distribution. Currently, 11% of all amphibian species do not have enough information for implement conservation measurements, and therefore recorded as data deficient by the International Union for Conservation of Nature (IUCN, Luedtke et al. 2023). Because of this incomplete knowledge, scientists use proxies for biodiversity, also known as biodiversity surrogates (Williams et al. 2006). Surrogates are accurately mapped environmental or taxonomic characteristics such as soil types, climatic conditions, or easily observed occurrences of species in the planning area (Albuquerque and Beier 2017, Beier and Albuquerque 2016). Examples of common biodiversity surrogates include the importance of sites for conservation, often expressed by Zonation (Di Minin et al. 2014), rarity-weighted richness (RWR, Williams et al. 1996), and species richness. Zonation is a commonly used proprietary software that aids spatial conservation planning

through a complementarity-based approach (Moilanen et al., 2009). Zonation aims to represent all conservation targets in the smallest number of sites. Similarly, RWR seeks to represent the maximum number of species in a given number of sites (Margules and Pressey 2000). RWR is a summation of the rarity scores of all the species at a select site and acts as a dependable method for representing species (Albuquerque and Beier 2015b). Rarity scores are calculated by taking the inverse of the number of species occurrences in one site (Albuquerque and Beier 2015b, Williams et al. 1996). RWR performs as an alternative spatial conservation planning tool that assigns higher priority rankings to sites offering unique species. Species richness is a common estimate of biodiversity, ranking sites by most overall species present (Albuquerque and Beier 2015b, Brown et al. 2007). In previous studies, both Zonation and RWR surrogates have successfully solved maximum coverage problems (Moilanen et al. 2009, William et al. 1996). Maximum coverage problems attempt to select the most amount of species represented across the sites selected when there are financial or resource limitations that do not allow for every site to be selected (Church et al. 1996, Alagador et al. 2020).

Another emerging factor influencing the spatial configuration of HPCA is climate. Recently, Albuquerque and Beier (2015a) investigated the distribution of HPCA in vertebrates, including amphibians, birds, and mammals, at a global scale, and they reported that climate-related predictors are the major drivers of the spatial configuration of HPCA. If climate has a pivotal influence on the spatial configuration of HPCA, then the location of these areas may change in the future. Thus, identifying HPCA without accounting for climate change may lead to quickly antiquated results. Exploring various

climate change scenarios could improve how sites are selected and have greater impacts on the conservation of species of concern (Albuquerque et al. 2018). To explore climate change impacts, studies often explore four Shared Socioeconomic Pathways (SSPs), as defined by the Intergovernmental Panel on Climate Change Special Report Emission Scenarios (Nakicenovic & Swart 2000) to model various scenarios depicting the predicted impacts of climate change on HPCA to the years 2081-2100. SSPs are pathways that represent possible outcomes for the ecosystem and society over a century timescale without the implementation of new climate policies ('O'Neill et al. 2014, Scenarios 2000).

The major goals of our study were to provide a geographic distribution of current HPCA for resident amphibian species in drylands of the SW United States and Mexico, and to elucidate potential changes between current and future HPCA's spatial configurations. Specifically, we aimed to (1) provide the geographical distribution of HPCA for North American dryland amphibians, (2) evaluate which proxy for biodiversity (Zonation, RWR, and species richness) is most effective for identifying HPCA, (3) identify the association between the spatial configuration of HPCA of amphibians and environmental variables, and (4) identify the potential effect of climate change on the spatial configurations of HPCA.

MATERIALS AND METHODS

STUDY AREA

Our study area includes the Southwest United States and Northern Mexico, comprising the largest continuous dryland area experiencing a major multi-year drought

(Hughes et al. 2008). The study area encompasses all four dryland subtypes: hyper-arid, arid, semi-arid, and dry sub humid, based on increasing aridity and decreasing moisture. Each subtype displays varying levels of biodiversity and species richness and encompasses 41.3% of land coverage on Earth altogether (Safriel et al. 2005). We used the Convention on Biological Diversity and the United Nations Convention to Combat Desertification (UNCCD) and Map (UNEP-UCMC. 2007) to define the dryland ecosystems across the SW United States and Northern Mexico. Drylands north of Nevada, Utah, and Colorado were excluded from the study area to primarily focus on the geographic area of the Southwest United States and Northern Mexico. We removed portions of northern California, central Colorado, and eastern Texas from our study area because they do not exhibit the same qualities as our other dryland systems, and the amphibian species present within them reflect this (Webb. 1950, Deitch et al. 2017).

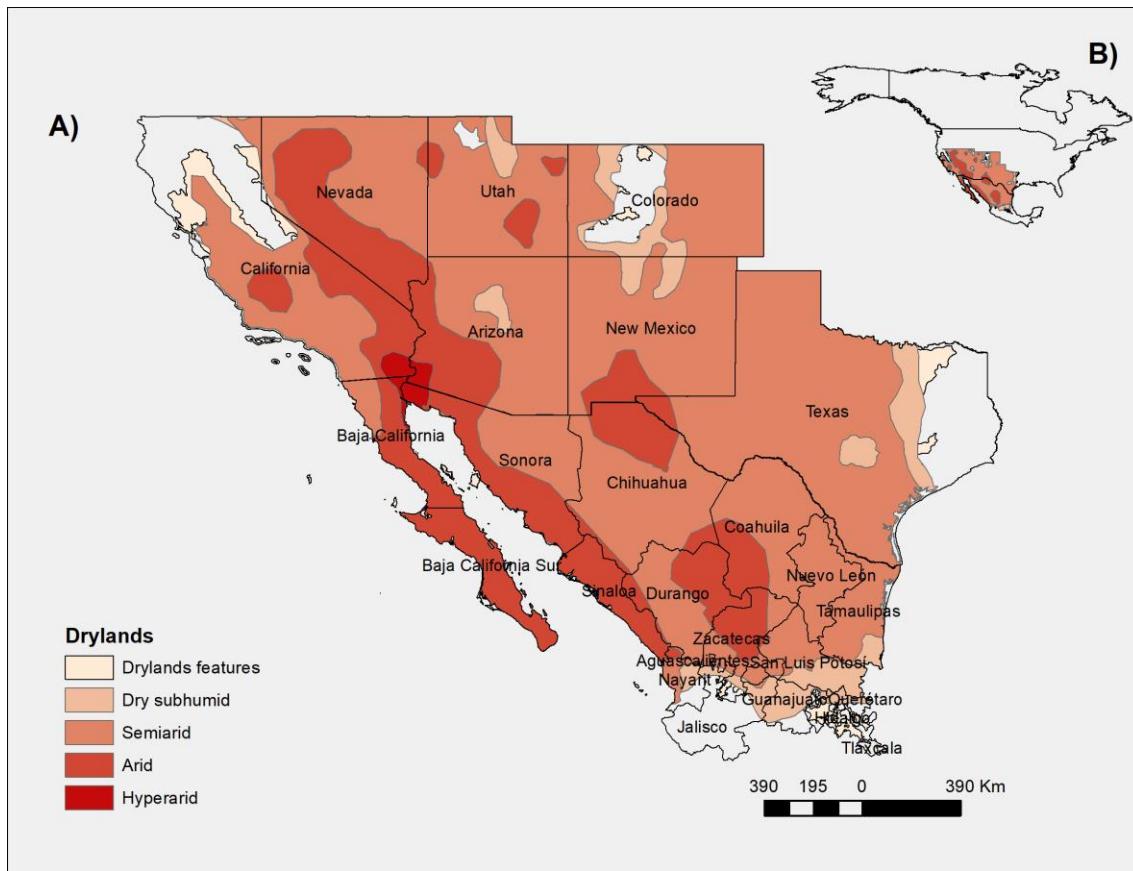


Figure 1. Geographic depiction of drylands in the Southwest United States and Mexico (A), and its location related to North America (B)

DATA SOURCE

Biological Data. We obtained global distribution range maps for 7,209 amphibian species from the IUCN Red List spatial data (IUCN 2022). We processed these range maps in *R* (R Core Team 2021). Then we used the referencing species' natural ranges on Amphibia Web (Amphibia Web 2023) to identify resident species, individuals with at least three-fourths of their annual cycle living in a given area (Red List Technical Group 2018) of the Southwest United States and Northern Mexico. This process left 211 amphibian species within our study area to conduct our analysis.

Environmental Data. We selected 34 environmental variables to determine the relationship between environmental changes and HPCA for amphibians, and all variables were processed in *R* for analysis. The first 19 were bioclimatic variables extracted from WorldClim (Fick and Hijmans 2017). We obtained 12 measures of solar radiation, expressed as monthly values from 1970-2000, from WorldClim (Fick and Hijmans 2017). We then used these solar radiation values to calculate solar radiation's mean, minimum, maximum, and standard deviation. Both bioclimate and solar radiation variables are at a 2.5-minute resolution. We also obtained ten topographic measures from EarthEnv (Robinson et al. 2014) and a Topographic wetness index (TWI), from Marthews et al. (2015a and 2015b). We used R and the *aggregate* (Hijmans 2023) function to rescale the topographic variables to 2.5-minute cells.

DATA PREPARATION

We compiled data from several sources and underwent a rigorous cleaning procedure, including removal of NAs, cropping data to our study area extent, and creating a grid cell. We removed records that lacked a coordinate system, did not overlap with our study area, and had errors, missing values, or incomplete data. To create a matrix of presence and absence, we overlaid each amphibian range map to a grid of ~2.5min cells, the same resolution as our environmental variables. We considered a 'presence', each grid cell overlapping the species range. Cells with no overlapping ranges were considered as 'absences'.

RARITY-WEIGHTED RICHNESS

We used the grid cell and presence/absence matrix to estimate species richness and RWR (William et al. 1996). Rather than identifying sites solely by the richness and amount of species, RWR identifies sites with overall richness, emphasizing the rarity of species (Albuquerque and Gregory 2017). We estimated our RWR values by multiplying our presence/absence values by the inverse sum of occurrences for that site, summing the values. When applied to these commonly designated locations with a lower priority ranking, RWR does not imply a lack of importance for conservation. Rather, the priority is linked to the conservation objective of attaining broad-scale protection within resource constraints. (William et al. 1996).

