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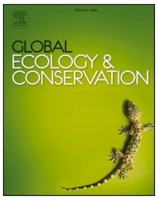

Amphibians at risk: Effects of climate change in the southwestern North American drylands

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ABSTRACT

Climate change can affect species' geographical range in several ways, leading to species' geographical range expansion and contraction. Amphibians are the most threatened vertebrate class, and deterioration is due, in part, to the loss of suitable habitat. This taxonomic group is especially sensitive because of their biphasic life cycles (aquatic and terrestrial) and microhabitat requirements. Herein, we propose a combined approach, which uses biological and life history information to understand species' sensitivity to climate change. The goals of our study were to (1) identify the contribution of environmental variables to the broad-scale distribution of amphibians in drylands of the southwestern United States and Mexico, (2) describe how the habitat suitability of amphibians can potentially respond to a range of climate change scenarios across drylands, and (3) identify amphibian traits related to increased vulnerability and adaptation to the specific pressures and mechanisms of climate change projected for the dryland areas. Results show that climate strongly influences the geographic distribution of amphibian diversity in drylands and that most amphibians are expected to lose habitat in the upcoming decades. This study also shows that areas with the greatest loss of high habitat suitability are related to temperature increases and precipitation reductions. Our results build a framework that will significantly improve the current state of knowledge on the drylands' biogeography while providing comprehensive information and analyses for decision-makers to conserve and protect endangered and threatened amphibian species and their habitats.

1. Introduction

Drylands are characterized by water scarcity and are formally defined by the ratio between average annual precipitation and potential evapotranspiration (Safriel et al., 2005; Prăvălie, 2016). These arid ecosystems encompass extraordinary endemism into four major systems: hyper-arid, arid, semiarid, and dry subhumid (Safriel et al., 2005). Drylands comprise several fragile environments that are becoming highly vulnerable to climate change, mainly because of the change in water availability, such as megadrought events (Cook et al., 2015). This climate vulnerability is even more pronounced in southwestern North America (Williams et al., 2022). Changes in water availability pose a significant threat to aquatic and terrestrial biodiversity, particularly to amphibians (Walls et al., 2013), one of the most endangered taxa on Earth (Stuart et al., 2004, D'Amen and Bombi 2009, Luedtke et al., 2023).

A significant question in biological conservation is understanding how dryland vulnerability to climate change may affect

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amphibians' distribution in the future. Previous dryland studies have reported that climate change is expected to cause significant species range shifts (SDNIMP, 2010, Albuquerque et al., 2018, and 2019, Yanahan and Moore, 2019). However, the evaluation of the influence of climate change on dryland species distribution has focused on plant species (e.g., SDNIMP, 2010, USDA, 2018, Albuquerque et al., 2018, and Albuquerque et al., 2019, Yanahan and Moore, 2019). In contrast, analyses involving amphibians have been conducted mostly for endemic species, such as *Anaxyrus microscaphus* - an endemic anuran of the North American drylands (Albuquerque et al., 2023). Griffis-Kyle et al. (2018) used NatureServe's climate change vulnerability tool to evaluate the vulnerability of seven amphibians in the southwest United States to climate change. However, no evaluation of the effect of climate change has been made on the overall distribution of amphibian species for drylands in the southwestern United States and northern Mexico. This evaluation is fundamental for understanding the geographic distribution of amphibian diversity and predicting how amphibian distribution may shift as a response to future climate alterations.

Over the last decades, studies have reported a significant decline in the abundance and extinction of amphibians globally (e.g., Pounds, 2001, Stuart et al., 2004, Luedtke et al., 2023). These are mainly associated with the spread of diseases and loss of suitable habitat (Luedtke et al., 2023), as well as heavy animal extraction and enigmatic decline (unknown explicit reasons) (Stuart et al., 2004). In general, habitat loss has significant adverse effects on biodiversity, including population decline, reduction of genetic diversity, breeding, dispersal, and species extinctions (Fahrigh, 1993, Luedtke et al., 2023).

Often linked to climate change, loss of suitable habitat is one of the greatest threats to amphibians (Cushman, 2006, Albuquerque et al., 2023, Luedtke et al., 2023), mainly because of their biphasic life cycles (aquatic and terrestrial) and microhabitat requirements (Bateman and Merritt, 2020). Thus, understanding the impact of climate change on amphibians' suitable habitat will significantly improve the knowledge of the drylands' biogeography while providing comprehensive information and analyses for decision-makers to conserve and protect endangered and threatened amphibian species and their habitats.

