CONSERVATION
SCIENCE PARTNERS

FINAL REPORT
12 May 2025

For the project entitled:

A framework for guiding management decisions for amphibians in an uncertain future

Submitted to:
Dr. Aparna Bamzai, Assistant Regional Administrator, North Central Climate Adaptation Science Center

By:

Dr. Amanda M. Kissel – Research Ecologist, U.S. Geological Survey Fort Collins Science Center

Dr. Erin Muths – Research Zoologist, U.S. Geological Survey Fort Collins Science Center

Mae Lacey, M.S. – Data Scientist, Conservation Science Partners

Dr. Viorel Popescu – Associate Research Scientist, Columbia University

Dr. Marissa Dyck – Postdoctoral Research Fellow, University of Victoria

Dr. Caitlin Littlefield – Senior Scientist, Conservation Science Partners

Administrative

Award PI: Dr. Caitlin Littlefield (*original award recipient was Dr. Amanda Kissel*)
Contact information: caitlin@csp-inc.org
Institution: Conservation Science Partners
Project Title: A framework for guiding management decisions for amphibians in an uncertain future
Agreement Number: USGS G21AC10833 (subaward to CSP 1561388)
Date of report: May 12, 2025
Period of time covered by report: October 1, 2021 – September 29, 2024
Actual total cost of the project: $175,933.50

Public Summary

Managing species in a rapidly changing climate requires knowledge of how species will respond to climate change and other threats while simultaneously developing management actions to reduce threats. Amphibians are one of the most threatened taxa on earth and often serve as the ‘canary in the coalmine’ for the health of ecosystems that countless other species and humans rely on. To understand the status of and guide management for the boreal toad (*Anaxyrus boreas boreas*), an imperiled amphibian species in the North Central region, we co-produced several products with the Boreal Toad Conservation Team. These products included 1) reconstructed seasonal hydrology patterns for historical boreal toad breeding wetlands and high elevation watersheds in the Southern Rocky Mountain Region (SRMR) from remotely sensed data, 2) current and future predictions of drying rates for historical breeding wetlands, 3) current and future predictions on the status of the boreal toad in the SRMR, and 4) a web tool to guide management actions. While the boreal toad is considered a ‘data rich’ species given data collection efforts that span multiple decades, many amphibian species are considered ‘data poor’, meaning managers lack data on the biology, ecology, or status of the species needed to make sound decisions. To address this knowledge gap, we also quantified drying patterns across watersheds for two ‘data poor’ species in the North Central region at risk from climate change: the Great Basin spadefoot toad (*Spea intermontana*) and the wood frog (*Lithobates sylvaticus*). These new data can guide management decisions for these species by allowing managers to understand habitat changes with respect to water availability, a crucial element for amphibian survival and persistence. Together, these products demonstrate how cutting-edge technology and analytical methods can produce a range of useful information to support amphibian conservation.

Project Summary

Managing species in an uncertain future is becoming an increasing reality for natural resource decision makers. Climate change is expected to exacerbate a myriad of different threats, such as habitat fragmentation, disease, and invasive species. However, data that can provide insight into how species might respond to climate change can help managers make informed decisions. For this project, we developed a climate-informed decision-support tool for the Boreal Toad Conservation Team (BTCT), a multi-agency group tasked with managing the imperiled boreal toad (*Anaxyrus boreas boreas*) in the Southern Rocky Mountain Region (SRMR), extending from southern Wyoming to northern New Mexico. We combined cutting edge remote sensing analyses and publicly available climate data with an advanced Bayesian dynamic multi-species occupancy model to explore the effects of climate change on boreal toad persistence in the SRMR. We developed novel hydrologic products, including a time series of surface area estimates spanning from 1985-2022 for historical toad breeding sites and watersheds within the SRMR, and developed hydrologic models for breeding sites to estimate the probability of a site drying in a given year. We used this hydrologic model to predict drying probabilities for sites into the future (2040-2069) under two climate change scenarios: representative concentration pathway (RCP) 4.5 representing a lower emissions scenario and RCP 8.5 representing a higher emissions scenario. The drying probabilities, along with other additional climate covariates hypothesized to affect toads, were then used in a multi-species dynamic occupancy model to determine the drivers of toad occupancy in the SRMR. Further, we used these modeled relationships to predict occupancy under the RCP 4.5 and RCP 8.5 climate scenarios. We found that the probability of toads occupying a site in the SRMR declined by over 40% between 2001 and 2019, and that further declines are likely to occur under both the RCP 4.5 and RCP 8.5 scenarios. Our hydrology and occupancy outputs and predictions are available to managers in the form of a web-based decision-support tool, which allows managers to explore these results at multiple management levels (individual sites, mountain ranges, and the SRMR as a whole) to guide decision making (e.g., translocations, habitat manipulation). As a proof of concept, we also used remote sensing data to quantify drying patterns at the watershed level for two species of conservation concern in the North Central Region: the Great Basin spadefoot toad (*Spea intermontana*) and wood frog (*Lithobates sylvaticus*). We found that most watersheds in these species' ranges within the North Central Region were drier in the latter half of our time series (2000-2022) than the prior 15 years (1985-1999). Together, these products demonstrate how cutting-edge technology and analytical methods can produce a range of useful information to support amphibian conservation in the North Central region.

