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RESEARCH ARTICLE

# The Impact of Climate Change on High-Priority Areas of Conservation for Amphibians in North American Drylands

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## ABSTRACT

**Aim:** The goals of this study were to (1) identify how climate change impacts the distribution of 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 and (3) explore how climate change will impact the distribution of HPCA and investigate the relationship between HPCA and protected area (PA) network.

**Location:** Southwest United States and Northern Mexico.

**Taxon:** Amphibians.

**Methods:** We used distribution maps for 209 amphibian species to estimate surrogates of amphibian diversity, assessed by rarity-weighted richness (RWR), site importance (Zonation) and species richness. Then, we used species accumulation curves to assess their efficiency in representing amphibians in the least number of sites. Next, we used the most effective surrogate to identify HPCA for amphibians. We used environmental variables, usually related to amphibian distribution, and random forest models to assess the impact of climate on the spatial configuration of HPCA in the current and future times. We also used PA networks to assess their representation.

**Results:** RWR produced a similar spatial configuration of HPCA as Zonation but could not depict the same level of connectivity. HPCAs were observed mainly across California, central Texas and western Mexico. The spatial distribution of HPCA was mostly influenced by precipitation, temperature and solar radiation. Climate change will influence the future distribution of HPCA. The overlay between HPCA and PA is weak.

**Main Conclusion:** Climate change is becoming an ever-increasing issue for conservation efforts, especially in dryland ecosystems where natural resources are already scarce for native species. Results show an alteration in the spatial configuration of amphibian HPCA, and much is still needed to protect and manage them.

## 1 | Introduction

The decline in amphibian population and abundance has been staggering in the last three decades, with 40.7% of amphibian species globally threatened (Pounds 2001; Stuart et al. 2004; Lannoo 2005; Luedtke et al. 2023). Many threats have been linked to amphibian population declines, including environmental pollution, invasive species, disease, anthropogenic habitat alteration and climate change (Lannoo 2005; Blaustein and Kiesecker 2002; Beebee and Griffiths 2005; Albuquerque, Bateman, et al. 2024; Albuquerque, Bateman, Ryan, et al. 2024). Climate change is amongst the most significant threats to amphibian diversity (Steigerwald 2021), especially in North American drylands (Albuquerque, Bateman, et al. 2024; Albuquerque, Bateman, Ryan, et al. 2024), areas often characterised by areas that receive less precipitation inputs (water scarcity) yet with a high biodiversity (Safriel et al. 2005).

Recent studies have shown that changes in extreme temperatures and precipitation regimes will modify the availability of suitable habitats across drylands, especially for amphibians (Griffis-Kyle et al. 2018). Albuquerque, Bateman, Ryan, et al. (2024) investigated the potential impacts of climate change on the geographical range of amphibians in drylands of North America, and they reported a significant loss of suitable habitat in the future. For example, many abundant species such as canyon treefrogs (*Hyla arenicolor*) and water frogs (family Ranidae) and specialised stream-breeding amphibians such as the Arizona toad (*Anaxyrus microscaphus*) are tied to water availability and may decrease when streams are regulated and diverted or base flows are reduced (Tockner et al. 2006; Railsback et al. 2016; Bateman et al. 2024; Albuquerque, Bateman, et al. 2024). The loss of suitable habitat has been considered a significant threat to the persistence of amphibian populations (Cushman 2006).

One way to identify suitable areas for conservation for imperilled species, such as amphibians, is to highlight potentially highly suitable areas for conservation (Albuquerque and Beier 2015b). High-priority conservation areas (HPCA) are essential to identifying crucial conservation areas for safeguarding species (Albuquerque and Beier 2015a). Their identification often relies on habitat suitability, species occurrence and richness and algorithms based on complementarity, rather than expert opinions, to prioritise sites for conservation (Moilanen et al. 2009; Albuquerque and Beier 2015b). Complementarity-based algorithms identify optimal or near-optimal sets of sites that collectively represent species in a small area (Moilanen et al. 2009). Because of amphibians' microhabitat requirements and biphasic cycle (aquatic and terrestrial), changes in habitat suitability can significantly reduce their distributional range, especially in drylands (Albuquerque, Bateman, Ryan, et al. 2024). Therefore, identifying HPCA can help provide information and data to prioritise and conserve amphibians' habitats (Albuquerque, Bateman, Ryan, et al. 2024).

Nevertheless, HPCA lack conservation actions (Le Saout et al. 2013; CBD 2022), such as protected areas (PAs). PAs are critically important in conserving biodiversity and preventing extinction (Le Saout et al. 2013). Lindenmayer (2024) reported that PA coverage was still inadequate to conserve all biodiversity and highlighted the need to expand them to prevent biodiversity loss. They also noted that more efforts were needed to meet the conservation for biodiversity target by 2030 (protect 30% or more of the Earth's surface). Despite the evidence of the lack of PA coverage in different parts of the Globe (e.g., Assunção-Albuquerque et al. 2012; Le Saout et al. 2013; Lindenmayer 2024; Dinerstein et al. 2024), the assessment of the efficiency of PA in representing HPCA for amphibians in the Southwest United States and North Mexico is still pending.

The delineation of HPCA depends on ensuring that most species are included in the conservation solution (representativeness; Watson et al. 2011). However, a major limitation to building a comprehensive HPCA network is the incomplete knowledge of species' geographical distribution (i.e., Wallacean shortfall, Lomolino 2004) and ecological needs. Since wall-to-wall inventories are not available in drylands, scientists use proxies for biodiversity, also known as biodiversity surrogates (Williams et al. 2006). Surrogates are accurately mapped environmental or taxonomic groups such as soil types, climatic conditions, or easily observed occurrences of species in the planning area (Rodrigues and Brooks 2007; Beier and Albuquerque 2016; Albuquerque and Gregory 2017). Examples of common biodiversity surrogates include the importance of areas for conservation, often expressed by complementarity-based solutions such as Zonation (Moilanen et al. 2009), rarity-weighted richness (RWR, Williams et al. 1996) and species richness.

Zonation is a spatial prioritisation solution often used to identify priority areas to support conservation actions (i.e., most important locations to retain biodiversity, Moilanen et al. 2009). Zonation produces a hierarchical priority ranking of geographic grid cells for each taxon from zero to one. It removes cells that are not indispensable to preserve biodiversity. Zonation is widely used to design and evaluate PA networks and plan for their expansion. It can also be used for habitat restoration and maintenance (Moilanen et al. 2009). Similarly, RWR seeks to represent the maximum number of species in a given number of sites (Williams et al. 1996). RWR is a summation of the scores calculated as the inverse of the number of species occurrences in one site (Albuquerque and Beier 2015b; Williams et al. 1996). Rarity scores can be a dependable method for representing species occurrences (Albuquerque and Beier 2015b). RWR is an alternative spatial conservation planning tool that assigns higher priority rankings to sites offering rare or endemic species. Species richness, often defined as the number of species within an area, is a common surrogate of biodiversity frequently used to prioritise areas for conservation (Albuquerque and Beier 2015b). However, its efficacy is questioned since, in most cases, richness has failed to preserve all biodiversity when compared to null models (Albuquerque and Beier 2015b; Astudillo-Scalia and de Albuquerque 2019; Astudillo-Scalia and Albuquerque 2020). In previous studies, solutions provided by Zonation and RWR surrogates represented the most species across sites when financial or resource limitations do not allow for every site to be sampled (Church et al. 1996; Williams, Gibbons, Margules, Rebelo, Humphries, et al. 1996; Moilanen et al. 2009; Albuquerque and Beier 2015a, 2015b).