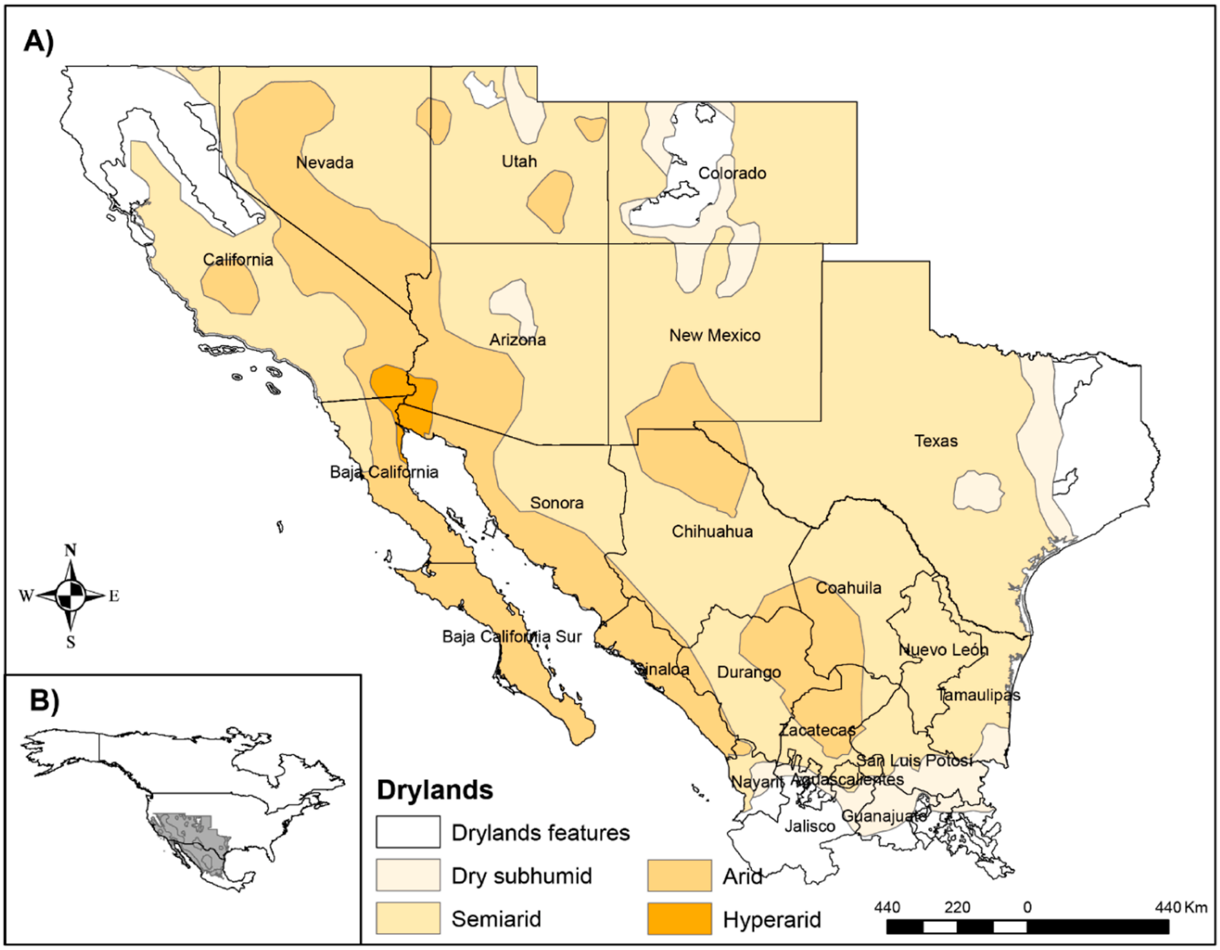

Fig. 1. Geographical distribution of the drylands in the southwest of the United States and northern Mexico according to the United Nations Convention to Combat Desertification (UNCCD) and Convention on Biological Conservation (UNEP-WCMC, 2007). Drylands are classified according to the United Nations Environment Program (UNEP) terminology: dry subhumid, semiarid, arid, and hyper-arid. The classification is based on a level of aridity or moisture deficit. The map also includes presumed drylands (white) - drylands features with the ratio of precipitation and potential evapotranspiration greater than 0.65 (the threshold used to identify drylands).

The influence of climate change on amphibians has been largely debated in the last two decades, and their effects are still controversial. Pounds (2001) proposed that pathogens and climate change are pivotal factors in population declines. Blaustein et al. (2002) investigated the effect of global warming on North American toads' breeding phenology, and their results were inconclusive. Carey and Alexander (2003) revised several studies on the impact of climate change on amphibians, and they concluded that no compelling evidence existed of the detrimental effects of climate change at the time of their publication. Years later, D′Amen and Bombi (2009) provided evidence that climate change significantly contributed to the disappearance of species in Italy. They reported that solar irradiation, associated with other stressors, was related to amphibians' decline. Griffis-Kyle et al. (2018) determined that the most vulnerable amphibians in the southwest United States were habitat specialists and species dependent on water. In other studies, population trends in temperate amphibians from North America and Europe have displayed mixed responses to climate as the specific driver of change (Muths et al., 2017). Because the response to climate change is heterogeneous, more information is needed to assess species' vulnerabilities.

Herein, we investigate the influence of climate on the overall amphibian species distribution across North American drylands. The ability of climate to explain species diversity patterns, especially richness, has been explored in previous studies. For example, Hawkins et al. (2003) investigated the impact of climate on vertebrates' distribution in different parts of the globe, including amphibians, and they concluded that energy alone, or in conjunction with water, is linked to broad-scale variation in richness. The energy hypothesis claims that large-scale patterns of species diversity will be better described by ambient energy inputs, such as temperature (Wright, 1983). The water-energy hypothesis, originally proposed to explain plant diversity (O'Brien, 1993), also applies to animals (Hawkins et al., 2003), especially amphibians – animals that often require water to complete their life cycle. Although these hypotheses were widely used to explain richness patterns, their application over amphibian species distribution is more of a limited knowledge.

We used a combined approach to assess climate change vulnerability. This approach includes species distribution models (SDMs) and a trait-based analysis (TBA). SDMs are widely used to determine the geographical distribution of poorly unknown terrestrial and aquatic species and quantify climate change's effect on species' distribution ranges (Parmesan et al., 2006). TBA uses the range of biological and life history information (e.g., habitat) to understand species' exposure and sensitivity to climate change (Hulme and Bernard-Verdier, 2017, Foden et al., 2019). TBA is often used in ecological risk assessment, bioassessment, or biomonitoring of species and ecosystems (Hulme and Bernard-Verdier, 2017). The goals of our study were to (1) identify the contribution of environmental variables to the broad-scale distribution of amphibians in drylands, (2) describe how the habitat suitability of amphibians can potentially respond to a range of climate change scenarios across drylands of the southwest of the United States and Mexico, (3) map areas of high loss of habitat suitability, (4) identify amphibian traits related to increased vulnerability and adaptation to the specific pressures and mechanisms of climate change projected for the dryland areas.