Purpose and Objectives

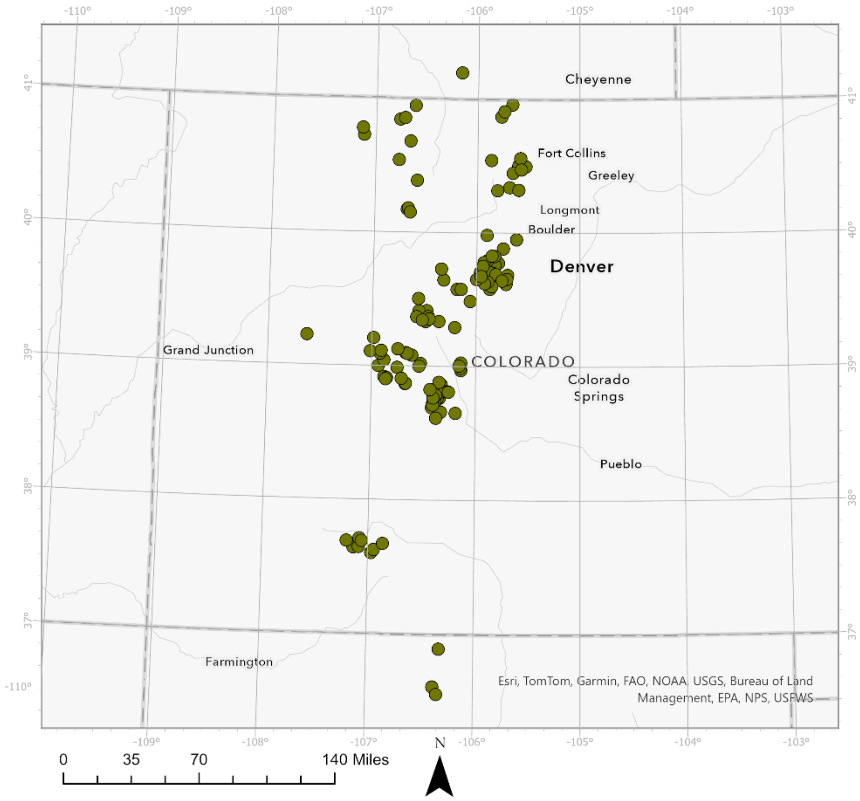
Conservation efforts aimed at the persistence of species and the habitats they depend on have typically focused on mitigating immediate threats. However, additional assessment of species' vulnerability to climate change, threats that may act synergistically with climate change (such as disease), and predictions of how a species will respond to management actions under a changing climate (Mantyka-Pringle et al. 2012) are needed to develop robust conservation and management plans. These comprehensive and forward-looking assessments are particularly important for amphibians. Amphibians are one of the most imperiled and under-studied taxa and are considered vulnerable to climate change along with many other additive and synergistic threats, such as disease and habitat loss (Stuart et al. 2004; Hoffmann et al. 2010; Hof et al. 2011; Grant et al. 2016). Amphibian declines, though widespread, vary in severity based on species traits, evolutionary history, local conditions, and susceptibility to climate change (Miller et al. 2018). Effectively managing for amphibian persistence requires ways to evaluate the vulnerability of species and their habitat to multiple threats, including climate change (Hof et al. 2011).