Another essential goal of designing HPCA is to ensure effectiveness in representing species in the current time that will persist in the future (Watson et al. 2011). Albuquerque and Beier (2015a) investigated the global distribution of HPCA in vertebrates, including amphibians, birds and mammals. They reported that climate-related predictors were major drivers of the spatial configuration of HPCA. Since climate change is expected to influence amphibian distribution (Luedtke et al. 2023), it is crucial to determine whether changes in the geographical distribution of amphibians will also impact the spatial configuration of their HPCA. Understanding the potential impacts of climate change on priority habitats is crucial for developing and implementing effective conservation and management plans.

Herein, we evaluate which proxy for biodiversity (Zonation, RWR and species richness) is most effective for identifying HPCA. Our research objectives are to (1) identify HPCA for amphibians in drylands of the Southwest United States and Northern Mexico, (2) investigate the potential impacts of climate change on the spatial configuration of HPCA and (3) assess if PAs represent HPCA.

## 2 | Methods

### 2.1 | Study Area

Our study area includes the Southwest United States and Northern Mexico (Figure 1), comprising one of the largest continuous dryland areas experiencing a major multi-year drought (Hughes and Diaz 2008). We used the Convention on Biological Diversity (CBD), the United Nations Convention to Combat Desertification (UNCCD) and Map (UNEP-WCMC 2007) to define the dryland ecosystems across the study area. They are usually determined by the ratio between precipitation and potential evapotranspiration (P/PET) and encompass four dryland subtypes: hyper-arid, arid, semi-arid and dry sub-humid. Dryland subtypes encompass 41.3% of land coverage on Earth and are defined by increasing aridity and decreasing moisture. They display varying levels of biodiversity and species richness (Safriel et al. 2005).

### 2.2 | Data Preparation

#### 2.2.1 | Estimating Presence and Absence

We obtained global distribution range maps for 7209 amphibian species from the International Union for the Conservation of Nature (IUCN) Red List spatial data (IUCN 2022). The IUCN distribution maps are established by considering known taxon occurrences, habitat, elevation limits and insights from experts regarding the taxon and its range (IUCN 2018). Ficetola et al. (2014) reviewed and assessed the quality of range maps in predicting the distribution of known amphibians and reported that range maps predicted their distribution well. We created a grid cell of about 10 × 10 min in *R* (R Core Team 2023) with the same extent as our study area and overlaid each amphibian range map to create a matrix of presence and absence. We removed records that lacked a coordinate system, did not overlap with our study area and had errors, missing values, or incomplete data. We considered presence by having each grid cell overlap with the species range. Cells without overlapping ranges were deemed absences. Next, we utilised the expert range maps provided by AmphibiaWeb (2023) to identify species likely to be year-round residents in the study area. Expert range maps are generally compiled from books or assessment reports, such as those offered by IUCN (please see AmphibiaWeb 2023 for more details on expert range maps), and illustrate the extent of species occurrences over time (e.g., 10–30 years—AmphibiaWeb 2023).

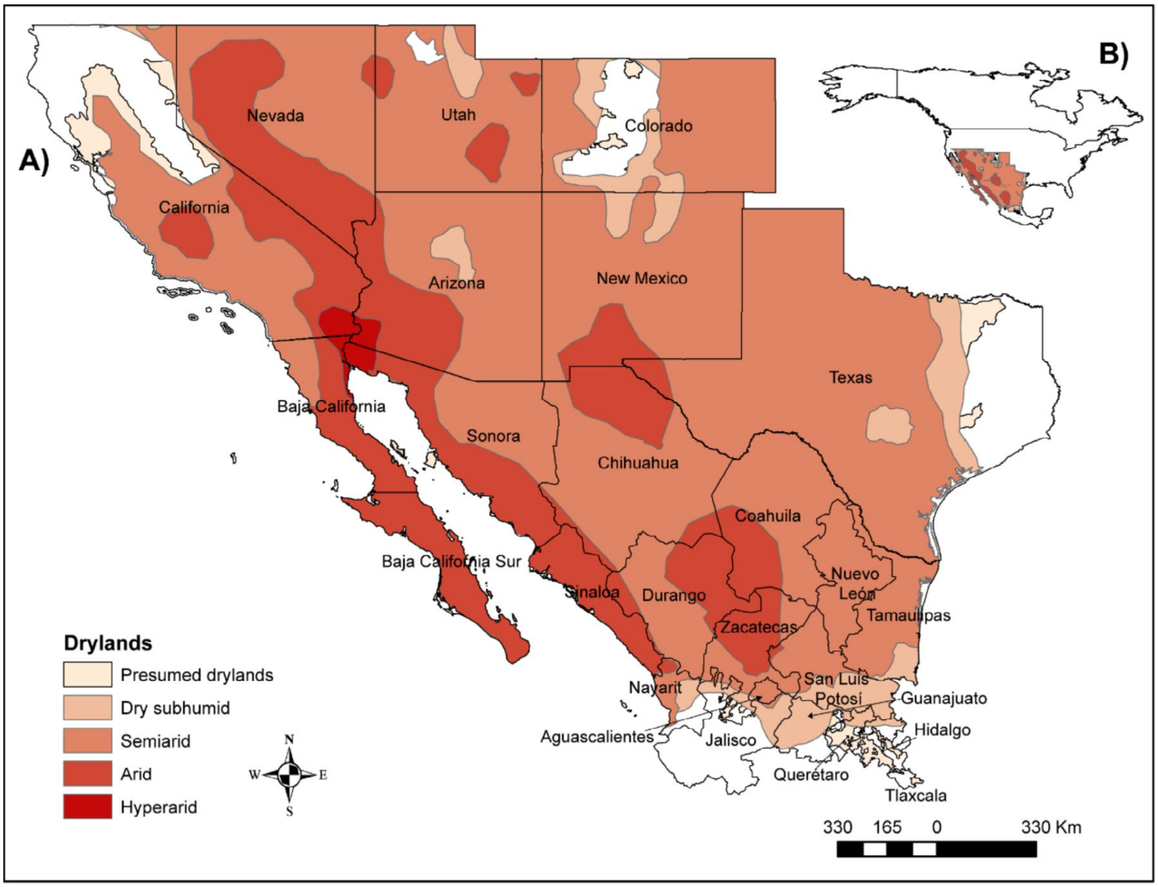

**FIGURE 1** | Geographic depiction of drylands in the Southwest United States and Mexico (A) and their location related to North America (B). The drylands delineations were obtained from the UNEP-WCMC (2007). The map also includes presumed drylands—an area with the precipitation/potential evapotranspiration (PET) ratio ≥ 0.65. Intended size of reproduction.

This process resulted in 209 amphibian species within our study area for our analysis.

### 2.2.2 | Environmental Variables

We selected 34 environmental variables to investigate the relationship between environmental changes and HPCA for amphibians. These included 19 bioclimatic variables and 12 solar radiation measurements, expressed as monthly values, from WorldClim (Fick and Hijmans 2017). We then used these solar radiation values to calculate the annual solar radiation's mean, minimum, maximum and standard deviation. Both bioclimatic and solar radiation variables are at a 10-min resolution. We also obtained 10 topographic measures from EarthEnv (Amatulli et al. 2018), representing median and standard deviations of elevation, slope, roughness, topographic position, topographic ruggedness and topographic wetness index (TWI) from Marthews, Dadso, Lehner, Abele, et al. (2015) and Marthews, Dadson, Lehner, Abele, et al. (2015). We used R (R Core Team 2023) and the *aggregate* (Hijmans 2024) function to rescale the topographic variables to 10-min cells.

## 2.3 | Estimating Surrogates of Biodiversity

We used the grid cell and presence/absence matrix to estimate species richness and RWR (Williams et al. 1996). We estimated richness by summing the species occurrences in each grid cell. We estimated RWR values by calculating the inverse of the number of cells where each species occurs (individual scores). Then, we summed the individual scores of all species within each grid cell (Williams et al. 1996). For example, if a species occurs in 1000 grid cells, its score would be 1/1000 or 0.001, whereas a species occurring in one grid cell would receive a score of 1.