2. Material and methods

2.1. Study area

The study area extends from the southwestern United States and northern Mexico (Fig. 1). Its representation was extracted from the World Drylands Areas UNEP-WCMC (2007), which was used to delineate relevant areas for the World Atlas of Desertification. The arid zones were identified through an aridity index (AI) calculated from the precipitation and potential evapotranspiration ratio. The World Atlas of Desertification defined drylands as zones with an AI value of less or equal to 0.65 (Middleton and Thomas, 1997; Prăvălie, 2016). Drylands adapt well to irregular rainfall patterns and extreme temperatures and provide multiple ecosystems and cultural services (e.g., nutrient cycling, pollination and seed dispersal, and primary production - Safriel et al., 2005). Although drylands are highly impacted by land degradation and climate change, only 8% of its global area is protected (Safriel et al., 2005). This amount is far from the 30% target proposed by the Convention on Biological Diversity (CBD) announced by 2030 (CBD, 2022).

2.2. Data preparation

2.2.1. Species data

We downloaded amphibian range maps from the IUCN (International Union for Conservation of Nature) Red List of Threatened Species (IUCN, 2022). We then overlapped the species' range to the dryland map (UNEP-WCMC, 2007) to identify the species with ranges intersecting with drylands. For each species, we calculated the percent of its range intersecting drylands (percent of dryland range). Then, we grouped species into two categories. One was based on their distribution across ecoregions and the other was based on the percent of dryland range. We classified species into three groups for the former: multi-ecoregion species had range maps intersecting drylands and other ecoregions. The second and third groups were dryland specialists and rare species (with their entire range within drylands). We classified rare species as those in the 25th percentile of dryland specialists' species with the smallest range across drylands (Gaston, 1994). For the second category, we defined two groups based on the quantiles of species' range. We classified those species at the 25th percentile as narrow-range and species with a range greater than the 25th percentile as wide-range. For example, it was possible for one species to be categorized as both in the multi-ecoregion group and in a narrow-range group (also found outside of drylands but within drylands has a small range). Similarly, other species could be in the multi-ecoregion and wide-range groups (also found outside of drylands but wide-spread across drylands).

2.2.2. Environmental data

We included a set of environmental variables grouped into four categories: (1) Energy and water-related variables: we used climate variables for the present time and future climatic projections from WorldClim (Hijmans et al., 2005, Fick and Hijmans 2017). This dataset provides *ca* 5 km x 5 km spatial resolution maps for 19 variables, representing measures of temperature and precipitation, including annual and seasonal means, extremes, and ranges. Further details about the calculation and description of bioclimatic variables are available at Hijmans et al. (2005); (2) Topography: We extracted the median and standard deviation of roughness, topographic position index, and the terrain ruggedness index(TRI) from the Global, remote-sensing supported environmental layers for assessing status and trends in biodiversity, ecosystems, and climate (EearthEnv- Amatulli et al., 2018); (3) Solar radiation: We obtained solar radiation values from the Worldclim database (Fick and Hijmans 20017); (4) Future climate projections - We acquired the future climatic projections from the Worldclim database (WorldClim, 2022). The data represent the Coupled Model Intercomparison Project Phase 6 (CMIP6) downscaled future projections. We included one period (2081–2100) and four Shared Economic Pathways (SSPs): 126 (sustainability - low emission scenario), 245 and 370 (Intermediate emission scenarios), and 585 (Highly unequal - high emission scenario) (O′Neill et al., 2017). SSPs represent different greenhouse gas emission and concentration scenarios (O′Neill et al., 2017). We also used eight global climate models (GCMs, Albuquerque et al., 2023 -Table S1).

2.3. *Model prediction and evaluation*

To better understand predictors of current amphibian species' distributions and habitat suitability, we used the occurrence data, obtained from the Global Biodiversity Information Facility (GBIF, 2022), and selected environmental variables (see below) to test the following hypothesis: current climate, especially water and energy predictors, restricts the broad-scale species distribution patterns of plants (Wright, 1983; Hawkins et al., 2003). Because most species are widely distributed across North America, we modeled the species to the extent of North America. The final results, however, are constrained to the study area. We followed van Proosdij et al. (2015) and removed narrow-range with less than 14 presences and wide-range species with more than 25 records, respectively.

Because the occurrence data were collected from heterogeneous sources and different sample efforts, we used the following steps to reduce the spatial aggregation among occurrence points (cleaned occurrence data): we created a regular grid with the same resolution of environmental variables (2.5 min). Then, we randomly selected one occurrence per site (Hijmans, 2012). We also removed records with no latitude and longitude, records outside the calibration area (North America), and records with missing or incomplete values. We randomly created a set of 10.000 background points (pseudo-absences) and combined them with the cleaned occurrence data. We then divided the data into testing (20%) and training (80%). We used the training data, environmental variables, and the *training* function (SDMTune package, Vignali et al., 2020) to parametrize a general Maxent model (Phillips et al., 2004; Elith et al., 2011). Maxent provides a detailed understanding of ecological relationships between environmental predictors and species distributions and evaluates which environmental variables contribute the most to optimizing the model's predictive performance (Guisan and Zimmermann, 2000). Next, we used the *varSel* function from the SDMTune package (Vignali et al., 2020) to remove highly correlated variables. The *varSel* processes a data-driven variable selection and a jackknife test to optimize the models and estimate the best-performing model (Vignali et al., 2020). To identify the least correlated variables with the highest contributions in the model, we used Spearman's $|\text{rho}| < 0.7$ (Vignali et al., 2020, Albuquerque et al., 2023). We calibrated and predicted the models at the spatial resolution of 2.5 min (same spatial resolution of the environmental variables).

We used the cleaned occurrence data, the set of selected environmental variables from the varSel process, and Maxent (through the *training* function from the SDMtune package, Vignali et al., 2020) to estimate habitat suitability values in the current time. We used the area under the curve (AUC) and true skill statistics (TSS) to assess the model prediction accuracy. AUC and TSS values are widely used to evaluate species distribution models (Allouche et al., 2006, Merow et al., 2013). We discarded models with AUC and TSS less than 0.7 (Albuquerque et al., 2023).