Amphibians are a unique vertebrate taxon due to their bi-phasic life history, in which most species require bodies of water for successful reproduction and recruitment (Wilbur 1980). While some amphibians are primarily terrestrial as adults and thus less dependent on water than fully aquatic species, changes to the timing and availability of breeding habitat due to climate change are still likely to have demographic consequences (Todd et al. 2010; Green 2017; Greenberg et al. 2017; Thompson et al. 2021; Nagel et al. 2021). Additionally, during the terrestrial phase of their life cycle, increasing temperatures, coupled with reduced water availability, have the potential to push individuals beyond critical physiological limits (Watling & Braga 2015; Lertzman-Lepofsky et al. 2020; Hoffmann et al. 2021; Greenberg & Palen 2021). Thus, understanding changes in water availability under future climate conditions is important for robust conservation and management decisions now and in the future.

While the decline in amphibians in recent decades has prompted long-term amphibian studies, particularly in North America (Miller & Grant 2015; Petrovan & Schmidt 2016; Bosch et al. 2018; Miller et al. 2018), these studies are generally focused on assessing demographic parameters, indices of abundance, or models predicting occupancy (Adams et al. 2013; Grant et al. 2016). Rarely are associated habitat data available at large scales to understand how changes in the environment, and water availability in particular, may be affecting these demographic rates (Brannelly et al. 2019; Thompson et al. 2021; Cayuela et al. 2021; Mims et al. 2023). However, recent technological advances allow us to reconstruct hydroperiods (i.e., seasonal patterns of water fluctuations) of wetlands over time, expanding our ability to understand how changes in water availability affect amphibians and other wetland obligate species (Kissel et al. 2020). These data can be used to evaluate the effects of wetland hydroperiod and water availability on individuals, populations, and species (Kissel et al. 2020), and/or to assess landscape scale patterns and identify potential climate refugia (Ryan et al. 2014; Pilliod et al. 2015; Cartwright et al. 2022).

To address the gap in available wetland data, we generated time series of surface water estimates at multiple landscape scales from remotely sensed data. When converted to biologically-relevant metrics, such as drying probability or change in surface water area, these data can then be used to develop mechanistic hypotheses regarding the effects of water availability on amphibian population dynamics, and to assess how landscape-scale shifts in water availability (i.e., due to climate change) may vary across a species range or management unit. We applied our framework to the boreal toad as a case study. We used the boreal toad as a model species for conservation planning under multiple threats and uncertainties, including climate change and disease.

To counter widespread declines in the Southern Rocky Mountain Region (SRMR, Fig. 1), Federal, State, and university partners developed a decision analysis (Gerber et al. 2018) to weigh tradeoffs in management strategies (e.g., translocation efforts, habitat manipulations, measures to prevent spread of disease) that maximize boreal toad persistence and distribution in the presence of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*), which is thought to have caused widespread declines in the SRMR (Muths et al. 2003; Pilliod et al. 2010; Russell et al. 2019). However, the analysis of Gerber et al. (2018) used historical/current data on the distribution of boreal toads and *Bd*, and did not consider potential synergistic effects of climate change. There is evidence that reduced snowpack and increased temperatures (as predicted under future climate change) will influence boreal toad and *Bd* dynamics (Murphy et al. 2011; Muths et al. 2020). Our analysis seeks to enhance our understanding of boreal toad and *Bd* dynamics by integrating these important additional factors.



Esri, TomTom, Garmin, FAO, NOAA, USGS, Bureau of Land Management, EPA, NPS, USFWS

Figure 1. Map of historical boreal toad breeding locations in the Southern Rocky Mountain Region, spanning from southern Wyoming to northern New Mexico.