We used the core area zonation (CAZ) marginal loss rule from Zonation software (Zonation 5 v2.2—Moilanen et al. 2022) to estimate priority rank values. The algorithm minimises biological loss by identifying cells with low species occurrences and giving a high priority value (Moilanen et al. 2009). The CAZ rule emphasises high complementarity and seeks to retain core areas for all species (Moilanen et al. 2009, 2022). Zonation often produces near-optimum solutions for target-based planning to meet the lowest cost targets (Moilanen 2007).

## 2.4 | Surrogate Evaluation

We built species accumulation curves to evaluate the efficacy of our surrogates in representing the maximum number of species in a minimum number of sites. This process consisted of the following five steps: (1) we created a data frame with all surrogates (richness, RWR and priority rank values) and the presence and absence values for resident amphibians, (2) we ordered each solution from the highest to the lowest value, (3) we counted the number of species accumulated across sites, (4) we built a random solution that consisted of counting the number of species accumulated across cells (randomly ordered) and (5) we used the surrogate and random solutions to estimate the Species Accumulation Index (SAI). SAI is commonly used to assess and contrast surrogates representing species (Rodrigues and Brooks 2007). SAI is defined by ($\mathrm{SAI} = S - R / O - R$). $S$ represents the total species count represented by the richness and RWR solutions. $R$ refers to the average species count represented by a random solution after 999 iterations. $O$ indicates the maximum species count that can be represented at least once across the sites indicated by the Zonation solution (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. We measured the effectiveness of each solution across 30 targets from 0.5% to 30%, increasing incrementally by 1% (Beier and Albuquerque 2016).

## 2.5 | Identifying HPCA

After identifying the surrogate (richness, RWR and priority-rank values) that yielded the best solution to select the maximum number of species in a minimum number of sites, we identified the top 30% of its value to identify HPCA for amphibians. We chose this percentage because the CBD expects 30% of natural areas to be protected by 2030 (CBD 2022).

## 2.6 | Identifying Drivers of HPCA Distribution

First, we reduced the dimensionality of the environmental data by implementing a varimax-rotated principal component analysis (PCA). PCA highlights sets of uncorrelated environmental variables and describes environmental gradients within the data (Albuquerque and Beier 2015a). We utilised 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. We identified the variables with the highest loadings for each chosen principal component. We used the Spearman correlation to relate variables with the highest loadings to the surrogate solution that yielded the best site representation results. We selected the variable that was most correlated with the surrogate. These were used as independent variables in the random forest model (selected variables).

We used random forest models to investigate the relationship between the surrogate values and the selected environmental variables, as indicated by the PCA (Albuquerque and Beier 2015a; Astudillo-Scalia and Albuquerque 2020). Random forest models were successfully used to model species distributions (Prasad et al. 2006) and the spatial configuration of HPCA in terrestrial (Albuquerque and Beier 2015a) and marine ecosystems (Astudillo-Scalia and Albuquerque 2020). The random forest approach uses multiple decision tree outputs to reach a single result (Breiman 2001). Specifically, the algorithm uses about 1/3 of the cases left out of the sample, also known as out of bag (OOB) data (Breiman 2001). OOB data are used as an estimator of variable importance. We ran our random forest model with the selected variables from the PCA and correlation analyses and the mean decrease in accuracy approach to investigate their importance in the model. This last was computed from a permutation of the OOB data (Liaw and Wiener 2002). In this process, the prediction error of the OOB data was estimated for each tree after the permutation of each predictor (Liaw and Wiener 2002). We used the mean square error (MSE) to evaluate the predictive performance of the random forest model. MSE was defined as the sum of the squared residuals divided by the number of trees (500). In general, MSE values close to 0 imply high-accuracy forecasts (Chicco et al. 2021). We used the *randomForest* package in R to run the random forest models and estimate the MSE (Liaw and Wiener 2002; R Core Team 2023). Models were set using the default model parameters.

### 2.7 | Investigating the Impact of Climate Change on the Distribution of HPCA

We used 10 global circulation models (GCMs, Table S1) obtained from Worldclim (n.d.) and the results from the random forest models to evaluate the impact of climate change on the distribution of HPCA. The GCMs include averaged values over 2081–2100 years. Each GCM includes future projections across four shared socioeconomic pathways (SSPs), each representing 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). For each SSP scenario, we produced 10 predictions, 1 for each GCM. We then averaged the projected values for each SSP to obtain a map of predicted complementarity values. We followed the same procedure to define the current HPCA and identify the projected HPCA for amphibians. We finally overlaid the maps with current and projected HPCA to identify areas of change and refuges (i.e., areas that are HPCA in the present and projected to continue in the future).

### 2.8 | Assessing the Coverage of HPCA by PAs

We used the World Database on Protected Areas (WDPA, UNEP-WCMC and IUCN 2024), the most comprehensive PAdatabase for terrestrial and marine realms (UNEP-WCMC 2019), to investigate the relationship between PA and HPCA in current and future times. To do so, we overlaid the HPCA layers to the WDPA and calculated the percentage of HPCA covered by PA.

## 3 | Results

The PCA analysis and the Kaiser criteria identified six axes with eigenvalues greater than one (Table S2). The first axis included topographical variables, and the second represented a combination of temperature and elevation. The third and fifth encompassed mostly temperature, precipitation and solar radiation variables. The fourth axis included measures of temperature and solar radiation. Altogether, the axes explained 90% of the environmental variance. Amongst the selected PCA axes, the variables most correlated with complementarity were mean diurnal range, annual precipitation, minimum temperature of coldest month, temperature annual range, precipitation of coldest quarter and median of the terrain ruggedness index.

Patterns of priority-rank values expressed by Zonation displayed high values throughout contiguous HPCA (corridors) across California, central Texas and western Mexico (Figure 2A). Zonation revealed isolated areas of high values in New Mexico, Arizona, Nevada and Utah. RWR produced similarly high values as priority-rank values but could not depict the same level of connectivity between high-value RWR areas (Figure 2B). Richness displayed high values in central Texas and along the Southwestern border of Mexico in our study area (Figure 2C). Secondary spots of high richness were also shown in Sinaloa, Tamaulipas and San Luis Potosí (Mexico).

The Zonation solution proved to be the best solution for representing amphibians in the dryland systems of the Southwest United States and Northern Mexico (Figure 2D). RWR performed nearly as well as Zonation in selecting the most species within the fewest 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 2D). Since Zonation was more efficient in selecting the most species in the smallest number of sites, the results thereafter are based on the abovementioned solution (Figure 2D).

The spatial distribution of HPCA shows a high concentration of priority areas in California, Northeast and Northwest Mexico and Texas (Figure 3). Secondary HPCA spots were also observed in New Mexico, Arizona, Colorado and Nevada (Figure 3). According to random forest models, measures of precipitation and temperature were the most influential variables in explaining the spatial distribution of priority-rank values and HPCA (Figure 4). The top four most influential variables were precipitation of the coldest quarter, annual precipitation, mean diurnal range and minimum temperature of the coldest month. The environmental variables explained 77.2% of the variance within our model (Figure 4). The MSE value was low (0.018, Figure S1).

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 SSP 370 (22%) and SSP 585 (23%). The most loss of HPCA was seen in the isolated dryland sites of Nevada, Utah, New Mexico and Arizona (Figure 5). The greatest gains of HPCA were seen along the western coast of Mexico and central Texas across all SSP (Figure 5). A high overlap between the current and the predicted future HPCA was also observed. The highest values were observed for the most optimistic scenarios, with an 82% (SSP 126) and 80% (SSP 245) overlap of suitable habitat between the current and future scenarios. The lowest overlap was noted in the most pessimistic scenarios (SSP 370—78% and SSP 585—77%). The overlap between HPCA and PA was low. Only 10.25% and 9.89% (average) of the PA covered HPCA at the current and future times, respectively (Figure 6).