We used the *varImp* function from the SDMTune package (Vignali et al., 2020) to calculate each variable contribution percentage. Then, we ranked the variables with the highest contributions for each model. We selected the three most influential variables and classified them into three groups: Top 1 (ranked as most important), Top 2 (ranked as second most important), and Top 3 (ranked as the third most important). We then calculated the frequency of each variable as Top 1, Top 2, and Top 3.

2.4. *Climate change simulations*

2.4.1. *Identifying areas of projected habitat loss*

We used the SDM for each species and eight GCMs to project the impact of the future climate environment on the spatial configuration of habitat suitability (predicted suitability) and forecast future ranges (predicted presence; Albuquerque et al., 2023). GCMs have been used extensively to address the impacts of climate change on species distribution and biodiversity (Buisson et al., 2010). We summed each species' projected presence maps (eight GCMs) and considered 100% occurrence as a predicted presence (combined projected map). We then overlayed the combined projected map to the current predicted presence map to find areas of potential loss of habitat (loss), gain, no change (potential refuge), and unsuitability. We overlaid the locations of loss to create maps of potential loss of suitable habitat.

We used the maps of potential loss of suitable habitat of the most pessimistic scenario (SSP 585) to identify the top 30% of cells with the highest projected habitat suitability loss, hereafter referred to as hotspots. Next, we estimated the current and predicted (SSP585 scenario) temperature and annual precipitation values. Future values were averaged for the eight GCMs. We then used paired Wilcoxon tests to compare current and averaged future values.

2.4.2. Effect of climate change on individual species range

We estimated the net loss for each species. Specifically, we subtracted the net number of future predicted presences (defined as the sum of no change and gain) from the number of predicted presences (current) and divided the number of current presences. We then multiplied the results by 100 (values expressed as percent). Negative percent values represent potential habitat loss, and positive values represent habitat gain. We calculated the average percent values across the four scenarios and classified species with negative percent (loss) as vulnerable to climate change (Vulnerable species). Climate change simulations were restricted to the dryland's extent.

2.4.3. Identifying factors most associated with vulnerability to climate change

We used extrinsic factors and traits to identify the characteristics associated with species with a net loss of suitable habitat. For each vulnerable species, we identified six extrinsic factors: (1) family, (2) population trend (e.g., decreasing, stable), (3) red list status (e.g., endangered, least concern, vulnerable), (4) systems (freshwater, terrestrial, both), (5) species range (narrow-range and wide-range), and (6) regionality (multi-ecoregion, specialists, and rare). Then, we calculated the mean percentage of loss of suitable habitat to produce a ranked list of extrinsic characteristics most associated with the potential loss of dryland habitat.

Based on the tenet that climate change potentially affects amphibian physiological aspects (e.g., body size, Daufresne et al., 2009) and that climate may influence some amphibians' large-scale body-size distribution (Ashton, 2002), we explored the relationship between the percent of habitat loss (species with a net loss of habitat) and body size. We obtained the traits and extrinsic factors from IUCN (2023), AmphibiaWeb (2023), and AmphiBIO (Oliveira et al., 2017).

3. Results

3.1. Evaluating the model's predictive performance

Of the 7209 worldwide amphibian species, 220 had ranges intersecting the North American drylands. From these, 217 had enough data for modeling. These included 171 (78.8%) multi-ecoregion species, 34 (15.7%) dryland specialists, and 12 (5.5%) rare species. Regarding the model evaluation, 162 (73.4%) species had AUC and TSS greater than 0.7. The median AUC and TSS values were generally high (Fig. 2). AUC values ranged from 0.87 to 1.0 (mean 0.98), while TSS ranged from 0.71 to 1.00 (mean 0.92).

3.2. Contribution of environmental variables to the broad-scale distribution of amphibians in Drylands

The species distribution models identified 31 predictors as the most influential (top) variables in the final model, i.e., the variables that contributed to the model fitness. Regarding the most significant variables (Top1), climate emerged as the most influential factor. The habitat suitability of 93 species (57.4%) was mainly influenced by 19 climate variables (Fig. 3). These include eleven energy-related variables (temperature measures), the most relevant for determining the distribution of 67 species (41.3%), and eight water-related predictors (precipitation variables). Precipitation was critical in determining habitat suitability for 26 species (28.3%).

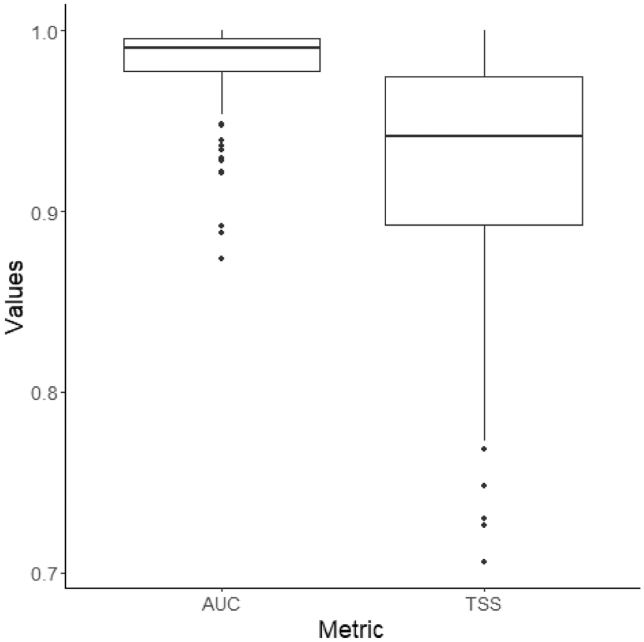

Fig. 2. Area under the curve (AUC) and true skill statistics (TSS) values for 162 species distribution models for amphibians in drylands of the southwest of the United States and Mexico.