THE IMPORTANCE OF A SITE FOR CONSERVATION

We implemented Zonation (Moilanen et al. 2009), a complementarity-based algorithm that estimates the importance of sites for conservation. Zonation produces a hierarchical priority ranking of the grid cells for each taxon from zero to one and removes cells that are not indispensable to the core area of the species (Albuquerque and Beier 2015b). Complementarity is the proportion of species that one region contributes to an area not otherwise represented in other sites (Vane-Wright et al. 1991, Colwell and Coddington 1994). We first extracted the Zonation values from our dataset for our study area. Then, to estimate the HPCA of complementarity, we selected the top 30% of grid cells from our study area (Albuquerque et al. 2024). We chose this percentage because the Convention on Biological Diversity (CBD) expects 30% of natural areas to be protected by 2030 (CBD 2022).

EVALUATING SURROGATES

We built species accumulation curves to evaluate the efficacy of our surrogate solutions for selecting HPCA. We also built species accumulation curves using random solutions (999 curves). The species accumulation curves were built for Zonation, RWR, and species richness and tested against a random solution. We implemented and evaluated a species accumulation curve for a random solution as our control surrogate to evaluate the efficiency of our surrogate approach. Zonation was used as our reference point in the species accumulation curve analysis because it produces near-optimum solutions and performs as a tool to measure the optimization of our surrogates.

We then added the surrogates to a Species Accumulation Index (SAI) to evaluate their efficacy. SAI is commonly used to assess and contrast substitute strategies (Rodrigues and Brooks 2007). It measures the number of species represented by the surrogate (RWR or richness), denoted by S . This value is compared against two reference points: R , which represents the average number of species that appear at least once in the same number of randomly chosen sites, and O , which indicates the highest possible number of species that can be represented at least once in that number of sites (Albuquerque and Beier 2015b). SAI values are rated from negative to positive infinity, with positive SAI values indicating the percent effectiveness of the surrogate. A negative SAI yields results worse than the random solution, and a zero SAI yields results no better than the random selection. The effectiveness of each solution was measured across 30 targets from 0.5% to 30%, increasing incrementally by 1% (Beier and Albuquerque 2016).

IDENTIFYING DRIVERS OF HPCA DISTRIBUTION

We minimized the dimensionality of the data by implementing a varimax-rotated principal component analysis (PCA) (Chan 2004). PCA highlights sets of uncorrelated environmental variables and describes environmental gradients within the data. We utilized the Kaiser rule (Kaiser 1960) to select components or factors to maintain in the PCA analyses. The Kaiser rule drops any component with eigenvalues or variance less than one. From the correlation matrix of the PCA scores, we identified the variables most correlated with each factor. Then, we selected the variables most correlated with complementarity values, as expressed by Zonation.

We used random forest models to investigate the relationship between HPCA selection and our environmental variables (Svetnik et al., 2003, Albuquerque et al. 2015a, Astudillo-Scalia et al. 2020). The Random Forest approach that uses multiple decision tree outputs to reach a single result (Breiman 2001). Specifically, the algorithm uses about 1/3 of the cases are left out of the sample, also known as Out of Bag data (OOB) (Breiman, 2001). OOB data is be used as an estimator of variable importance. We ran our random forest model with the raw variables to investigate the importance of variables.

CLIMATE CHANGE SCENARIOS

The four SSP pathways each represented a different future scenario with varying emissions predictions: ssp 126 represented low emission scenarios, ssp 245 and ssp 370 represented intermediate emission scenarios, and ssp 585 represented high emission scenarios ('O'Neill et al. 2014, Scenarios 2000). Our maps display the top 30% of complementarity values.

RESULTS

The PCA analysis and the Keiser criteria identified six axes with eigenvalues greater than one (Table 1). The first axis included topographical variables, while the second represented a combination of temperature and elevation. The third and fifth encompassed mostly temperature and energy variables. The fourth axis included measures of temperature and solar radiation. Altogether, the axes explained 90% of environmental variance. Among the selected PCA axes, the variables most correlated with complementarity were mean diurnal range, minimum temperature of coldest month, temperature annual range, precipitation of coldest quarter, precipitation of wettest quarter, and terrain ruggedness index- median.

Table 1

Principal components analysis of the environmental variables obtained for the SW United States and México drylands. Variables include measures of temperature, precipitation, solar radiation, and topography. Bold values represent the highest correlation with each PC score. Variables highlighted in red are the variables most correlated to complementarity values as expressed by Zonation (correlation coefficients are displayed in the Correlation column).

Variables	PCA Scores						Correlation
	RC1	RC4	RC2	RC6	RC3	RC5	
Bioclimates							
Annual Mean Temperature	-0.13	0.47	0.85	0.14	0.04	0.11	0.239
Mean Diurnal Range	-0.1	-0.06	-0.3	0.01	0.78	0.23	-0.199
Isothermality	0.19	0.84	0.01	0.2	0.41	0	0.261
Temperature Seasonality	-0.23	-0.91	-0.1	-0.22	-0.11	0.11	-0.425

Max Temperature of Warmest Month	-0.27	-0.13	0.89	-0.07	0.17	0.11	0.008
Min Temperature of Coldest Month	0.04	0.64	0.75	0.13	0.01	-0.08	0.368
Temperature Annual Range	-0.24	-0.86	-0.26	-0.2	0.11	0.17	-0.457
Mean Temperature of Wettest Quarter	-0.23	0.23	0.51	0.3	0.06	0.6	-0.026
Mean Temperature of Driest Quarter	0.15	0.28	0.64	-0.09	0.26	-0.43	0.310
Temperature of Warmest Quarter Mean	-0.27	0.03	0.94	0.03	0.01	0.16	0.065
Temperature of Coldest Quarter	-0.01	0.67	0.71	0.18	0.09	0.02	0.332
Annual Precipitation	0.1	0.24	0.05	0.82	-0.45	-0.15	0.450
Precipitation of Wettest Month	0.17	0.39	0.1	0.87	-0.09	-0.1	0.458
Precipitation of Driest Month	-0.11	-0.19	-0.1	0.23	-0.87	0.08	0.017
Precipitation Seasonality	0.03	0.58	0.18	0.42	0.56	-0.03	0.209
Precipitation of Wettest Quarter	0.19	0.4	0.05	0.87	-0.05	-0.13	0.459
Precipitation of Driest Quarter	-0.08	-0.17	-0.06	0.26	-0.87	0.05	0.072

Precipitation of Warmest Quarter	0.14	0.34	0.01	0.83	-0.05	0.28	0.192
Precipitation of Coldest Quarter	0.21	-0.12	0.09	0.32	-0.24	-0.79	0.497
Solar radiation							
Solar radiation - minimum	0.12	0.62	0.32	0.27	0.36	0.41	0.191
Solar radiation - maximum	0.01	-0.88	0.02	-0.25	0.25	-0.19	-0.192
Solar radiation - mean	0.14	-0.17	0.33	0	0.71	0.21	-0.035
Solar radiation - standard deviation	-0.07	-0.85	-0.14	-0.3	-0.05	-0.36	-0.208
Topography							
Elevation - median	0.32	-0.07	-0.86	-0.05	0.17	0.18	-0.165
Elevation - standard deviation	0.97	0.08	-0.07	0.02	0.06	0.01	0.128
Roughness- median	0.94	0.08	-0.14	0.17	-0.01	-0.09	0.157
Roughness - standard deviation	0.97	0.08	-0.09	0.02	0.05	-0.01	0.128
Slope - median	0.93	0.07	-0.14	0.16	-0.02	-0.1	0.153
Slope - standard deviation	0.98	0.08	-0.11	0.04	0.04	-0.03	0.134
Topographic position index- median	-0.56	-0.08	-0.16	0.09	-0.08	0.03	-0.110
Topographic position index--	0.96	0.1	-0.1	0.15	0.04	-0.03	0.160

standard deviation							
Terrain ruggedness index- median	0.94	0.08	-0.14	0.18	-0.01	-0.09	0.161
Terrain ruggedness index - standard deviation	0.97	0.08	-0.08	0.01	0.05	0	0.129
Topographic index	-0.87	0.01	0.23	-0.07	0	0.07	-0.139
SS loadings	9.09	6.38	5.51	3.96	3.77	1.89	
Cumulative Var	0.27	0.45	0.62	0.73	0.84	0.90	

Patterns of Zonation, RWR, and HPCA displayed high values throughout continuous corridors across California, central Texas, and western Mexico. Richness displayed high values in central Texas and along the Southwestern border of Mexico in our study area. Secondary spots of high richness values were also displayed in SW and NE Mexico (Sinaloa, Tamaulipas, and San Luis Potosí). Zonation was displayed as the best depiction of the high values with the solution. It also reveals isolated areas of high values in New Mexico, Arizona, Nevada, and Utah that did not yield the same results under the other solutions. RWR produced similarly high values as Zonation but could not depict the same level of connectivity between the isolated HPCA.