## 4 | Discussion

Our findings are important to help fill gaps in information on the conservation of amphibians across North American drylands. Ours is the first attempt to evaluate the effectiveness of amphibian surrogates in this often-overlooked biome. We summarise the spatial configuration of priority conservation areas

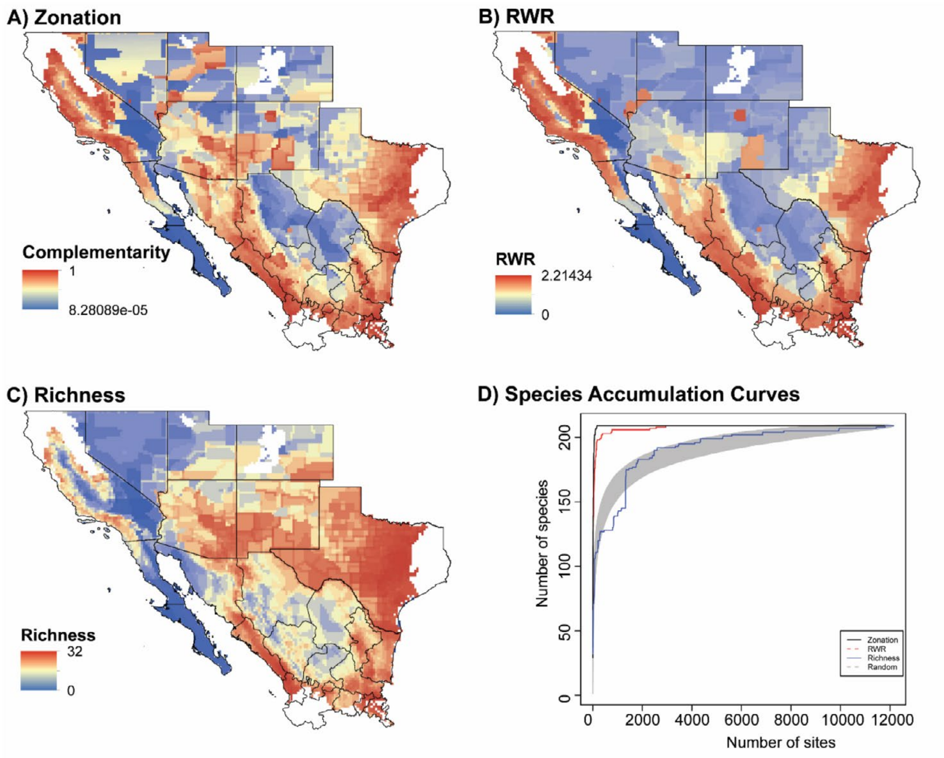

**FIGURE 2** | Geographic distribution of (A) priority rank values, estimated by Zonation, (B) rarity-weighted richness (RWR) and (C) species richness. The (D) species accumulation curves (SAC) depicting Zonation, RWR, richness and random solutions are also displayed. SAC shows the number of sites each solution needed to reach the target number of amphibian species in the study. Intended size of reproduction.

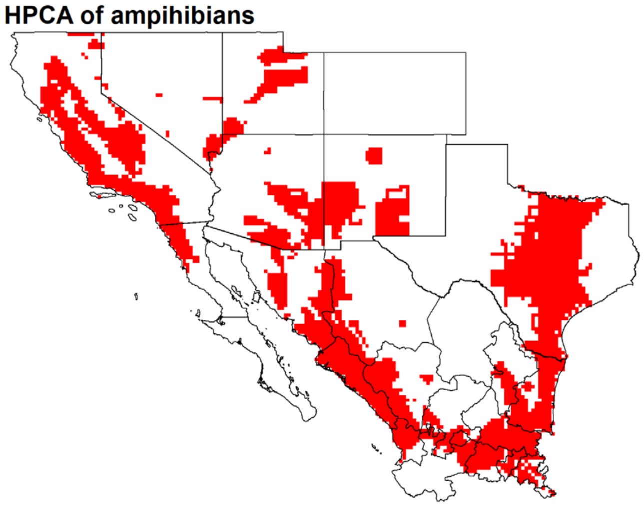

**FIGURE 3** | Geographic distribution of high-priority conservation areas (HPCA) for amphibians in Southwest drylands according to the Zonation solution. HPCA represent the top 30% of the priority-rank values. Intended size of reproduction.

and their drivers and identify the potential impacts of climate change on HPCA.

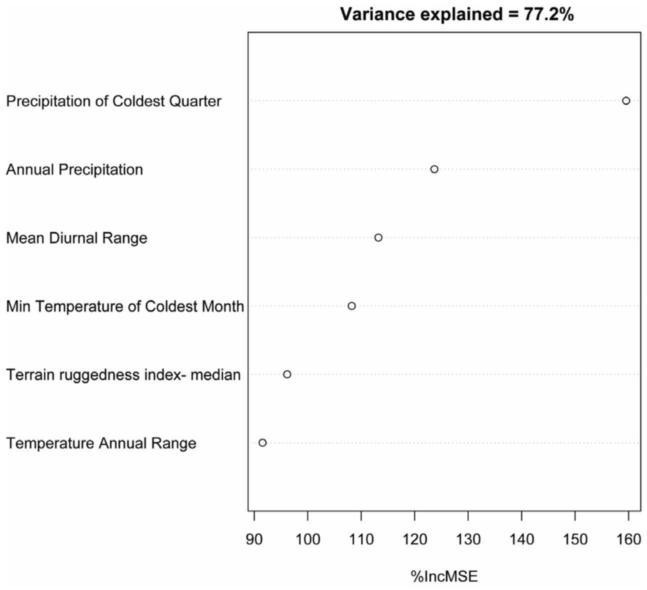

**FIGURE 4** | Variable importance for the random forest model, identifying which variables were most important to the spatial configurations of important conservation areas for amphibians in drylands of the Southwest United States and Mexico. %IncMSE—mean decrease accuracy. Results also indicate how the model accuracy decreases when that variable is removed. Intended size of reproduction.

## 4.1 | Surrogate Analysis

Our results showed that Zonation was the most successful surrogate for identifying the HPCA for amphibians within the dryland systems of the Southwest United States and Northern Mexico. The efficiency of Zonation has been tested in several scenarios, including biomes, extents and spatial resolution. For example, Beier and Albuquerque (2015) investigated the