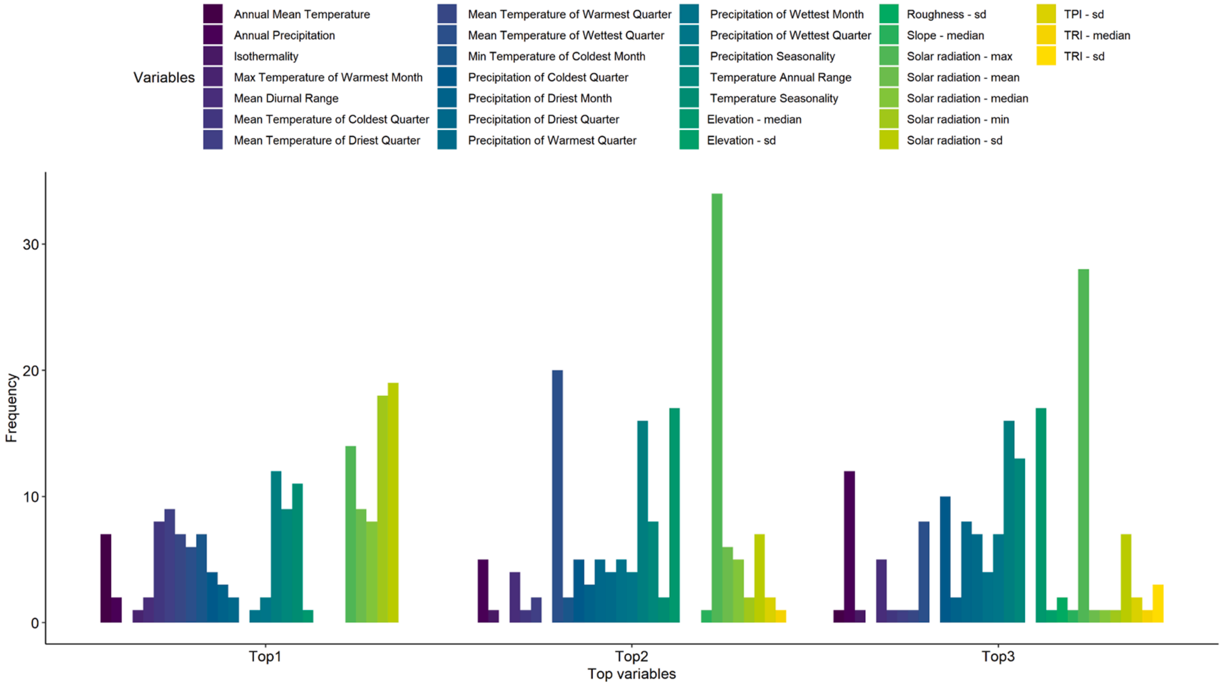

Fig. 3. Frequency of variables ranked as most important. Variables were grouped into four groups: Top 1 (ranked as most important), Top 2 (ranked as second most important), and Top 3 (ranked as the third most important). Acronyms are TPI - topographic position index, TRI- terrain ruggedness index, and SD – standard deviation.

The second and third most influential factors were solar radiation (68 species – 42%) and topography (1 species – 0.6%) (Fig. 3).

3.3. *Response to a range of climate change scenarios*

The geographical distribution of areas of projected loss of habitat suitability is illustrated in Fig. 4. The highest overall habitat loss was expected to happen in the most pessimistic scenario (SSP 585), especially in the semiarid and dry subhumid areas of the Gulf of Mexico (northwestern Mexico and southwestern Texas), eastern Texas, and southeastern Tamaulipas (Fig. 4). Secondary potential areas of high projected habitat loss were observed in arid regions of the Gulf of California (Sinaloa state) and Guanajuato.

The hotspots analysis (i.e., areas of highest projected habitat loss) for the SSP 585 scenario showed that temperature changes were more prominent than precipitation (Fig. 5). The median current and future temperatures were 19.0–24.8 °C, respectively. For precipitation, the median values were 611.6 mm (current) and 587.61 mm (future). Paired Wilcoxon analyses indicated temperature and precipitation values (current and future) differed significantly (p-value < 0.001, Fig. 5).

Most amphibians (129 species – 80%, Table S1) are projected to lose their dryland range, while 33 species (20%) are expected to gain drylands suitable habitats. Projections of loss of suitable habitat ranged from 34% (median, SSP 126 scenario) to 50% (SSP 585) (Figure S1).

3.4. *Factors associated with vulnerability to climate change*

The extrinsic factors analyses included the species negatively impacted by climate change, and results are expressed for averaged values (across the four SSPs, Table S1). Most species negatively affected by climate change and, therefore, expected to reduce their distribution range, were critically endangered (CR) species and those with increasing population trends that live in terrestrial systems and from the family Leptodactylidae (Fig. 6). Endangered and stable species are also expected to lose a significant portion of their dryland habitat (Fig. 6). Regarding the species range within drylands, multi-ecoregions and species with their entire range within the drylands (specialists) are the most affected by climate change. Terrestrial species with increasing status are the most impacted.

Regarding the relationship between projected habitat suitability loss and body weight, the correlation between potential habitat loss and body mass shows no relationship ($p = 0.8883$). Data on body mass for vulnerable species was available for 116 species (129 total).