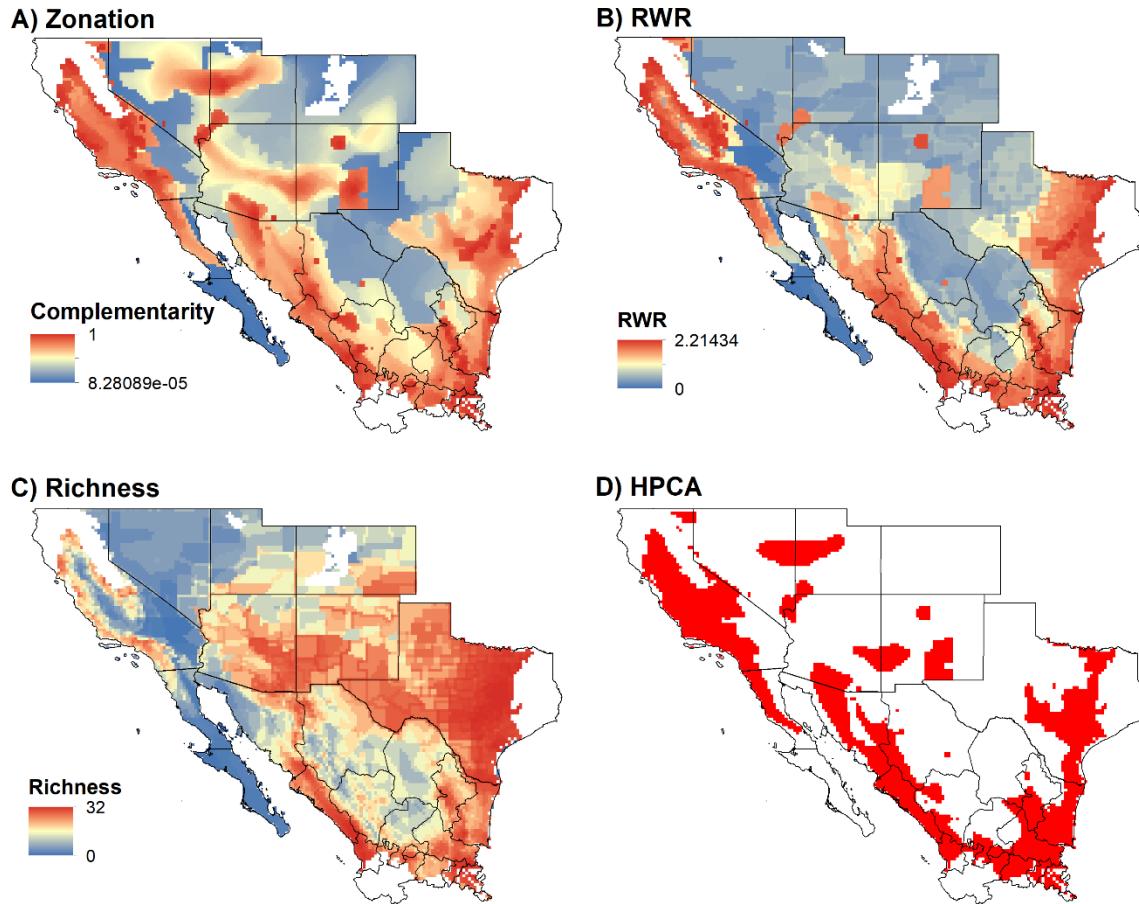


Figure 2. Geographic distribution of high priority conservation areas for amphibians in Southwest drylands using different methods to select sites (A) Zonation, (B) rarity-weighted richness, (C) species richness. (D) D represents the high priority conservation areas (HPCA) identified as the most important areas for amphibian conservation.

Zonation proved to be the best solution for representing amphibians in the dryland systems of the Southwest United States and Northern Mexico. RWR performed nearly as well as the Zonation solution in selecting the most amount of species within the fewest number of sites. Species richness, however, was a poor solution for selecting species with richness performing no better than the random solution simulations of our model.

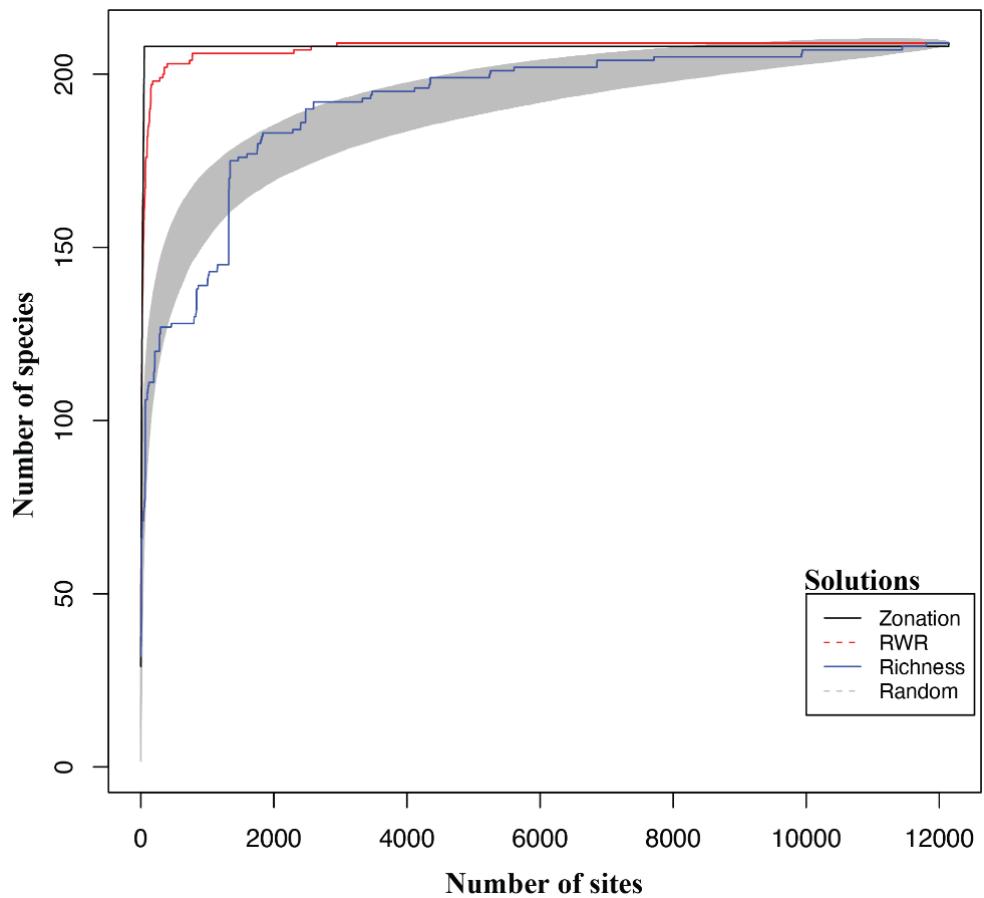


Figure 3. Species accumulation curves depicting Zonation, rarity-weighted richness (RWR), richness, and random solutions selecting species for conservation and the number of sites each solution needed to reach the target number of amphibian species in the study (220).

According to random forest models, precipitation and energy were the most influential variables in explaining the spatial distribution of site complementarity and HPCA (Figure 4). The top four most influential variables were precipitation of the coldest quarter, mean diurnal range, minimum temperature of the coldest month, and

precipitation of the wettest quarter. The environmental variables explained 78.47% of the variance within our model.

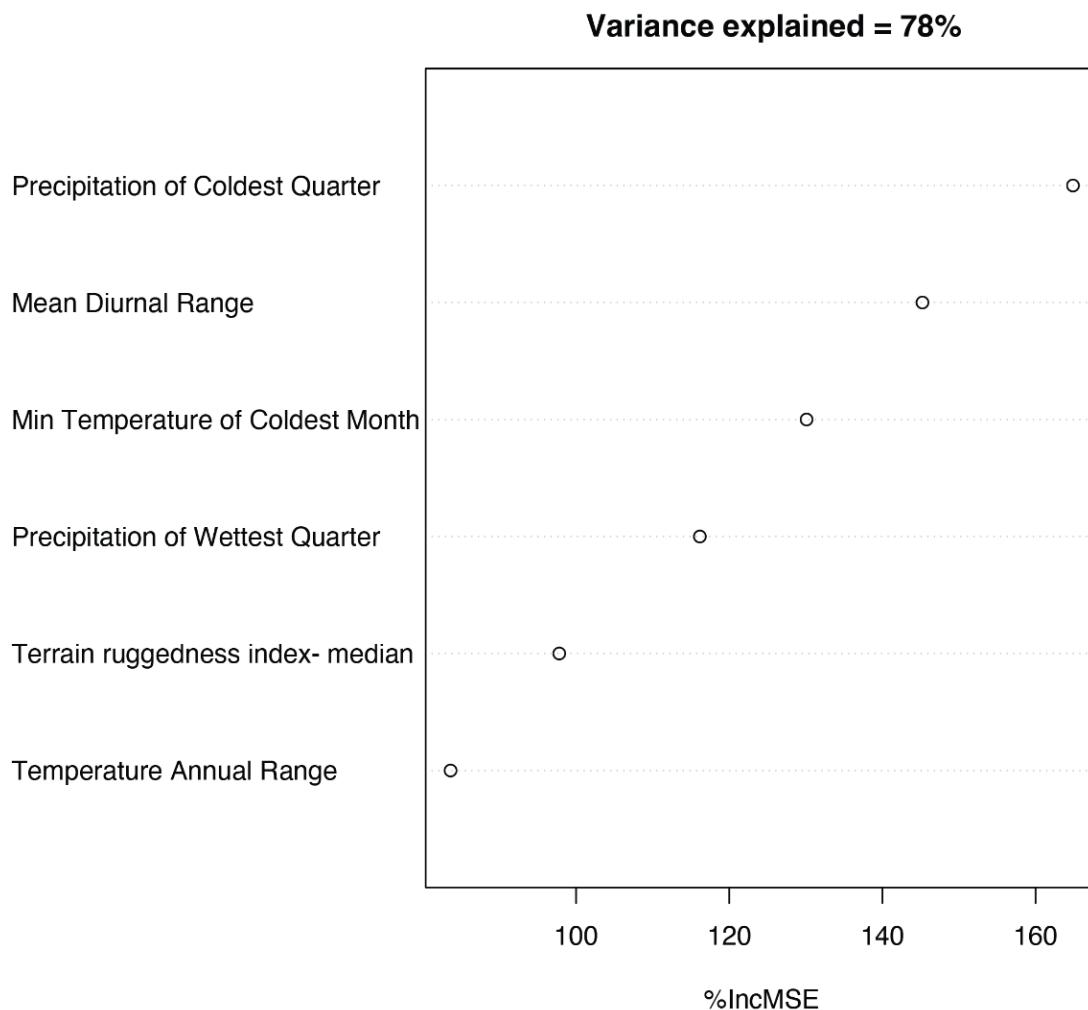


Figure 4. Variable importance for random forest model, identifying which variables were most important to the spatial configurations of important conservation areas for amphibians in drylands of SW United States and Mexico. %IncMSE- Mean Decrease Accuracy. Results also indicate how the model accuracy decreases when that variable is removed.

The climate change scenarios displayed overall changes in the HPCA for all four scenarios for 2081-2100 (Figure 5). The greatest changes in HPCA were observed for ssp370 (30.09%) and ssp585 (32.09%). The most loss of HPCA was seen in the isolated dryland sites of Nevada, Utah, New Mexico, and Arizona. The most gains of HPCA were seen along the western coast of Mexico and central Texas across all climate change scenarios.