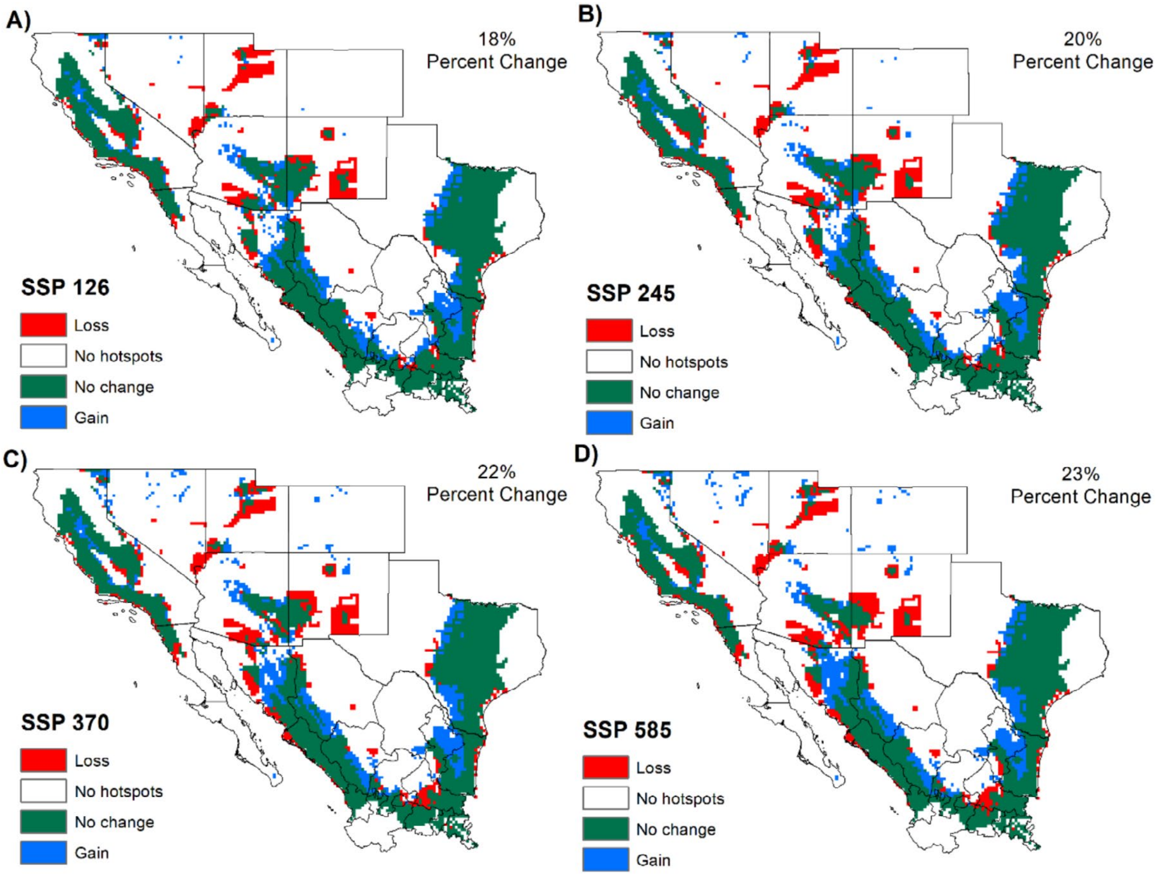

**FIGURE 5** | Future geographic distribution of high-priority conservation areas for amphibians in Southwest drylands. Red cells represent a predicted loss, white cells represent no HPCA, green cells represent no change and blue cells represent a predicted gain. Intended size of reproduction.

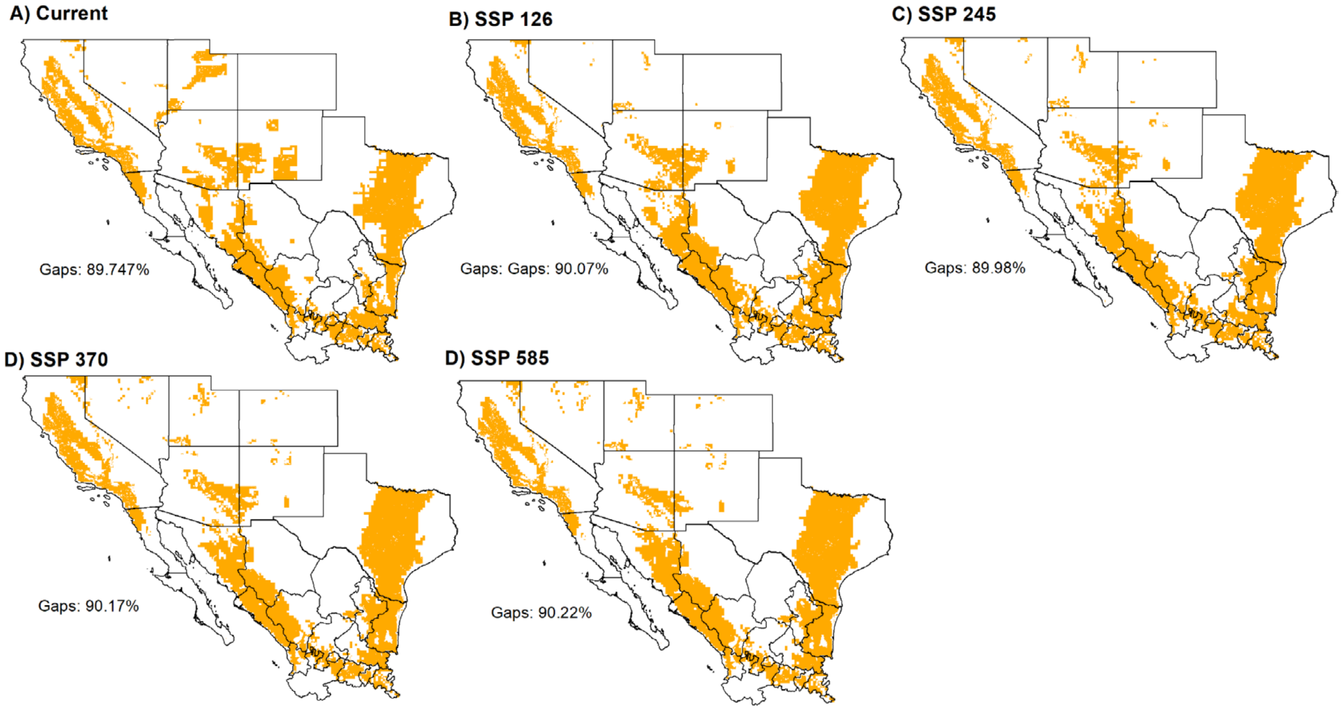

**FIGURE 6** | Geographic distribution of gaps in high-priority conservation areas (HPCA) for amphibians in current and project times (shared socioeconomic pathways SSP 126, SSP 245, SSP 370 and SSP 585). Orange areas represent HPCA, not represented by protected areas. The percentage of unrepresented HPCA is also displayed. Intended size of reproduction.

efficiency of biotic and abiotic surrogates for species representation in eight terrestrial datasets, including animals and plants. They reported that Zonation provided efficient solutions to represent species in a minimal number of sites in all cases. Its success in prioritising species might be related to how Zonation selects core areas for all species and its heuristic algorithm and process of iteratively removing the least valuable cells and keeping the most important ones until the end (Moilanen et al. 2005).

Another powerful approach was RWR as an efficient surrogate of amphibians in the drylands southwest of the United States and Mexico (Figure 2). The efficiency of RWR as a surrogate for species representation has been assessed in previous studies in terrestrial (e.g., Albuquerque and Beier 2015a, 2015b; Albuquerque and Gregory 2017) and marine realms (Astudillo-Scalia and de Albuquerque 2019). They reported that RWR outperformed richness because the latter seeks to prioritise sites with the highest number of species (greedy algorithm). At the same time, RWR selects sites with a higher number of rare species and species composition (non-greedy algorithm). These studies also reported that RWR can be an efficient surrogate for biodiversity when optimising conservation efficiency and offers alternative solutions to Zonation.

According to our SAI results, identifying HPCA through richness was less efficient at representing amphibians. Our results show that richness performed worse than Zonation, RWR and random solutions at selecting species (Figure 2). Our results are in tandem with previous studies that richness is not a viable metric to predict or identify areas for conservation (e.g., Albuquerque and Beier 2015b; Astudillo-Scalia and Albuquerque 2020). The poor performance of richness could be explained by the homogeneity of the species assemblage in areas with high species richness, meaning areas with high species richness have greater numbers of overlapping species with other sites. Richness is a historic statistic for conservation planning. Still, its simplicity results in the spatial overlap that can cause an under-representation of species compared to Zonation and other rarity index approaches (Astudillo-Scalia and Albuquerque 2020).