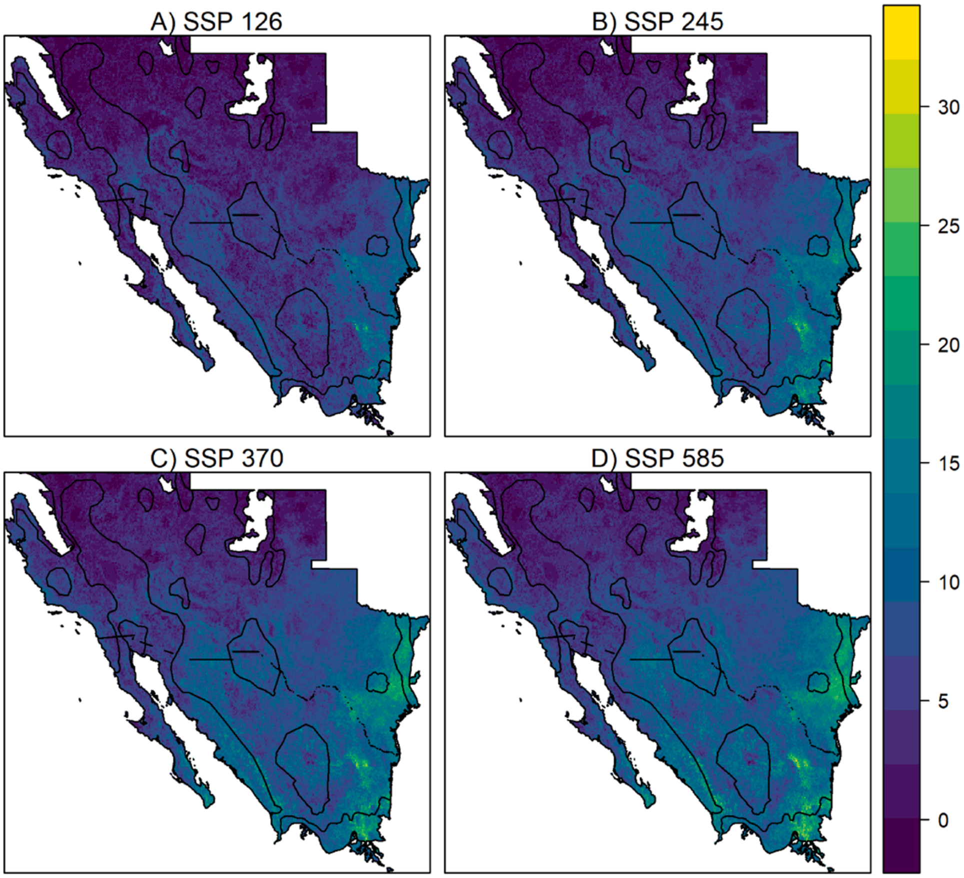

Fig. 4. Geographic distribution of projected loss of suitable habitat in drylands. Colors depict the number of cells predicted to lose their suitability across four Shared Economic Pathways (SSPs): 126 (sustainability - low emission scenario), 245 and 370 (Intermediate emission scenarios), and 585 (Highly unequal - high emission scenario).

4. Discussion

4.1. *The influence of the environment on amphibian habitat suitability*

Our results indicate that climate, represented by ambient energy and water measures, primarily influenced the broad-scale distribution of amphibians in North American drylands. The high importance of energy and water variables might be related to amphibian life history and behavioral biology, especially thermoregulation. Amphibians are ectotherms and need these sources for thermoregulatory regulation to maintain their body temperature within an optimal range and maximize their growth and development (Blaustein and Bancroft, 2007; Kearney et al., 2009). In addition to influencing habitat suitability, temperature, and rainfall can also affect amphibian's phenology of reproduction, metamorphosis, growth, and hibernation/inactive seasons (Steigerwald, 2021). Several biological aspects of amphibians depend on air or water temperature. For example, Berven (1982) reported that temperature limits growth rate and body size. Sullivan (1992) reported that the calling activity of males occurs at air temperatures of 8–18°C. Dodd (2023) suggested that egg hatching and larval development depend significantly on the stream water temperature. Bateman et al. (2024) report that calling activity is connected to spring flooding and rising temperatures. Our study also takes a step further and provides support that energy and water are significant in explaining species distribution, herein represented by habitat suitability.

Results suggest that solar radiation is the second most influential driver of amphibian distribution across the drylands of the Southwest of the United States and Mexico. Radiation was also the second most influential factor explaining the distribution and habitat suitability of *Anaxyrus microscaphus* in Arizona (USA), an endemic arid land riparian species (Albuquerque et al., 2023). They showed that the relationship between solar radiation and habitat suitability is strongly non-linear, as suitability values decreased significantly at high solar radiation values (Albuquerque et al., 2023). The importance of sunlight might be linked to physiological aspects since ectothermic species often use sunlight to help thermoregulate their internal temperature (Blaustein and Bancroft, 2007). However, our results highlight a concern since high solar radiation levels, especially ultraviolet rays (UV-B), are often linked to amphibian decline (Blaustein and Belden, 2005). Multifactorial studies show that ultraviolet rays, in combination with abiotic (e.g., temperature) and biotic (e.g., disease) factors, are likely to affect the persistence of the amphibian population, species growth,