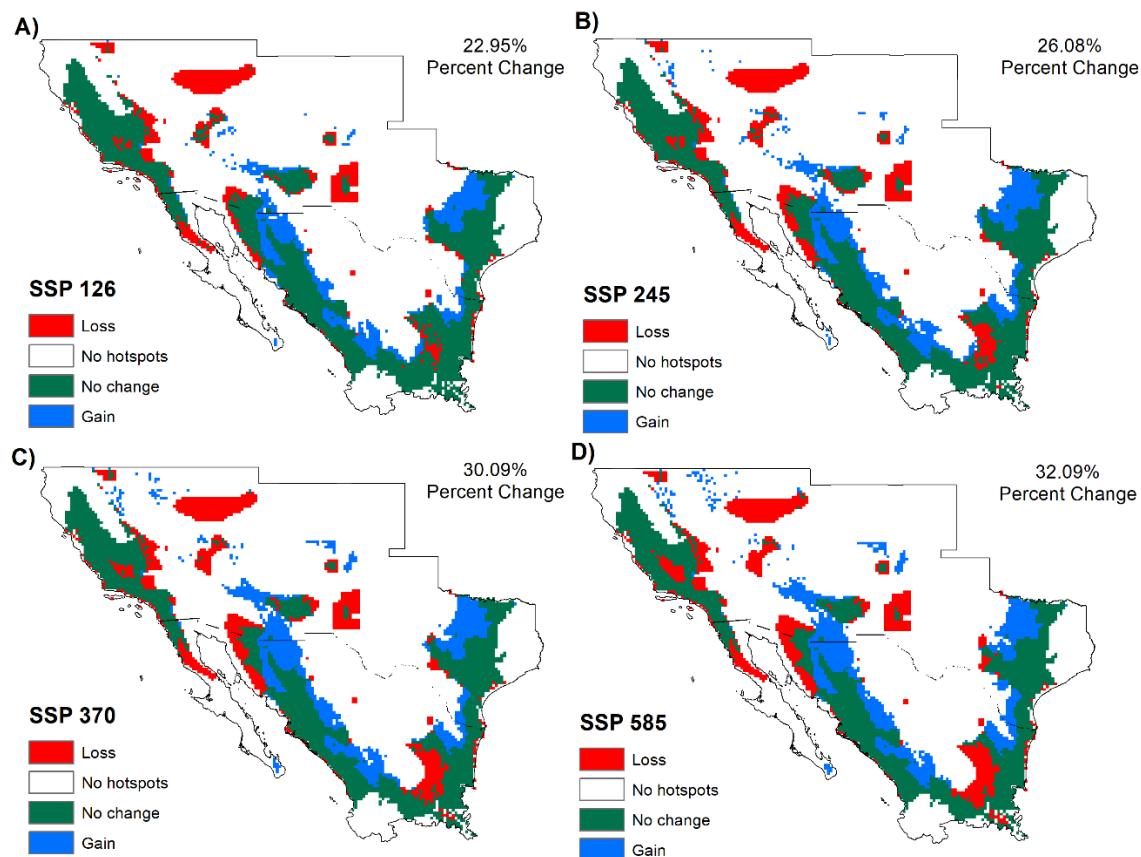


Figure 5. Future geographic distribution of high priority conservation areas for amphibians in Southwest drylands. Red cells represent a predicted loss, white cells represent no HPCA, green cells represent no change, and blue cells represent a predicted gain.

The climate change scenarios also display significant overlap between the current HPCA and the predicted future HPCA. The highest values were observed for the most optimistic scenarios (SSP 126 and 245), with a 77.05% overlap of suitable habitat between the two models. The lowest overlap was noted in the most pessimistic scenarios (SSP 370 – 69.91%, and SSP 570 - 67.91%).

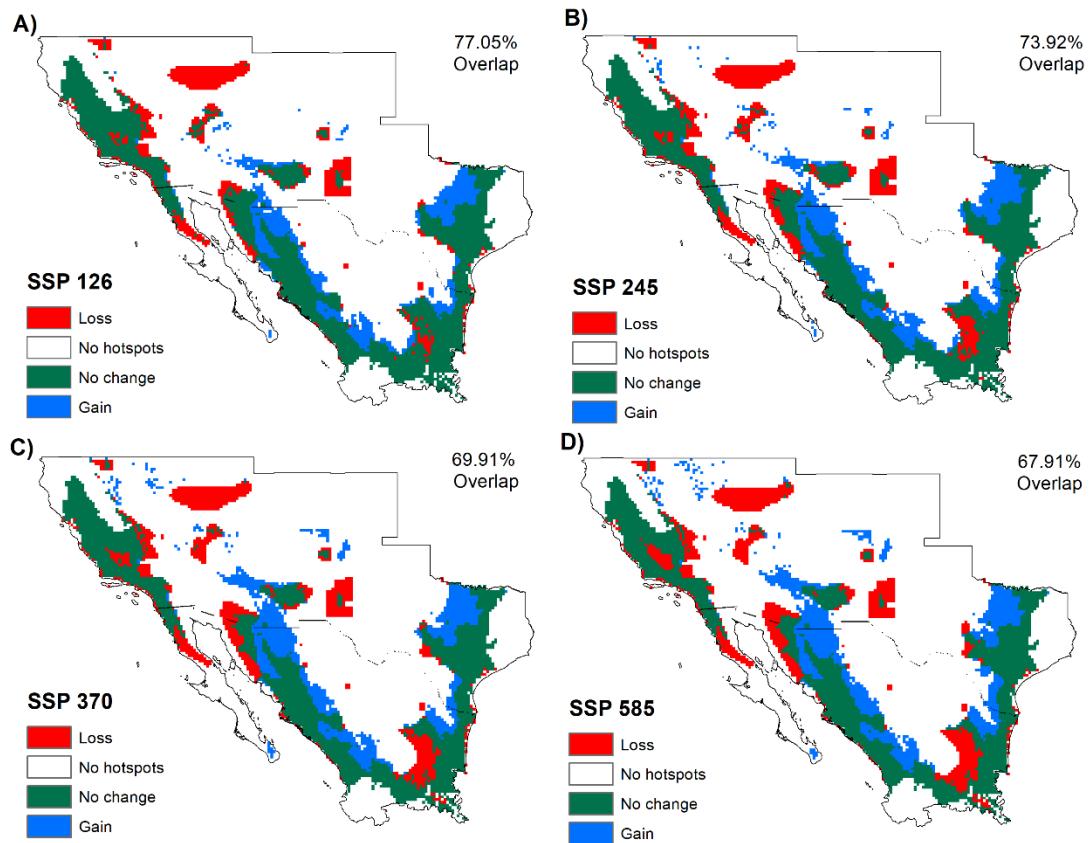


Figure 6. Geographic distribution for predicted overlap between current HPCA and future HPCA in the Southwest drylands. Red cells represent a predicted loss, white cells represent no HPCA, green cells represent no change, and blue cells represent a predicted gain.

DISCUSSION

SURROGATE ANALYSIS

Zonation was the most successful surrogate for identifying the HPCA for amphibians within the dryland systems of the Southwest United States and Northern Mexico. Zonation was chosen as the standard surrogate because hierarchical prioritization produces near-optimum solutions for target-based planning to meet the lowest cost targets (Moilanen 2007). Zonation works best due to its heuristic algorithm and process of iteratively removing the least valuable cells and keeping the most important ones until the end (Di Minin et al. 2014). The algorithm identifies that a least valuable cell would have low species occurrences while a high-priority cell would have many occurrences (Di Minin et al. 2014). The Zonation approach identified the HPCA for amphibian conservation and showed the connectivity between the more isolated HPCA found in Arizona, New Mexico, Utah, and Nevada (Figure 1).

Results indicated that RWR was an efficient surrogate of amphibians in the drylands southwest of the United States and Mexico. Rarity indices such as RWR have proven to be efficient surrogates for biodiversity when optimizing efficiency when planning conservation (Astudillo-Scalia and Albuquerque 2019). RWR has proven to be a reliable measure of complementarity and could be used as an alternative approach to Zonation for conservation planning, and is supported by previous studies evaluating rarity indices within terrestrial systems (Albuquerque and Beier 2015b, Albuquerque et al. 2019). RWR identifies HPCA with isolated range-restricted species while simultaneously illustrating sites with assemblages of rare and common species (Albuquerque and Gregory 2017). Rarity indices also offer alternative solutions Zonation by prioritizing

sites with endemic, vulnerable, or rare species rather than more common ones (Astudillo-Scalia and Albuquerque 2019).

According to our SAI results, identifying HPCA through richness was less efficient at representing amphibians. Our results show richness performed worse than Zonation and RWR at selecting species, performing no better than the random solution based on our SAI (Figure 2). Our results are in tandem with previous studies that have displayed that richness is not a viable metric to predict or identify areas for conservation (Fleishman et al. 2006). The poor performance of richness could be explained by the homogeneity of the species assemblage in areas with high species richness within the study, meaning areas with high species richness have greater numbers of overlapping species with other sites. In contrast, areas with rarer endemic species occur in areas with low overall species richness. Richness is a historic statistic for conservation planning, but its simplicity results in the spatial overlap that can cause under-representation of species compared to Zonation and other rarity indice approaches (Astudillo-Scalia and Albuquerque 2020). Richness as a surrogate highlights significant overlap between species ranges, which results in redundancy when selecting HPCA (Albuquerque and Gregory 2017).

BIOGEOGRAPHY

Our study is unique in its novelty as it is the first to investigate the spatial configurations of HPCA for amphibians in the drylands of the Southwest United States and Northern Mexico. HPCA included a wide range of amphibians in arid ecosystems (Figure 1). The geographic HPCA for amphibians displays two continuous corridors from

California to Baja California, and from Southern Arizona along the western coast of Mexico, across the southern border of the study area, and back up the eastern coast of Mexico through Central Texas. HPCA are also seen in isolated areas in the SW United States, most notably in Nevada, Arizona, New Mexico, and Utah. Climate conditions, especially water availability, primarily constrain the spatial configuration of HPCA observed herein. Ours agrees with previous studies that support our results by identifying water, temperature, and solar radiation as driving factors for amphibian distributions (Hawkins et al. 2003, Wake and Vredenburg 2008, Albuquerque et al. 2024).

Our results provide support for the tenet that environmental variables strongly influence the spatial configuration of HPCA in terrestrial (Albuquerque and Beier 2015a, Albuquerque et al. 2019) and marine (Astudillo-Scalia and Albuquerque 2020) realms. In all these cases, climate, represented by water and energy-related variables, was the most influential over the location of HPCA. The relevance of water-related variables to the spatial distribution of HPCA of amphibians could be related to their life-history as many species have biphasic life cycles with aquatic larval forms. Water as a resource is integral to amphibian life history because their semi-permeable skin lacks structures to prevent water loss (Thorston 1955). Water is also a requirement for amphibians that conduct cutaneous respiration, which is more efficient and important to them than respiration via the lungs (Wake and Vredenburg 2008). Desiccation threatens amphibians living in drylands, especially amphibians in the Southwest United States, which has been experiencing intense drought conditions for the past decade and is predicted to continue (Seager et al. 2007). The high importance of energy-related variables in explaining the

spatial distribution of HPCA could be related to amphibians' physiology. Amphibians are ectothermic vertebrates that require environmental inputs, such as air temperature, to aid them in thermoregulation, and as ectotherms, they are particularly sensitive to temperature changes, both high and low, in their environment (Huey 1982). Body temperature influences amphibian metabolic rates and activity (Buckley et al. 2012).