### 4.2 | Biogeography

The spatial configuration of HPCA for amphibians displayed 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. The spatial configuration of HPCA might be related to environmental constraints to amphibian distribution, since our results indicate that climate conditions, especially water availability, are the primary drivers of the spatial configuration of HPCA in this study. Our results provide support for the tenet that environmental variables, and climate in particular, strongly influence the priority rank values and spatial configuration of HPCA in terrestrial (Albuquerque and Beier 2015a; Albuquerque et al. 2019) and marine (Astudillo-Scalia and Albuquerque 2020) realms. The relevance of water-related variables to explain the spatial distribution of HPCA in amphibians could be related to their life history in several ways. For example, precipitation is linked to the changes in amphibians' timing of cyclical events (phenology). Dalpasso et al. (2023) investigated the impact of precipitation change on the phenology of *Pelobates fuscus* (Common Spadefoot toad), and they reported that precipitation and temperature changes may affect *P. fuscus* migration patterns towards an earlier start of the breeding migrations. Rainfall patterns also affect amphibians' seasonal activity through toads' emergence from underground (Márquez et al. 2016).

Water is vital to amphibian life history due to their semi-permeable skin, which lacks structures to prevent water loss (Thorson 1955). It is also essential for amphibians that perform cutaneous (skin) respiration (Wake and Vredenburg 2008). Desiccation threatens amphibians living in drylands, especially those 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). 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 harbour unique habitats that contain rich pockets of biodiversity (Gudka et al. 2014) that dryland amphibians can exploit.

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. As ectotherms, they are susceptible to temperature changes, both high and low, in their environment (Huey 1982). Body temperature influences amphibian metabolic rates and activity (Buckley et al. 2012).

### 4.3 | Potential Impacts of Climate Change

Our results identified changes in the HPCA spatial configuration from the current model to the future model under simulated climate change, which indicates that climate change may influence overall amphibian habitat suitability. Any change in habitat suitability is critical for dryland amphibian conservation due to the lack of currently available habitat suitability that the taxa face in arid environments (Dayton and Fitzgerald 2006). Despite the potential changes in the spatial configuration of HPCA, results show substantial overlap between the current and the predictive future HPCA, displayed as areas of no change in Figure 5. Depending on the climate change scenario, the overlap varied from 77% (SSP 585) to 82% (SSP 126), showing that the overlap decreased with more pessimistic scenarios. This overlap between the current and future scenarios is important because it displays suitable habitats for dryland amphibians that will remain after simulated climate change (Refugia areas). The mismatch between the current and future spatial configuration of HPCA indicates that conservation plans should consider climate change.

Spatial analysis tools have allowed scientists to predict how climate change will impact habitat suitability and how it will impact species distributions. However, climate change may also cause previously PAs to no longer efficiently protect species as a changing climate drives species' distribution to alter from their historical ranges (Albuquerque, Bateman, et al. 2024; Albuquerque, Bateman, Ryan, et al. 2024). Conventional conservation practices do not always account for changes in habitat 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). This study provides evidence that climate should be regarded as a potential indicator for future amphibian conservation projects in the drylands of North America.

### 4.4 | Implications for Conservation

Identifying HPCA for amphibians can help managers and conservationists fill gaps in amphibian conservation and propose strategies for reinforcing conservation plans in PAs (Albuquerque and Beier 2015a). The spatial configurations of HPCA are important because they can act as a broad-scale framework for conservation managers to identify the most important areas to begin finer-scale conservation attempts.

Despite the impacts of climate change, the proposed HPCA framework predicted no significant changes in the habitat suitability of the two continuous corridors highlighted at the current time (Figures 3 and 5). These corridors could act as refugia for dryland amphibian species and offer connectivity amongst suitable habitats. Interestingly, the models also show potential areas of gain of habitat suitability that are well connected to the current corridor. The integration of future gain areas into core portions of unaffected corridors (Figure 5) could allow for the migration of at-risk amphibian populations to more suitable habitats.

Another significant finding of our study is the low representation of HPCA by PAs, since only 11.6% of HPCA are represented by the PA network. These results show that much is still needed to protect and manage at least 30% of the Earth's land (CBD 2022). Similar to the discoveries by Lindenmayer (2024) and Dinerstein et al. (2024), we demonstrate that PAs are inadequate in representing biodiversity. In our case, results may represent a significant loss in the fight against amphibian decline. This mismatch may indicate that the establishment of PAs in the drylands of North America does not account for HPCA for amphibians. Our results can help managers and conservationists identify sets of complementary priority areas to expand the current PA network, provide adequate representativeness of amphibians and conserve their habitat.

We understand that identifying PAs is not the only step to halt biodiversity loss (Lindenmayer 2024). By identifying the minimum number of sites collectively representing most or all amphibians, our results can help managers and conservationists minimise the cost of expanding PA to conserve at least 30% of amphibians' HPCA.

### 4.5 | Limitations of the Study

Since knowledge of amphibian occurrence distribution is still incomplete, our models used coarse occurrence data, expressed by range maps, for most amphibian species within our study area. Because range maps may lead to an overestimation of species protection level when planning PAs (Di Marco et al. 2016), we acknowledge that the spatial resolution of our analysis can mask our PA results. The low overlap between HPCA and PA can also be influenced by our study's spatial extent and resolution, since PA networks are not necessarily designed at the same scale at which HPCA was proposed.

Our approach also did not account for important factors for spatial conservation prioritisation, such as disturbance, landscape connectivity, and biotic interactions (Lannoo 2005; Moilanen et al. 2009). Although these models are not designed to be tools for local conservation efforts due to the scale, they represent a valid approach to understanding how suitable habitats can change under future climate scenarios over a broad extent, especially when the study area extends to multiple countries. Effective conservation plans are created at local and regional levels, requiring stakeholders and government bodies to enact pertinent policies (Fleishman and Brown 2019). Our study aims not to replace local conservation efforts but to support them. Further research is needed at the local level for effective conservation policy to be enacted (Epele et al. 2021).

It is important to highlight that climate change is not the sole threat to amphibians. Factors like chemical pollution, invasive species, and disease have been linked to amphibian decline and extinctions and, therefore, play a key role in shaping the proposed refuge areas (Figures 4 and 5). For example, Chytridiomycosis, a disease caused by an aquatic fungus (*Batrachochytrium dendrobatidis*), has devastated amphibian populations around the globe, including North America (Cheng et al. 2011). In this sense, when the information is available, these factors should be incorporated into the HPCA process to reach a more precise prioritisation analysis.

### 4.6 | Conclusion

In contrast to Zonation and RWR solutions, which performed considerably better than random solutions, richness was the worst-performing method for selecting amphibians. 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. Our results demonstrate that environmental variables strongly influence the spatial configurations of amphibian HPCA. Water and energy variables, specifically precipitation, solar radiation, and temperature, proved to be the most influential variables in determining these spatial configurations. Our results display changes in the HPCA distribution due to climate change. Finally, we show that the proposed HPCA of amphibians in the drylands of North America is far from achieving the 30% protection target established by the CBD. It is important to highlight that we used coarse data to assess the impact of climate on HPCA and that conservation actions are mostly applied at a local scale. Despite its limitations, it is imperative to understand its novelty and utility. It is the first to offer a conservation tool for amphibian conservation in the drylands of the Southwest United States and Northern Mexico.

## Author Contributions

Fábio Suzart de Albuquerque and Jared E. Johnson conceived and designed the research, conducted the data analyses, produced the figures and wrote the manuscript. Heather L. Bateman and Adam Stein helped with editing and writing the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data that support the findings of this study are available in International Union for the Conservation of Nature, at https://www.iucn.org. These data were derived from the following resources available in the public domain: IUCN, https://www.iucnredlist.org.