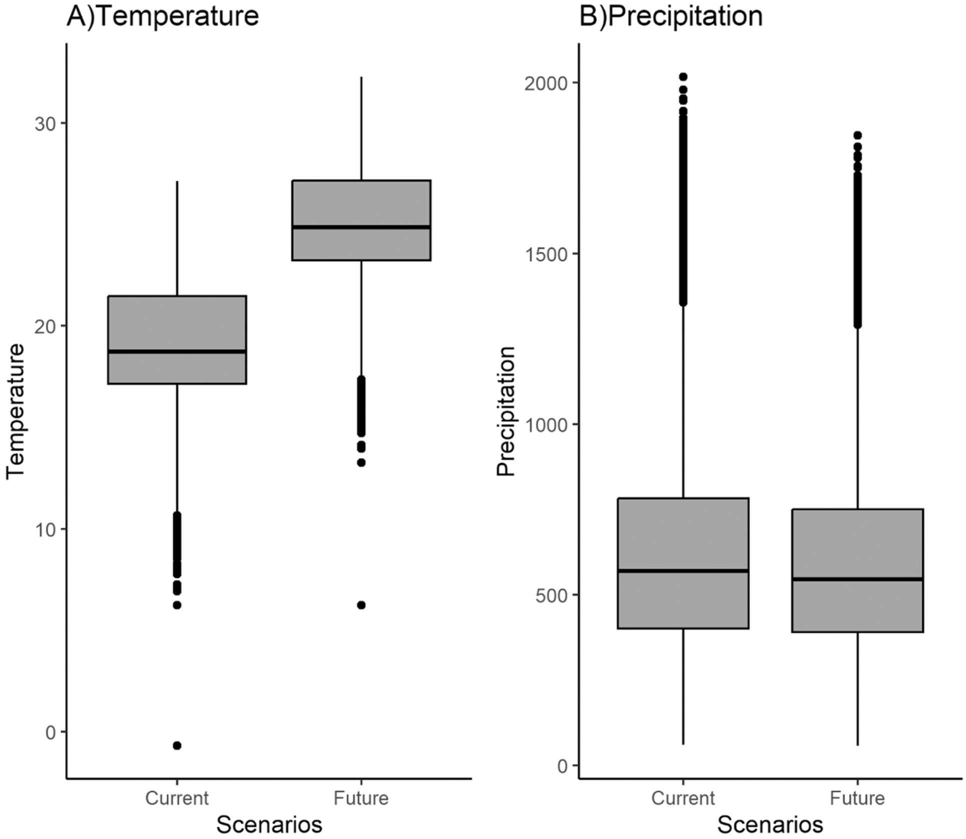

Fig. 5. Boxplot of the (A) temperature and (B) precipitation values for the current and future scenarios in areas of highest projected loss (hotspots). Future predictions were calculated as the average of the eight global circulation models for the most pessimistic Shared Economic Pathways – SSP 585 (Highly unequal - high emission scenario). Paired Wilcoxon analyses indicated temperature values (A) and precipitation(B) differed significantly (p-value < 0.001).

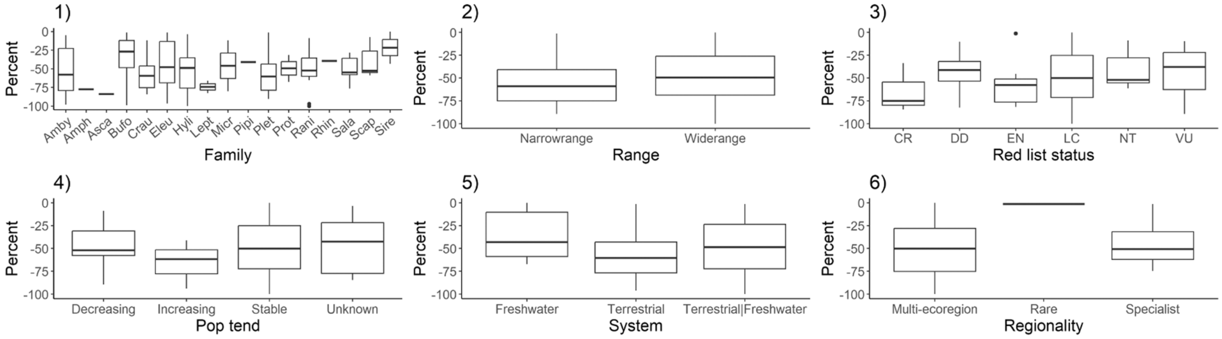

Fig. 6. Boxplot of the percentage of projected changes in habitat suitability for vulnerable species, that is, species projected to lose habitat suitability in the upcoming decades. Groups are arranged into (1) family, (2) population trend (e.g., decreasing, stable), (3) species range (narrow-range and wide-range), (4) systems (e.g., freshwater, terrestrial), (5) red list status (e.g., endangered, least concern, vulnerable), and (6) regionality (multi-ecoregion, specialists and rare). Values are for the average loss among the four Shared Economic Pathways (SSPs): 126 (sustainability - low emission scenario), 245 and 370 (Intermediate emission scenarios), and 585 (Highly unequal - high emission scenario). Acronyms are Amby-Ambystomatidae, Amph-Amphiumidae, Asca-Ascaphidae, Bufo-Bufonidae, Crau-Craugastoridae, Eleu-Eleutherodactylidae, Hyli-Hylidae, Lept-Leptodactylidae, Micr-Microhylidae, Pipi-Pipidae, Plet-Plethodontidae, Prot-Proteidae, Rani-Ranidae, Rhin-Rhinophrynidae, Sala-Salamandridae, Scap-Scaphiopodidae, and Sire-Sirenidae.

development, and behavior, especially under future warming scenarios (Blaustein and Belden, 2005 and references therein).

Our results confirm topography as a crucial environmental characteristic influencing amphibians' distribution (Ribeiro et al., 2018). The importance of elevation in shaping amphibian's habitat suitability could be related to temperature. Often, amphibians at low elevations experience higher ambient temperatures than species found in mid and high elevations. Individuals inhabiting cold high-elevation areas experience restricted activity and breeding seasons, negatively affecting the production of clutches and broods per season (Morrison and Hero 2003). As temperatures increase as predicted, amphibians from high elevations will be further constricted in the southwest United States (Griffis-Kyle et al., 2018), similar to other taxa where high-elevation species have already experienced extirpations (Beever et al., 2016).