Dry climates pose a unique challenge to amphibians due to the lack of available water and the increased risk of desiccation, especially in dry and hot climates. However, many dryland amphibians have developed unique adaptations such as becoming fossorial, covering their bodies in wax, etc., allowing amphibian persistence in a hostile environment (Shoemaker 1988). Besides their adaptations, the United States and Northern Mexico's dryland systems harbor unique habitats that contain rich pockets of biodiversity (Gudka et al. 2014) that dryland amphibians can exploit.

The importance of the spatial configurations of our HPCA lies within their ability to act as a broad-scale framework for conservation managers to identify the most important areas to begin finer-scale conservation attempts. Effective conservation plans are created at local and regional levels because they require stakeholders and government bodies to enact pertinent policies (Fleishman and Brown 2019). Our study does not intend to overshadow local conservation attempts but rather empower them by investigating the larger picture and identifying HPCA across the drylands of the southwest.

IMPACTS OF CLIMATE CHANGE

Our future climate change models serve as predictions for the HPCA from 2081 to 2100. The SSP models act as a reference to estimate the influence climate change and

various policy approaches will have on the environment ('O'Neill et al. 2014). Our results display a significant change in the HPCA from the current model to the future model under simulated climate change. Our climate change analysis displays an overall change in suitability for amphibians, ranging from a 23% change in the most optimistic scenario to 32% in the most pessimistic scenario (Figure 5). Any change in suitability is alarming for dryland amphibian conservation due to the lack of currently available suitability the taxa faces in arid environments (Dayton and Fitzgerald 2006). Our climate change scenarios also included overlap between the current HPCA and the predictive future HPCA models. There was a predicted 77.05% to 67.91% overlap between the most optimistic to pessimistic scenarios (SSP 126- SSP 585, Figure 6). This overlap between the current and future models is important because it displays suitable habitats for dryland amphibians that will remain after simulated climate change. By employing predictive modeling such as the SSP climate change scenarios, conservation managers can identify sites most at risk of degradation and plan for these scenarios. Conservation managers can also focus their efforts on the green/ unchanged areas because many areas that gained suitability in the future were connected to core portions of unaffected habitat (Figures 5 & 6). In addition, creating corridors for migration to the predicted HPCA could allow for the movement of at-risk amphibian populations to more suitable habitats.

Spatial analysis tools have allowed scientists to predict how climate change will impact habitat suitability and how it impacts species distributions. However, climate change may also cause previously protected areas to no longer efficiently protect species as a changing climate drives species' distribution to alter from their historic ranges

(Alagador et al. 2014). For future research, we suggest identifying unprotected areas that offer high conservation value to dryland amphibians. Conventional conservation practices do not always account for changes in suitability and species range over time in light of climate change, and we advocate the integration of a dynamic complementarity-based conservation approach that accounts for these predicted shifts (Araújo 2009). Results also provide evidence that climate should be regarded as a potential indicator for future amphibian conservation projects in the drylands of the Southwest United States and Northern Mexico.

We understand the limitations of our study as we did not account for landscape connectivity within our models. Our models used occurrence data for all the amphibian species within our study area, but we did not include specific biological information about each species in our model. Our models are curated to represent a macroecological approach to selecting suitable areas for conserving amphibians in drylands. Further research is needed at the local level for effective conservation policy to be enacted (Epele et al. 2021). We implemented a robust climate change analysis for the HPCA across our study area, and we did not account for non-climate-related variables that may be contributing to amphibian declines, such as biological pressures, disease, natural disasters, and human-caused habitat degradation (Lanoo 2005). Although these models are not designed to be tools for local conservation efforts due to the scale, the models represent the state of the best science available to accomplish this type of investigation to understand how suitable habitats can change under future climate scenarios. With the limitations of this study, it is imperative to understand its novelty and utility as it is the

first to offer a conservation tool for amphibian conservation in the drylands of the Southwest United States and Northern Mexico.

CONCLUSION

Zonation and RWR solutions fared far better than random solutions at selecting amphibians, while richness failed. We advocate for conservation managers to implement complementarity-based solutions, such as Zonation or RWR, rather than richness when selecting conservation areas to best protect amphibians in the drylands of the Southwest and Northern Mexico.

Results show the environmental variables have a strong relationship with the spatial configurations of the HPCA. Water and energy variables, specifically precipitation, solar radiation, and temperature, proved to be the most influential variables in determining these spatial configurations and have been linked as drivers for amphibian richness (Hawkins et al. 2003). Our results align with other studies, where high precipitation and solar radiation values were linked to high habitat suitability for amphibians (Albuquerque et al. 2024).

Our results display a substantial change in the HPCA due to climate change. Our most optimistic scenario, ssp126, representing low predicted emissions, saw a 23% change in the suitable range for amphibians. The ssp585 scenario representing high predicted emissions saw a 32% change in suitable habitat across the study area. These results portray an alarming alteration in current amphibian suitability, with the isolated dryland sites in Nevada, New Mexico, Arizona, and Utah receiving the most predicted loss of suitable habitat.

REFERENCES

Alagador, D., Cerdeira, J. O., & Araújo, M. B. (2014). Shifting protected areas: scheduling spatial priorities under climate change. *Journal of applied ecology*, 51(3), 703-713.

Alagador, D., & Cerdeira, J. O. (2020). Revisiting the minimum set cover, the maximal coverage problems and a maximum benefit area selection problem to make climate-change-concerned conservation plans effective. *Methods in Ecology and Evolution*, 11(10), 1325-1337.

Albuquerque, F., & Beier, P. (2015a). *Global Patterns and environmental correlates of high-priority conservation areas for vertebrates*. *Journal of Biogeography*, 42(8), 1397–1405. <https://doi.org/10.1111/jbi.12498>

Albuquerque, F., & Beier, P. (2015b). Rarity-weighted richness: *A simple and reliable alternative to integer programming and heuristic algorithms for minimum set and maximum coverage problems in Conservation Planning*. *PLOS ONE*, 10(3). <https://doi.org/10.1371/journal.pone.0119905>

Albuquerque, F. S., & Gregory, A. (2017). The geography of hotspots of rarity weighted richness of birds and their coverage by Natura 2000. *PLOS ONE*, 12(4). <https://doi.org/10.1371/journal.pone.0174179>

Albuquerque, F., & Beier, P. (2017). Improving the use of environmental diversity as a surrogate for species representation. *Ecology and Evolution*, 8(2), 852–858. <https://doi.org/10.1002/ece3.3651>

Albuquerque, F., Benito, B., Rodriguez, M. Á. M., & Gray, C. (2018). Potential changes in the distribution of *Carnegiea gigantea* under future scenarios. *PeerJ*, 6, e5623.

Albuquerque, F., Astudillo-Scalia, Y., Loyola, R., & Beier, P. (2019). Towards an understanding of the drivers of broad-scale patterns of rarity-weighted richness for vertebrates. *Biodiversity and Conservation*, 28, 3733-3747.

Albuquerque, F. S., Bateman, H. L., Ryan, M. J., & Montgomery, B. (2024). Model transferability and predicted response of a dryland anuran to climate change in the Southwest United States. *Journal of Biogeography*.

AmphibiaWeb. 2023. <<https://amphibiaweb.org>> University of California, Berkeley, CA, USA. Accessed 19 Apr 2023.

Araújo, M. B. (2009). Climate change and spatial conservation planning. In Moilanen, A., Wilson, K.A., Possingham, H.P., 2009. *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools*. Oxford University Press. Great Britain. 304pp.

Astudillo-Scalia, Y., & de Albuquerque, F. S. (2019). Evaluating the performance of rarity as a surrogate in site prioritization for biodiversity conservation. *Global Ecology and Conservation*, 18, e00639.

Astudillo-Scalia, Y., & Albuquerque, F. (2020). Why should we reconsider using species richness in spatial conservation prioritization?. *Biodiversity and Conservation*, 29, 2055-2067.

Beebee, T. J., & Griffiths, R. A. (2005). The amphibian decline crisis: a watershed for conservation biology?. *Biological conservation*, 125(3), 271-285.

Beier, P., & Albuquerque, F. (2016). *Evaluating β diversity as a surrogate for species representation at fine scale*. PLOS ONE, 11(3). <https://doi.org/10.1371/journal.pone.0151048>

Blaustein, A. R., & Kiesecker, J. M. (2002). Complexity in conservation: lessons from the global decline of amphibian populations. *Ecology letters*, 5(4), 597-608.

Breiman, L. (2001). Random forests. *Machine learning*, 45, 5-32.

Buckley, L. B., Hurlbert, A. H., & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, 21(9), 873-885.

Brown, R. L., Jacobs, L. A., & Peet, R. K. (2007). Species richness: small scale. *Els.*

CBD. 2022. Nations Adopt Four Goals, 23 Targets for 2030 in Landmark UN Biodiversity Agreement. Available at: <https://www.cbd.int/article/cop15-cbd-press-release-final-19dec2022>

Chan, Y. H. (2004). Biostatistics 302. Principal component and factor analysis. *Singapore Med J*, 45(12), 558-565.

Church, R. L., Stoms, D. M., & Davis, F. W. (1996). Reserve selection as a maximal covering location problem. *Biological conservation*, 76(2), 105-112.

Colwell, R. K., & Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 345(1311), 101-118.

Cushman, S. A. (2006). Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological conservation*, 128(2), 231-240.

Dayton, G. H., & Fitzgerald, L. A. (2006). Habitat suitability models for desert amphibians. *Biological conservation*, 132(1), 40-49.

Decena, S. C. P., Avorque, C. A., Decena, I. C. P., Asis, P. D., & Pacle, B. (2020). Impact of habitat alteration on amphibian diversity and species composition in a lowland tropical rainforest in Northeastern Leyte, Philippines. *Scientific reports*, 10(1), 10547.

Deitch, M. J., Sapundjieff, M. J., & Feirer, S. T. (2017). Characterizing precipitation variability and trends in the 'world's Mediterranean-climate areas. *Water*, 9(4), 259.

Di Minin, Enrico, Victoria Veach, Joonas Lehtomäki, Federico Montesino Pouzols, and Atte Moilanen. "A quick introduction to Zonation." (2014).