## References

Albuquerque, F., Y. Astudillo-Scalia, R. Loyola, and P. Beier. 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., and P. Beier. 2015a. "Global Patterns and Environmental Correlates of High-Priority Conservation Areas for Vertebrates." *Journal of Biogeography* 42, no. 8: 1397–1405. https://doi.org/10.1111/jbi.12498.

Albuquerque, F., and P. Beier. 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, no. 3: e0119905.

Albuquerque, F. S., H. Bateman, and J. Johnson. 2024. "Amphibians at Risk: Effects of Climate Change in the Southwestern North American Drylands." *Global Ecology and Conservation* 51: e02944. https://doi.org/10.1016/j.gecco.2024.e02944.

Albuquerque, F. S., H. L. Bateman, M. J. Ryan, and B. Montgomery. 2024. "Model Transferability and Predicted Response of a Dryland Anuran to Climate Change in the Southwest United States." *Journal of Biogeography* 51: 120–130.

Albuquerque, F. S., and A. Gregory. 2017. "The Geography of Hotspots of Rarity Weighted Richness of Birds and Their Coverage by Natura 2000." *PLoS One* 12, no. 4: e0174179. https://doi.org/10.1371/journal.pone.0174179.

Amatulli, G., S. Domisch, M.-N. Tuanmu, et al. 2018. "A Suite of Global, Cross-Scale Topographic Variables for Environmental and Biodiversity Modeling." *Scientific Data* 5: 180040. https://doi.org/10.1038/sdata.2018.40.

AmphibiaWeb. 2023. "AmphibiaWeb." University of California. Accessed April 19, 2023. https://amphibiaweb.org.

Araújo, M. B. 2009. "Climate Change and Spatial Conservation Planning." In *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools*, edited by A. Moilanen, K. A. Wilson, and H. P. Possingham. Oxford University Press.

Assunção-Albuquerque, M. J. T., J. M. Rey-Benayas, M. A. Rodríguez, and F. S. Albuquerque. 2012. "The Geography of High-Value Biodiversity Areas for Terrestrial Vertebrates in Western Europe and Their Coverage by Protected Area Networks." *Web Ecology* 12: 65–73.

Astudillo-Scalia, Y., and F. Albuquerque. 2020. "Why Should We Reconsider Using Species Richness in Spatial Conservation Prioritization?" *Biodiversity and Conservation* 29: 2055–2067.

Astudillo-Scalia, Y., and F. S. de Albuquerque. 2019. "Evaluating the Performance of Rarity as a Surrogate in Site Prioritization for Biodiversity Conservation." *Global Ecology and Conservation* 18: e00639.

Bateman, H. L., M. A. Huck, H. Klingel, and D. M. Merritt. 2024. "Cue the Chorus: Canyon Treefrog Calling Phenology on the Falling Limb of Spring Floods and Warming Nights." *Ecology* 105, no. 4: e4287.

Beebee, T. J., and R. A. Griffiths. 2005. "The Amphibian Decline Crisis: A Watershed for Conservation Biology?" *Biological Conservation* 125, no. 3: 271–285.

Beier, P., and F. Albuquerque. 2016. "Evaluating β Diversity as a Surrogate for Species Representation at Fine Scale." *PLoS One* 11, no. 3: e0151048. https://doi.org/10.1371/journal.pone.0151048.

Beier, P., and F. S. Albuquerque. 2015. "Environmental Diversity is a Reliable Surrogate for Species Representation." *Conservation Biology* 29: 1401–1410. https://doi.org/10.1111/cobi.12495.

Blaustein, A. R., and J. M. Kiesecker. 2002. "Complexity in Conservation: Lessons From the Global Decline of Amphibian Populations." *Ecology Letters* 5, no. 4: 597–608.

Breiman, L. 2001. "Random Forests." *Machine Learning* 45: 5–32.

Buckley, L. B., A. H. Hurlbert, and W. Jetz. 2012. "Broad-Scale Ecological Implications of Ectothermy and Endothermy in Changing Environments." *Global Ecology and Biogeography* 21, no. 9: 873–885.

CBD. 2022. "Nations Adopt Four Goals, 23 Targets for 2030 in Landmark UN Biodiversity Agreement." Accessed April 2023. https://www.cbd.int/article/cop15-cbd-press-release-final-19dec2022.

Cheng, T. L., S. M. Rovito, D. B. Wake, and V. T. Vredenburg. 2011. "Coincident Mass Extirpation of Neotropical Amphibians With the Emergence of the Infectious Fungal Pathogen *Batrachochytrium dendrobatidis*." *Proceedings of the National Academy of Sciences of the United States of America* 108: 9502–9507. https://doi.org/10.1073/pnas.1105538108.

Chicco, D., M. J. Warrens, and G. Jurman. 2021. "The Coefficient of Determination R-Squared is More Informative Than SMAPE, MAE, MAPE, MSE and RMSE in Regression Analysis Evaluation." *PeerJ Computer Science* 7: e623. https://doi.org/10.7717/peerj-cs.623.

Church, R. L., D. M. Stoms, and F. W. Davis. 1996. "Reserve Selection as a Maximal Covering Location Problem." *Biological Conservation* 76, no. 2: 105–112.

Cushman, S. A. 2006. "Effects of Habitat Loss and Fragmentation on Amphibians: A Review and Prospectus." *Biological Conservation* 128, no. 2: 231–240.

Dalpasso, A., D. Seglie, P. Eusebio Bergò, et al. 2023. "Effects of Temperature and Precipitation Changes on Shifts in Breeding Phenology of an Endangered Toad." *Scientific Reports* 13: 14573. https://doi.org/10.1038/s41598-023-40568-w.

Dayton, G. H., and L. A. Fitzgerald. 2006. "Habitat Suitability Models for Desert Amphibians." *Biological Conservation* 132, no. 1: 40–49.

Dinerstein, E., A. R. Joshi, N. R. Hahn, et al. 2024. "Conservation Imperatives: Securing the Last Unprotected Terrestrial Sites Harboring Irreplaceable Biodiversity." *Frontiers in Science* 2: 1349350. https://doi.org/10.3389/fsci.2024.1349350.

Di Marco, M., S. H. Butchart, P. Visconti, G. M. Buchanan, G. F. Ficetola, and C. Rondinini. 2016. "Synergies and Trade-Offs in Achieving Global Biodiversity Targets." *Conservation Biology* 30, no. 1: 189–195.

Epele, L. B., M. G. Grech, L. M. Manzo, et al. 2021. "Identifying High Priority Conservation Areas for Patagonian Wetlands Biodiversity." *Biodiversity and Conservation* 30: 1359–1374.

Ficetola, G. F., C. Rondinini, A. Bonardi, V. Katariya, E. Padoa-Schioppa, and A. Angulo. 2014. "An Evaluation of the Robustness of Global Amphibian Range Maps." *Journal of Biogeography* 41, no. 2: 211–221.

Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37, no. 12: 4302–4315.

Fleishman, E., and H. Brown. 2019. "Use of Macroecology to Integrate Social Justice and Conservation." *Global Ecology and Biogeography* 28, no. 10: 1512–1518.

Griffis-Kyle, K. L., K. Mougey, M. Vanlandeghem, S. Swain, and J. C. Drake. 2018. "Comparison of Climate Vulnerability Among Desert Herpetofauna." *Biological Conservation* 225: 164–175.

Gudka, M., J. Davies, L. Poulsen, et al. 2014. "Conserving Dryland Biodiversity: A Future Vision of Sustainable Dryland Development." *Biodiversity* 15, no. 2–3: 143–147.

Hijmans, R. 2024. "_terra: Spatial Data Analysis_. R Package Version 1," 7–83. https://CRAN.R-project.org/package=terra.