4.2. *The effect of climate change on habitat suitability*

Climate change simulation results unveil a concerning threat since a significant portion of suitable habitat is expected to disappear in all scenarios for all amphibian groups. Considering the climate is the primary driver of most amphibians in our study, the effect of climate change on habitat suitability was somewhat expected. However, the projected habitat loss was surprising since about 48% of areas considered suitable in the present are expected to become unsuitable in the future (Fig. 5). Habitat loss is regarded as one of the major causes of amphibian decline (Wake, 1991, Luedtke et al., 2023). Habitat loss may influence the reduction of suitable habitats and spatial configuration of habitats, leading to isolation and habitat fragmentation (Gray and Brown, 2005). Habitat isolation can have a significant effect on amphibian persistence (Carr and Fahrig, 2001), and it is often linked to the reduction of species dispersion (Gibbs, 1998) and genetic diversity (Carr and Fahrig, 2001). Previous studies have shown habitat alterations were among the most significant factors contributing to the decline of frogs (Gray and Brown, 2005). The loss of suitable habitat can increase the risk of extinction (Fahrigh, 1993).

Our results showed that the highest habitat loss predicted in drylands is related to overarching changes in annual temperatures and a decrease in annual precipitation. The increase in temperature in drylands may directly impact amphibians' physiological requirements. The significant increase in temperature could result in several direct impacts, including species' body condition (e.g., individual fitness, Reading, 2007) and immune functioning (e.g., increase their susceptibility to pathogens and parasites, Kilpatrick et al., 2010). Being ectotherms, a significant increase in temperature would force species to move to keep their internal temperature in an optimal range (Kearney et al., 2009). The reduction of precipitation could play a significant role in increasing land degradation by desertification. This last process is intrinsically related to the loss of vegetation coverage and, consequently, the reduction of primary productivity (Safriel et al., 2005). Vegetation suppression is often associated with herptile abundance and species decline (Luedtke et al., 2023).

The potential effect of habitat loss on the species vulnerable to climate change can also disclose a significant risk for imperiled species, especially critically endangered species. Critically endangered species are probably at the margins of their global range and are considered to be at extreme risk of extinction in the wild (IUCN 2023). Our results, therefore, uncover a concerning scenario for some amphibians since the loss of suitable habitat may shrink their geographical range even more. Reduced suitable habitat can create smaller patches of isolated populations, increasing habitat fragmentation and susceptibility to extinction (Cushman, 2006). In a similar pattern, we found that the family of anurans that would be predicted to experience the least contraction of range is Bufonidae, the true toads. This family has a nearly global distribution, and although the family has habitat specialists, especially in tropical areas, several life history traits (e.g., large body size, toxins, high fecundity) have made this family highly adaptable (Van Bocxlaer et al., 2010).

The findings suggest that dryland specialists and rare species are included in the list of vulnerable species for species unique to drylands. Dryland specialists and rare species have their range entirely within the drylands. Since species classified as specialists and rare are not expected to increase their range across the dryland area, losing suitable habitat for these species could result in extreme habitat shrinking and isolation. Because amphibians often have relatively low dispersal ability (Marsh and Trenham, 2001), the fragmentation of dryland specialists and rare species could offer a challenging barrier to their conservation. On the other hand, negatively affected multi-ecoregion species are expected to lose a significant portion of their habitat (within drylands). Yet, they still can persist in habitats outside drylands. For example, in our study, Ascaphidae – the tailed frog, was the family (represented by a single species) with the greatest habitat loss (within drylands). Another multi-ecoregion species are amphibians in the family Sirenidae – neotenic aquatic salamanders with the least habitat loss. This suggests that some multi-ecoregion species might persist in dryland areas.

Previous studies have questioned whether climate change directly or indirectly caused the amphibian population to decline (e.g., Carey and Alexander, 2003). Our study did not aim to prove causality. Instead, we focused on habitat suitability (based on the probability of occurrence). Since amphibians are often considered limited dispersers and highly philopatric (Blaustein et al., 2002), the changes in habitat may reflect a significant concern to amphibians' conservation. Yet, it is unknown to conclude whether the suppression of suitable habitats will contribute to extinction scenarios. Amphibians are known to adapt to adverse conditions. One example is the northern cricket frog (*Acris crepitans*), one vulnerable to climate change. Although *A. crepitans* has experienced a significant population decline due to habitat loss in the last century, this cricket frog seems to be able to adapt to adverse environmental and landscape conditions (Gray and Brown, 2005).

Amphibians are known for their molecular evolution and plasticity, especially plastic changes in physiology and plasticity (Steigerwald, 2021 and references therein). Even with this plasticity, it is still unknown if the extent of trait change will be enough to couple the habitat loss (Meester et al., 2018), especially in a radically changing environment. Thus, we urge managers and conservationists to consider habitat loss and other factors (e.g., disease, Luedtke et al., 2023) in drylands as a significant threat to amphibians' persistence, especially species from the dryland specialist rare group. The maps presented herein could help identify areas most likely to lose habitat suitability. Managers could use critical locations to monitor droughts, breeding ponds, wetland habitat, and exposure to desiccation, factors often associated with amphibian population decline (Daszak et al., 2005).

5. Conclusions

Our study is the first to identify that climate, represented by ambient temperature and precipitation measures, is primarily associated with highly suitable areas for amphibians in drylands. We also confirmed the association of solar radiation with amphibian habitat suitability. Ours is also the first to provide quantitative estimates of the potential loss of habitat suitability of amphibians across North American drylands to relate the perfect loss to extrinsic factors and traits and show that critically endangered and endangered species are the most affected species. This study also provides the locations where habitat loss is most expected. Besides improving the biogeography of amphibians in drylands, this study also provides comprehensive information and analyses for decision-makers to conserve and protect amphibian's habitats. In addition, our findings open up a new possibility of collaboration among biogeography, conservation biology, evolution, and animal disease. Future studies can explore family-level patterns and investigate evolutionary aspects (e.g., life history, morphology, behavior) of climate vulnerability. Studies can also explore species' vulnerability to disease combined with habitat loss from climate change or how climate might alter disease prevalence.

CRediT authorship contribution statement

Fábio Albuquerque: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Heather Bateman:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Jared Johnson:** Investigation, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data supporting this study's findings are available at the Global Biodiversity Information Facility, WorldClim and EnvEarth, and are publicly available

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02944.

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