Epele, L. B., Grech, M. G., Manzo, L. M., Macchi, P. A., Hermoso, V., Miserendino, M. L., ... & Cañedo-Argüelles, M. (2021). Identifying high priority conservation areas for Patagonian wetlands biodiversity. *Biodiversity and Conservation*, 30, 1359-1374.

Fick, S.E. & R.J. Hijmans, 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37 (12): 4302-4315.

Fleishman, E., Noss, R. F., & Noon, B. R. (2006). Utility and limitations of species richness metrics for conservation planning. *Ecological indicators*, 6(3), 543-553.

Fleishman, E., & Brown, H. (2019). Use of macroecology to integrate social justice and conservation. *Global Ecology and Biogeography*, 28(10), 1512-1518.

Griffis-Kyle, K. L., Mougey, K., Vanlandeghem, M., Swain, S., & Drake, J. C. (2018). Comparison of climate vulnerability among desert herpetofauna. *Biological Conservation*, 225, 164-175.

Gudka, M., Davies, J., Poulsen, L., Schulte-Herbrüggen, B., MacKinnon, K., Crawhall, N., ... & Smith, J. (2014). Conserving dryland biodiversity: a future vision of sustainable dryland development. *Biodiversity*, 15(2-3), 143-147.

Hamer, A. J., & McDonnell, M. J. (2008). Amphibian ecology and conservation in the urbanising world: a review. *Biological conservation*, 141(10), 2432-2449.

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J. F., Kaufman, D. M., ... & Turner, J. R. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84(12), 3105-3117.

Heinrichs, J. A., Bender, D. J., & Schumaker, N. H. (2016). Habitat degradation and loss as key drivers of regional population extinction. *Ecological Modelling*, 335, 64-73.

Hijmans R (2023). *_raster: Geographic Data Analysis and Modeling_*. R package version 3.6-14, <<https://CRAN.R-project.org/package=raster>>.

Hinderer, R. K., Litt, A. R., & McCaffery, M. (2021). Habitat selection by a threatened desert amphibian. *Ecology and Evolution*, 11(1), 536-546.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. Pp. 25–91 in C. Gans and FH Pough, eds. *Biology of the Reptilia, physiology C: physiological ecology*. Vol. 12.

Hughes, M. K., & Diaz, H. F. (2008). Climate variability and change in the drylands of Western North America. *Global and Planetary Change*, 64(3-4), 111-118.

IUCN. 2022. The IUCN Red List of Threatened Species. Version 2022-2. <https://www.iucnredlist.org>. Accessed on 10 February 2023.

Kaiser, H. F. (1960). The application of electronic computer to factor analysis. *Educational and Psychological Measurement*, 20, 141-151.

Lannoo, M. J. (Ed.). (2005). *Amphibian declines: the conservation status of United States species*. Univ of California Press.

Luedtke, J. A., Chanson, J., Neam, K., Hobin, L., Maciel, A. O., Catenazzi, A., ... & Stuart, S. N. (2023). Ongoing declines for the 'world's amphibians in the face of emerging threats. *Nature*, 622(7982), 308-314.

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, 405(6783), 243-253.

Marthews, T.R., Dadso, S.J., Lehner, B., Abele, S. & Gedney, N. (2015a). High resolution global topographic index values for use in large-scale hydrological modelling. *Hydrol. Earth Syst. Sci.*, 19, 91–104; doi:10.5194/hess-19-91-2015.

Marthews, T.R., Dadson, S.J., Lehner, B., Abele, S. & Gedney, N. (2015b). High resolution global topographic index values. NERC Environmental Information Data Centre. <https://doi.org/10.5285/6b0c4358-2bf3-4924-aa8f-793d468b92be>

Moilanen, A., Franco, A.M.A., Early, R., Fox, R., Wintle, B., and C.D. Thomas. (2005). Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proc. R. Soc. Lond. B Biol. Sci.*, 272: 1885-1891.

Moilanen, A. (2007). Landscape zonation, benefit functions and target-based planning: unifying reserve selection strategies. *Biological Conservation*, 134(4), 571-579.

Moilanen, A., Wilson, K.A. & Possingham, H.P. (eds) (2009) *Spatial conservation prioritization*. Oxford University Press, Oxford

Nakicenovic, N., & Swart, R. (2000). Intergovernmental panel on climate change special report on emissions scenarios.

O'Neill, B. C., Kriegler, E., Riahi, K., Ebi, K. L., Hallegatte, S., Carter, T. R., ... & Van Vuuren, D. P. (2014). A new scenario framework for climate change research: the concept of shared socioeconomic pathways. *Climatic change*, 122, 387-400.

Platz, J. E., & Mecham, J. S. (1979). *Rana chiricahuensis*, a new species of leopard frog (*Rana pipiens* complex) from Arizona. *Copeia*, 383-390.

Pounds, J. A. (2001). Climate and amphibian declines. *Nature*, 410(6829), 639-640.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Red List Technical Working Group. "The IUCN Red List of Threatened Species". *IUCN Red List of Threatened Species*, www.iucnredlist.org/resources/spatial-data-download. Accessed 1 Feb. 2024.

Robinson, N., Regetz, J., and Guralnick, R. P. (2014). EarthEnv-DEM90: A nearly-global, void-free, multi-scale smoothed, 90m digital elevation model from fused ASTER and SRTM data. *ISPRS Journal of Photogrammetry and Remote Sensing*, 87:2014, 57-67. Available at <http://www.sciencedirect.com/science/article/pii/S0924271613002360>.

Rodrigues, A. S., & Brooks, T. M. (2007). *Shortcuts for biodiversity conservation planning: the effectiveness of surrogates*. *Annu. Rev. Ecol. Evol. Syst.*, 38, 713-737.

Safriel, U., Adeel, Z., Niemeijer, D., Puigdefabregas, J., White, R., Lal, R., ... & King, C. (2005). Dryland systems. In *Ecosystems and human well-being: current state and trends* (pp. 623-662). Island Press.

Scenarios, E. (2000). IPCC Special Report. *Cambridge Univ, Cambridge*.

Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., ... & Naik, N. (2007). Model projections of an imminent transition to a more arid climate in southwestern North America. *Science*, 316(5828), 1181-1184.

Shoemaker, V. H. (1988). Physiological ecology of amphibians in arid environments. *Journal of Arid Environments*, 14(2), 145-153.

Stebbins, R. C. (1985). A field guide to western amphibians and reptiles. *Peterson Field Guide Series*. Houghton Mifflin Company, Boston, MA.

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S., Fischman, D. L., & Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, 306(5702), 1783-1786.

Svetnik, V., Liaw, A., Tong, C., Culberson, J. C., Sheridan, R. P., & Feuston, B. P. (2003). Random forest: a classification and regression tool for compound classification and QSAR modeling. *Journal of chemical information and computer sciences*, 43(6), 1947-1958.

Team, S. E. S. A. (2008). CHIRICAHUA LEOPARD FROG.

Thorson, T. B. (1955). The relationship of water economy to terrestrialism in amphibians. *Ecology*, 36(1), 100-116.

Vane-Wright, R. I., Humphries, C. J., & Williams, P. H. (1991). What to protect?—Systematics and the agony of choice. *Biological conservation*, 55(3), 235-254.

Wake, D. B., & Vredenburg, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences*, 105(supplement_1), 11466-11473.

Webb, W. L. (1950). Biogeographic regions of Texas and Oklahoma. *Ecology*, 31(3), 426-433.

Williams, P., Gibbons, D., Margules, C., Rebelo, A., Humphries, C., & Pressey, R. (1996). A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology*, 10(1), 155–174.
<https://doi.org/10.1046/j.1523-1739.1996.10010155.x>

Williams, P., Faith, D., Manne, L., Sechrest, W., & Preston, C. (2006). Complementarity analysis: Mapping the performance of surrogates for biodiversity. *Biological Conservation*, 128(2), 253-264.

UNEP-WCMC 2007. A spatial analysis approach to the global delineation of dryland areas of relevance to the CBD Programme of Work on Dry and Subhumid Lands. Dataset based on spatial analysis between WWF terrestrial ecoregions (WWF-US, 2004) and aridity zones (CRU/UEA; UNEPGRID, 1991). Dataset checked and refined to remove many gaps, overlaps and slivers (July 2014). Cambridge (UK): UNEP-WCMC.

APPENDIX I
ENVIRONMENTAL VARIABLES

Bioclimatic	Description
Annual Mean Temperature	Average annual temperature from 1970-2000
Mean Diurnal Range	(Mean of monthly (max temp - min temp))
Isothermality	(BIO2/BIO7) ($\times 100$)
Temperature Seasonality	(standard deviation $\times 100$)
Max Temperature of Warmest Month	Yearly value from 1970-2000 of the month with the highest temperature
Min Temperature of the Coldest Month	Yearly value from 1970-2000 of the month with the lowest temperature
Temperature Annual Range	(Max Temperature – Min Temperature)
Mean Temperature of Wettest Quarter	Average temperature from 1970-2000 for the wettest $\frac{1}{4}$ of the year
Mean Temperature of Driest Quarter	Average temperature from 1970-2000 for the driest $\frac{1}{4}$ of the year
Mean Temperature of Warmest Quarter	Average temperature from 1970-2000 for the warmest $\frac{1}{4}$ of the year
Mean Temperature of Coldest Quarter	Average temperature from 1970-2000 for the coldest $\frac{1}{4}$ of the year
Annual Precipitation	Yearly value from 1970-2000
Precipitation of the Wettest Month	Rainfall value from 1970-2000 of the month with the most rainfall

Precipitation of Driest Month	Rainfall value from 1970-2000 of the month with the least rainfall
Precipitation Seasonality	(Coefficient of Variation)
Precipitation of Wettest Quarter	Rainfall value from 1970-2000 for the $\frac{1}{4}$ of the year with the most rainfall
Precipitation of Driest Quarter	Rainfall value from 1970-2000 for the $\frac{1}{4}$ of the year with the least rainfall
Precipitation of Warmest Quarter	Rainfall value from 1970-2000 for the $\frac{1}{4}$ of the year with the highest temperatures
Precipitation of Coldest Quarter	Rainfall value from 1970-2000 for the $\frac{1}{4}$ of the year with the lowest temperatures
Solar Radiation	Description
Solar Radiation Minimum Value	Average minimum values from 1970-200
Solar Radiation Maximum Value	Average maximum values from 1970-200
Solar Radiation Mean	Average values from 1970-200
Solar Radiation Standard Deviation	Standard deviation of the values from 1970-2000
Topography	Description
Elevation 5 km median	5 km resolution of the median elevation value