Huey, R. B. 1982. "Temperature, Physiology, and the Ecology of Reptiles." In *Biology of the Reptilia, Physiology C: Physiological Ecology*, edited by C. Gans and F. H. Pough, vol. 12, 25–91. Academic Press.

Hughes, M. K., and H. F. Diaz. 2008. "Climate Variability and Change in the Drylands of Western North America." *Global and Planetary Change* 64, no. 3–4: 111–118.

IUCN. 2018. "Mapping Standards and Data Quality for the IUCN Red List Categories and Criteria. Version 1.16. Mapping_Standards_Version_1.16_2018." Accessed April 18, 2025.

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

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*. University of California Press.

Le Saout, S., M. Hoffmann, Y. Shi, et al. 2013. "Protected Areas and Effective Biodiversity Conservation." *Science* 342: 803–805. https://doi.org/10.1126/science.1239268.

Liaw, A., and M. Wiener. 2002. "Classification and Regression by randomForest." *R News* 2, no. 3:18–22. https://CRAN.R-project.org/doc/Rnews/.

Lindenmayer, D. 2024. "Key Steps Toward Expanding Protected Areas to Conserve Global Biodiversity." *Frontiers in Science* 2: 1426480. https://doi.org/10.3389/fsci.2024.1426480.

Lomolino, M. V. 2004. "Conservation Biogeography." In *Frontiers of Biogeography: New Directions in the Geography of Nature*, edited by M. V. Lomolino and L. R. Heaney, 293–296. Sinauer Associates.

Luedtke, J. A., J. Chanson, K. Neam, et al. 2023. "Ongoing Declines for the World's Amphibians in the Face of Emerging Threats." *Nature* 622, no. 7982: 308–314.

Márquez, R., J. F. Beltrán, D. Llusia, M. Penna, and P. M. Narins. 2016. "Synthetic Rainfall Vibrations Evoke Toad Emergence." *Current Biology* 26, no. 24: R1270–R1271. https://doi.org/10.1016/j.cub.2016.11.005.

Marthews, T. R., S. J. Dadso, B. Lehner, S. Abele, and N. Gedney. 2015. "High Resolution Global Topographic Index Values for Use in Large-Scale Hydrological Modelling." *Hydrology and Earth System Sciences* 19: 91–104. https://doi.org/10.5194/hess-19-91-2015.

Marthews, T. R., S. J. Dadson, B. Lehner, S. Abele, and N. Gedney. 2015. *High Resolution Global Topographic Index Values*. NERC Environmental Information Data Centre. https://doi.org/10.5285/6b0c4358-2bf3-4924-aa8f-793d468b92be.

Moilanen, A. 2007. "Landscape Zonation, Benefit Functions and Target-Based Planning: Unifying Reserve Selection Strategies." *Biological Conservation* 134, no. 4: 571–579.

Moilanen, A., A. M. A. Franco, R. Early, R. Fox, B. Wintle, and C. D. Thomas. 2005. "Prioritizing Multiple-Use Landscapes for Conservation: Methods for Large Multi-Species Planning Problems." *Proceedings of the Royal Society B: Biological Sciences* 272: 1885–1891.

Moilanen, A., P. Lehtinen, I. Kohonen, E. Virtanen, J. Jalkanen, and H. Kujala. 2022. "Novel Methods for Spatial Prioritization With Applications in Conservation, Land Use Planning and Ecological Impact Avoidance." *Methods in Ecology and Evolution*, Early View. https://doi.org/10.1111/2041-210X.13819.

Moilanen, A., K. A. Wilson, and H. P. Possingham, eds. 2009. *Spatial Conservation Prioritization*. Oxford University Press.

O'Neill, B. C., E. Kriegler, K. Riahi, et al. 2014. "A New Scenario Framework for Climate Change Research: The Concept of Shared Socioeconomic Pathways." *Climatic Change* 122: 387–400.

Pounds, J. A. 2001. "Climate and Amphibian Declines." *Nature* 410, no. 6829: 639–640.

Prasad, A. M., L. R. Iverson, and A. Liaw. 2006. "Newer Classification and Regression Tree Techniques: Bagging and Random Forests for Ecological Prediction." *Ecosystems* 9: 181–199.

R Core Team. 2023. "R: A Language and Environment for Statistical Computing." R Foundation for Statistical Computing. https://www.R-project.org/.

Railsback, S. F., B. C. Harvey, S. J. Kupferberg, M. M. Lang, S. McBain, and H. H. Welsh Jr. 2016. "Modeling Potential River Management Conflicts Between Frogs and Salmonids." *Canadian Journal of Fisheries and Aquatic Sciences* 73, no. 5: 773–784.

Rodrigues, A. S., and T. M. Brooks. 2007. "Shortcuts for Biodiversity Conservation Planning: The Effectiveness of Surrogates." *Annual Review of Ecology, Evolution, and Systematics* 38: 713–737.

Safriel, U., Z. Adeel, D. Niemeijer, et al. 2005. "Dryland Systems." In *Ecosystems and Humanwell-Being: Current State and Trends*, 623–662. Island Press.

Seager, R., M. Ting, I. Held, et al. 2007. "Model Projections of an Imminent Transition to a More Arid Climate in Southwestern North America." *Science* 316, no. 5828: 1181–1184.

Shoemaker, V. H. 1988. "Physiological Ecology of Amphibians in Arid Environments." *Journal of Arid Environments* 14, no. 2: 145–153.

Steigerwald, E. 2021. *"Impacts of Climate Change on Amphibians" AmphibiaWeb*. University of California. Accessed November 23, 2024. https://amphibiaweb.org/declines/climatechange.html.

Stuart, S. N., J. S. Chanson, N. A. Cox, et al. 2004. "Status and Trends of Amphibian Declines and Extinctions Worldwide." *Science* 306, no. 5702: 1783–1786.

Thorson, T. B. 1955. "The Relationship of Water Economy to Terrestrialism in Amphibians." *Ecology* 36, no. 1: 100–116.

Tockner, K., I. Klaus, C. Baumgartner, and J. V. Ward. 2006. "Amphibian Diversity and Nestedness in a Dynamic Floodplain River (Tagliamento, NE-Italy)." *Hydrobiologia* 565: 121–133.

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)*. UNEP-WCMC.

UNEP-WCMC. 2019. *User Manual for the World Database on Protected Areas and World Database on Other Effective Area-Based Conservation Measures 1.6*. UNEPWCMC.

UNEP-WCMC and IUCN. 2024. *Protected Planet: The World Database on Protected Areas (WDPA)/Database on Other Effective Area-Based Conservation Measures*. UNEP-WCMC and IUCN. www.protectedplanet.net.

Wake, D. B., and V. T. Vredenburg. 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, no. supplement_1: 11466–11473.

Watson, J. E. M., H. S. Grantham, K. A. Wilson, and H. P. Possingham. 2011. "Systematic Conservation Planning: Past, Present and Future." In *Conservation Biogeography*, edited by R. J. Ladle and R. J. Whittaker, 301. Willey-Blackwell.

Williams, P., D. Faith, L. Manne, W. Sechrest, and C. Preston. 2006. "Complementarity Analysis: Mapping the Performance of Surrogates for Biodiversity." *Biological Conservation* 128, no. 2: 253–264.

Williams, P., D. Gibbons, C. Margules, A. Rebelo, C. Humphries, and R. Pressey. 1996. "A Comparison of Richness Hotspots, Rarity Hotspots, and Complementary Areas for Conserving Diversity of British Birds." *Conservation Biology* 10, no. 1: 155–174. https://doi.org/10.1046/j.1523-1739.1996.10010155.x.

Worldclim. n.d. "Future Climate Data." Accessed July 2022. https://www.worldclim.org/data/cmip6/cmip6climate.html.

## Supporting Information

Additional supporting information can be found online in the Supporting Information section.