Elevation 5 km standard deviation	5 km resolution of the standard deviation of elevation values
Roughness median	Median roughness value
Roughness standard deviation	Standard deviation of roughness values
Slope median	Median slope values
Slope standard deviation	Standard deviation of slope values
Topographic Position index median	Median value of the difference between the elevation of each cell and the mean elevation of its neighboring cell
Topographic Position Index standard deviation	Standard deviation of the difference between the elevation of each cell and the mean elevation of its neighboring cell
Topographic Roughness Index median	Median value of the average of the elevation difference among neighboring cells
Topographic Roughness Index standard deviation	Standard deviation of the average of the elevation difference among neighboring cells
Topographic Wetness Index	(TWI, $\ln(a/\tan\beta)$)

APPENDIX II
RESIDENT AMPHIBIAN SPECIES AND THEIR LIFE CYCLE

	BINOMIAL	Common Name	Life Cycle
1	<i>Acris crepitans</i>	Northern Cricket Frog	Metamorphosis
2	<i>Agalychnis dacnicolor</i>	Mexican Leaf Frog	Metamorphosis
3	<i>Ambystoma californiense</i>	California Tiger Salamander	Metamorphosis
4	<i>Ambystoma gracile</i>	Northwestern Salamander	Metamorphosis
5	<i>Ambystoma granulosum</i>	Granular Salamander	Direct Development
6	<i>Ambystoma macrodactylum</i>	Long-Toed Salamander	Metamorphosis
7	<i>Ambystoma maculatum</i>	Spotted Salamander	Metamorphosis
8	<i>Ambystoma mavortium</i>	Barred Tiger Salamander	Metamorphosis
9	<i>Ambystoma opacum</i>	Marbled Salamander	Metamorphosis
10	<i>Ambystoma rosaceum</i>	Tarahumara Salamander	Metamorphosis
11	<i>Ambystoma silvense</i>	Durango Salamander	Metamorphosis
12	<i>Ambystoma talpoideum</i>	Mole Salamander	Paedomorphic
13	<i>Ambystoma texanum</i>	Small Mouth Salamander	Metamorphosis
14	<i>Ambystoma tigrinum</i>	Tiger Salamander	Metamorphosis
15	<i>Ambystoma velasci</i>	Mexican Tiger Salamander	Paedomorphic
16	<i>Amphiuma tridactylum</i>	Three-Toed Amphihuma	Paedomorphic
17	<i>Anaxyrus americanus</i>	American Toad	Metamorphosis
18	<i>Anaxyrus boreas</i>	Western Toad	Metamorphosis
19	<i>Anaxyrus californicus</i>	Arroyo Toad	Metamorphosis
20	<i>Anaxyrus canorus</i>	Yosemite Toad	Metamorphosis
21	<i>Anaxyrus cognatus</i>	Great Plains Toad	Metamorphosis
22	<i>Anaxyrus compactilis</i>	Plateau Toad	Metamorphosis
23	<i>Anaxyrus debilis</i>	Green Toad	Metamorphosis
24	<i>Anaxyrus exsul</i>	Black Toad	Metamorphosis
25	<i>Anaxyrus fowleri</i>	Fowler's Toad	Metamorphosis
26	<i>Anaxyrus houstonensis</i>	Houston Toad	Metamorphosis
27	<i>Anaxyrus kelloggi</i>	Little Mexican Toad	Metamorphosis
28	<i>Anaxyrus mexicanus</i>	Southwestern Toad	Metamorphosis
29	<i>Anaxyrus microscaphus</i>	Arizona Toad	Metamorphosis
30	<i>Anaxyrus nelsoni</i>	Armargosa Toad	Metamorphosis
31	<i>Anaxyrus punctatus</i>	Red-Spotted Toad	Metamorphosis
32	<i>Anaxyrus retiformis</i>	Sonoran Green Toad	Metamorphosis
33	<i>Anaxyrus speciosus</i>	Texas Toad	Metamorphosis
34	<i>Anaxyrus woodhousii</i>	Woodhouse Toad	Metamorphosis
35	<i>Aneides ferreus</i>	Clouded Salamander	Direct Development
36	<i>Aneides flavipunctatus</i>	Speckled Black Salamander	Direct Development

37	<i>Aneides hardii</i>	Sacramento Mountain Salamander	Direct Development
38	<i>Aneides lugubris</i>	Arboreal Salamander	Direct Development
39	<i>Aneides vagrans</i>	Wandering Salamander	Direct Development
40	<i>Aquiloeurycea cephalica</i>	Red-Legged False Brook Salamander	Direct Development
41	<i>Aquiloeurycea galeanae</i>	Galeana false brook salamander	Direct Development
42	<i>Aquiloeurycea scandens</i>	Tamaulipan False Brook Salamander	Direct Development
43	<i>Ascaphus truei</i>	Tailed Frog	Metamorphosis
44	<i>Batrachoseps attenuatus</i>	California Slender Salamander	Direct Development
45	<i>Batrachoseps campi</i>	Inyo Mountains Salamander	Direct Development
46	<i>Batrachoseps diabolicus</i>	Hell Hallow Salamander	Direct Development
47	<i>Batrachoseps gabrieli</i>	San Gabriel Slender Salamander	Direct Development
48	<i>Batrachoseps gavilanensis</i>	Gabilan Mountains Slender Salamander	Direct Development
49	<i>Batrachoseps gregarius</i>	Gregarious Slender Salamander	Direct Development
50	<i>Batrachoseps incognitus</i>	San Simeon Slender Salamander	Direct Development
51	<i>Batrachoseps kawia</i>	Sequoia Slender Salamander	Direct Development
52	<i>Batrachoseps luciae</i>	Santa Lucia Salamander	Direct Development
53	<i>Batrachoseps major</i>	Garden Slender Salamander	Direct Development
54	<i>Batrachoseps minor</i>	Lesser Slender Salamander	Direct Development
55	<i>Batrachoseps nigriciventris</i>	Black Bellied Salamander	Direct Development
56	<i>Batrachoseps pacificus</i>	Channel Island Slender Salamander	Direct Development
57	<i>Batrachoseps regius</i>	Kings River Slender Salamander	Direct Development
58	<i>Batrachoseps reliktus</i>	Relictual Slender Salamander	Direct Development

59	<i>Batrachoseps robustus</i>	Kern Plateau Salamander	Direct Development
60	<i>Batrachoseps simatus</i>	Kern Canyon Slender Salamander	Direct Development
61	<i>Batrachoseps stebbinsi</i>	Tehachapi Slender Salamander	Direct Development
62	<i>Bolitoglossa platydactyla</i>	Brood-footed Salamander	Direct Development
63	<i>Chiropterotriton chondrostega</i>	Gristle-Headed Splayfoot Salamander	Direct Development
64	<i>Chiropterotriton cieloensis</i>	El Cielo Salamander	Direct Development
65	<i>Chiropterotriton cracens</i>	Graceful Splayfoot Salamander	Direct Development
66	<i>Chiropterotriton infernalis</i>	Purification System Salamander	Direct Development
67	<i>Chiropterotriton magnipes</i>	Bigfoot Splayfoot Salamander	Direct Development
68	<i>Chiropterotriton miquihuana</i>	Miquihuana Splayfoot Salamander	Direct Development
69	<i>Chiropterotriton multidentatus</i>	Toothy Splayfoot Salamander	Direct Development
70	<i>Chiropterotriton orculus</i>	Cope's Flat-Footed Salamander	Direct Development
71	<i>Chiropterotriton priscus</i>	Primeval Splayfoot Salamander	Direct Development
72	<i>Chiropterotriton terrestris</i>	Terrestrial Splayfoot Salamander	Direct Development
73	<i>Craugastor augusti</i>	The Barking Frog	Metamorphosis
74	<i>Craugastor batrachylus</i>	Taumalipan Arboreal Robber Frog	Metamorphosis
75	<i>Craugastor berkenbuschii</i>	Burkenbusch's Robber Frog	Metamorphosis
76	<i>Craugastor decoratus</i>	Adorned Robber Frog	Metamorphosis
77	<i>Craugastor hobartsmithi</i>	Smith's Pigmy Robber Frog	Metamorphosis
78	<i>Craugastor loki</i>	Common Leaf Litter Frog	Metamorphosis
79	<i>Craugastor mexicanus</i>	Mexican Robber Frog	Metamorphosis
80	<i>Craugastor occidentalis</i>	Taylor's Barking Frog	Metamorphosis
81	<i>Craugastor pygmaeus</i>	Pigmy Free-Fingered Frog	Metamorphosis
82	<i>Craugastor rhodopis</i>	Polymorphic Robber Frog	Metamorphosis
83	<i>Craugastor tarahumaraensis</i>	Tarahumara Barking Frog	Metamorphosis

84	<i>Craugastor vocalis</i>	Taylor's Stream Frog	Metamorphosis
85	<i>Desmognathus auriculatus</i>	Southern Dusky Salamander	Metamorphosis
86	<i>Dicamptodon ensatus</i>	California Giant Salamander	Metamorphosis
87	<i>Dicamptodon tenebrosus</i>	Costal Giant Salamander	Metamorphosis
88	<i>Dryophytes arenicolor</i>	Canyon Treefrog	Metamorphosis
89	<i>Dryophytes chrysoscelis</i>	Cope's Grey Treefrog	Metamorphosis
90	<i>Dryophytes cinereus</i>	North American Green Treefrog	Metamorphosis
91	<i>Dryophytes eximius</i>	Mountain Treefrog	Metamorphosis
92	<i>Dryophytes plicatus</i>	Ridged Treefrog	Metamorphosis
93	<i>Dryophytes squirellus</i>	Squirrel Treefrog	Metamorphosis
94	<i>Dryophytes versicolor</i>	Eastern Gray Treefrog	Metamorphosis
95	<i>Dryophytes wrightorum</i>	Arizona Treefrog	Metamorphosis
96	<i>Eleutherodactylus campi</i>	Rio Grande Chirping Frog	Metamorphosis
97	<i>Eleutherodactylus cystignathoides</i>	Lowland Chirping Frog	Metamorphosis
98	<i>Eleutherodactylus dennisi</i>	Long-Footed Frog	Metamorphosis
99	<i>Eleutherodactylus guttulatus</i>	Spotted Chirping Frog	Metamorphosis
100	<i>Eleutherodactylus interorbitalis</i>	Spectacled Chirping Frog	Metamorphosis
101	<i>Eleutherodactylus longipes</i>	Huasteca Chirping Frog	Metamorphosis
102	<i>Eleutherodactylus marnockii</i>	Cliff Chirping Frog	Metamorphosis
103	<i>Eleutherodactylus nitidus</i>	Shiny Peeping Frog	Metamorphosis
104	<i>Eleutherodactylus orarius</i>	Coastal Whistling Frog	Metamorphosis
105	<i>Eleutherodactylus pallidus</i>	Pale Chirping Frog	Metamorphosis
106	<i>Eleutherodactylus saxatilis</i>	Marbled Robber Frog	Metamorphosis
107	<i>Eleutherodactylus teretistes</i>	Whistling Frog	Metamorphosis
108	<i>Eleutherodactylus verrucipes</i>	Bigear Chirping Frog	Metamorphosis
109	<i>Eleutherodactylus wixarika</i>	Wixarika Chirping Frog	Metamorphosis
110	<i>Engystomops pustulosus</i>	Tungara Frog	Metamorphosis
111	<i>Ensatina eschscholtzii</i>	Ensatina Salamander	Direct Development
112	<i>Eurycea chisholmensis</i>	Salado Salamander	Paedomorphic
113	<i>Eurycea latitans</i>	Cascade Cavern Salamander	Paedomorphic
114	<i>Eurycea nana</i>	San Marcos Salamander	Paedomorphic

115	<i>Eurycea naufragia</i>	Georgetown Salamander	Paedomorphic
116	<i>Eurycea neotenes</i>	Texas Salamander	Paedomorphic
117	<i>Eurycea pterophila</i>	Fern Bank Salamander	Paedomorphic
118	<i>Eurycea quadridigitata</i>	Dwarf Salamander	Metamorphosis
119	<i>Eurycea rathbuni</i>	Texas Blind Salamander	Paedomorphic
120	<i>Eurycea robusta</i>	Blanco Blind Salamander	Unknown
121	<i>Eurycea sosorum</i>	Barton Spring Salamander	Unknown
122	<i>Eurycea tonkawae</i>	Jollyville Plateau Salamander	Paedomorphic
123	<i>Eurycea tridentifera</i>	Comal Blind Salamander	Paedomorphic
124	<i>Eurycea troglodytes</i>	Valdina Farms Salamander	Paedomorphic
125	<i>Eurycea waterlooensis</i>	Austin Blind Salamander	Paedomorphic
126	<i>Exerodonta smaragdina</i>	Emerald Treefrog	Metamorphosis
127	<i>Gastrophryne carolinensis</i>	Eastern Narrow-Mouthed Toad	Metamorphosis
128	<i>Gastrophryne elegans</i>	Elegant Narrow-Mouthed Toad	Metamorphosis
129	<i>Gastrophryne olivacea</i>	Western Narrow-Mouthed Toad	Metamorphosis
130	<i>Hydromantes brunus</i>	Limestone Salamander	Direct Development
131	<i>Hydromantes platycephalus</i>	Mount Lyell Salamander	Direct Development
132	<i>Hydromantes shastae</i>	Shasta Salamander	Direct Development
133	<i>Hypopachus ustus</i>	Two-Spaded Narrow-Mouth Toad	Metamorphosis
134	<i>Hypopachus variolosus</i>	Sheep Frog	Metamorphosis
135	<i>Incilius alvarius</i>	Sonoran Desert Toad	Metamorphosis
136	<i>Incilius marmoreus</i>	Weigmann's Toad	Metamorphosis
137	<i>Incilius mazatlanensis</i>	Sinaloa Toad	Metamorphosis
138	<i>Incilius mccoyi</i>	McCoy's Toad	Metamorphosis
139	<i>Incilius nebulifer</i>	Gulf Coast Toad	Metamorphosis
140	<i>Incilius occidentalis</i>	Pine Toad	Metamorphosis
141	<i>Isthmura bellii</i>	Bell's Salamander	Direct Development
142	<i>Isthmura gigantea</i>	Giant False Brook Salamander	Direct Development
143	<i>Isthmura sierraoccidentalis</i>	Pine Oak Salamander	Direct Development
144	<i>Leptodactylus fragilis</i>	Mexican White Lipped Frog	Metamorphosis

145	<i>Leptodactylus melanotus</i>	Reddish-Brown White Lipped Frog	Metamorphosis
146	<i>Lithobates berlandieri</i>	Rio Grande Leopard Frog	Metamorphosis
147	<i>Lithobates blairi</i>	Plains Leopard Frog	Metamorphosis
148	<i>Lithobates catesbeianus</i>	American Bullfrog	Metamorphosis
149	<i>Lithobates chiricahuensis</i>	Chiricahua Leopard Frog	Metamorphosis
150	<i>Lithobates fisheri</i>	Las Vegas Valley Leopard Frog	Metamorphosis
151	<i>Lithobates forreri</i>	Forrer's Grass Frog	Metamorphosis
152	<i>Lithobates johni</i>	Moore's Frog	Metamorphosis
153	<i>Lithobates magnaocularis</i>	Northwest Mexico Leopard Frog	Metamorphosis
154	<i>Lithobates montezumae</i>	Montezuma Leopard Frog	Metamorphosis
155	<i>Lithobates neovolcanicus</i>	Transverse Volcanic Leopard Frog	Metamorphosis
156	<i>Lithobates onca</i>	Relict Leopard Frog	Metamorphosis
157	<i>Lithobates pipiens</i>	Northern Leopard Frog	Metamorphosis
158	<i>Lithobates pustulosus</i>	Mexican Cascades Frog	Metamorphosis
159	<i>Lithobates spectabilis</i>	Showy Leopard Frog	Metamorphosis
160	<i>Lithobates subaquavocalis</i>	Ramsey Canyon Leopard Frog	Metamorphosis
161	<i>Lithobates tarahumarae</i>	Tarahumara Frog	Metamorphosis
162	<i>Lithobates yavapaiensis</i>	Lowland Leopard Frog	Metamorphosis
163	<i>Necturus beyeri</i>	Gulf Coast Waterdog	Metamorphosis
164	<i>Notophthalmus meridionalis</i>	Black-Spotted Newt	Metamorphosis
165	<i>Notophthalmus viridescens</i>	Eastern Newt	Metamorphosis
166	<i>Plethodon albagula</i>	Western Slimy Salamander	Direct Development
167	<i>Plethodon neomexicanus</i>	Jemez Mountain Salamander	Direct Development
168	<i>Pseudacris cadaverina</i>	California Treefrog	Metamorphosis
169	<i>Pseudacris clarkii</i>	Spotted Chorus Frog	Metamorphosis
170	<i>Pseudacris crucifer</i>	Spring Peeper	Metamorphosis
171	<i>Pseudacris fouquettei</i>	Cajun Chorus Frog	Metamorphosis
172	<i>Pseudacris maculata</i>	Boreal Chorus Frog	Metamorphosis
173	<i>Pseudacris regilla</i>	Pacific Treefrog	Metamorphosis
174	<i>Pseudacris streckeri</i>	Stecker's Chorus Frog	Metamorphosis
175	<i>Pseudoeurycea gadovii</i>	Gadow's Salamander	Direct Development
176	<i>Pseudoeurycea leprosa</i>	Leprous False Brook Salamander	Direct Development

177	<i>Rana boylii</i>	Foothill Yellow-Legged Frog	Metamorphosis
178	<i>Rana cascadae</i>	Cascades Car	Metamorphosis
179	<i>Rana draytonii</i>	California Red-Legged Frog	Metamorphosis
180	<i>Rana luteiventris</i>	Columbia Spotted-Frog	Metamorphosis
181	<i>Rana muscosa</i>	Southern Mountain Yellow-Legged Frog	Metamorphosis
182	<i>Rana pretiosa</i>	Oregon Spotted Frog	Metamorphosis
183	<i>Rana sierrae</i>	Sierra Nevada Yellow-Legged Frog	Metamorphosis
184	<i>Rheohyla miotympanum</i>	Small-Eared Treefrog	Metamorphosis
185	<i>Rhinella marina</i>	Cane Toad	Metamorphosis
186	<i>Rhinophryne dorsalis</i>	Mexican Burrowing Toad	Metamorphosis
187	<i>Sarcohyla arborescens</i>	Lesser Bromeliad Treefrog	Metamorphosis
188	<i>Sarcohyla charadricola</i>	Puebla Treefrog	Metamorphosis
189	<i>Sarcohyla hapsa</i>	Northern Streamside Treefrog	Metamorphosis
190	<i>Sarcohyla robertorum</i>	Robert's Treefrog	Metamorphosis
191	<i>Scaphiopus couchii</i>	Couch's Spadefoot	Metamorphosis
192	<i>Scaphiopus hurterii</i>	Hurter's Spadefoot	Metamorphosis
193	<i>Scinax staufferi</i>	Middle American Snouted Treefrog	Metamorphosis
194	<i>Siren intermedia</i>	Lesser Siren	Metamorphosis
195	<i>Siren lacertina</i>	Greater Siren	Metamorphosis
196	<i>Smilisca baudinii</i>	Common Mexican Treefrog	Metamorphosis
197	<i>Smilisca dentata</i>	Upland Burrowing Treefrog	Metamorphosis
198	<i>Smilisca fodiens</i>	Northern Casque-Headed Frog	Metamorphosis
199	<i>Spea bombifrons</i>	Plains Spadefoot	Metamorphosis
200	<i>Spea hammondii</i>	Western Spadefoot	Metamorphosis
201	<i>Spea intermontana</i>	Great Basin Spadefoot	Metamorphosis
202	<i>Spea multiplicata</i>	Mexican Spadefoot	Metamorphosis
203	<i>Taricha granulosa</i>	Roughskinned Newt	Metamorphosis
204	<i>Taricha rivularis</i>	Red-Bellied Newt	Metamorphosis
205	<i>Taricha sierrae</i>	Sierra Newt	Metamorphosis
206	<i>Taricha torosa</i>	California Newt	Metamorphosis
207	<i>Tlalocohyla picta</i>	Painted Treefrog	Metamorphosis
208	<i>Tlalocohyla smithii</i>	Dwarf Mexican Treefrog	Metamorphosis
209	<i>Trachycephalus typhonius</i>	Common Milk Frog	Metamorphosis

210	<i>Triprion spatulatus</i>	Shovel Headed Treefrog	Metamorphosis
211	<i>Xenopus laevis</i>	African Clawed Frog	Metamorphosis