Capitalizing on several decades of observed declines of boreal toad populations in the SRMR, the Boreal Toad Conservation Team (BTCT) implemented a monitoring program for a subset of breeding sites, with toad detection/non-detection data collected annually since 2001. These observational data, coupled with *Bd* data collected at sites where boreal toads were detected and reconstructed hydroperiods for current and historical breeding sites, allowed us to develop time-series predictions of changes in boreal toad occupancy. We also used these data to forecast future changes under several general circulation models (GCMs) and greenhouse gas representative concentration pathways (RCP). The results of these analyses were then communicated via an interactive web mapping application that was developed in consultation with managers at Colorado Parks and Wildlife to provide a decision-support tool for amphibian managers. While our original intention was to update the decision-support tool developed by Gerber et al. (2018) by co-producing updated management strategies, members of the BTCT had limited capacity to participate in an additional, facilitated decision analysis workshop. Additionally, as the project evolved and modeling results became available, we determined that the volume of data outputs warranted a separate decision-support tool. However, our results could help inform an updated structured decision making process in the future, as capacity allows.

While the boreal toad is considered a ‘data rich’ species given data collection efforts that span multiple decades, many amphibian species are considered ‘data poor’, meaning managers lack data on the biology, ecology, or status of the species needed to make sound decisions. To address this gap in knowledge, we also quantified drying patterns across watersheds for two ‘data poor’ species in the North Central region at risk from climate change: the Great Basin spadefoot toad and the wood frog. These two species were chosen in collaboration with Ross Hinderer and Lisa Eby (original Co-PIs on this award), who developed a climate change vulnerability analysis for amphibians in the North Central Region (Hinderer et al. 2024). Both species were listed as a species of greatest conservation need in the states of Wyoming and Colorado (Hinderer et al. 2024). These new data can guide management decisions for these species by allowing managers to understand habitat changes with respect to water availability, a crucial element for amphibian survival and persistence. Together, these products demonstrate how cutting-edge technology and analytical methods can produce a range of useful information to support amphibian conservation for ‘data poor’ and ‘data rich’ species.

Organization and approach

Spectral Mixture Analysis

Spectral mixture analysis (SMA) is a remote sensing method that uses the spectral signature of a Landsat pixel to identify the composition of the landscape (e.g., vegetation, bare ground, water) (Adams et al. 1986; Adams & Gillespie 2018). SMA is particularly useful because it estimates the land cover composition of each individual 30 x 30 m Landsat pixel, which facilitates more detailed analyses of landscape composition without sacrificing temporal resolution or availability (i.e., we can take full advantage of the roughly 40 years' worth of Landsat imagery available to the public, as opposed to being restricted to recently collected high-resolution imagery that only covers the last decade).

We used an SMA model to estimate the percent of surface water from Landsat satellite images (Halabisky et al. 2016) at two different landscape levels: 1) boreal toad breeding wetlands in the SRMR (individual, historical and current), and 2) Hydrologic Unit Code (HUC) 12 watersheds within the SRMR that include suitable habitat for boreal toads. Additionally, to demonstrate the utility of the method to inform management of data poor species, we developed SMA models for HUC12 watersheds within the known range of two additional amphibian species (the wood frog and the Great Basin spadefoot) that lack biological data and are of conservation concern.

We implemented the SMA for all available Landsat images from 1985 to 2022 during the toad active season (May - October) for boreal toad breeding sites, and during the driest months (June-August) at the HUC12 watershed level (for boreal toads, Great Basin spadefoots, and wood frogs). We reduced the overall number of months examined for the HUC12 watershed analyses due to computational limitations of running the SMA at a broader spatial extent. The SMA was conducted in Google Earth Engine (GEE; Gorelick et al. 2017) using the blue, green, red, near infrared, shortwave infrared 1, and shortwave infrared 2 bands (bands 1-5 and 7 for Landsat 5; bands 2-7 for Landsat 8 and 9). Due to this difference in bands, the SMA was run for (a) Landsat 5 and (b) Landsat 8 and 9 separately before combining all outputs into a single data frame (Fig. 2).

Representative samples of different components of the physical landscape, known as spectral endmembers (e.g., vegetation cover, water, and bare earth) were used to 'unmix' the composition of each pixel within a given image (Fig. 2 Step 1). The endmember can be a single value for each band derived from the mean spectral value for a representative group of pixels at a single location (e.g., a portion of a large lake) across a broad time period (i.e., static), or a series of values extracted from the same pixel over time that may change depending on the variation of spectral values for the focal pixel (i.e., dynamic). We used a set of static endmembers representing water, shallow/murky water, meadow, trees, and bare earth to derive the fractional abundance of each of these land cover categories within each pixel (Fig. 2 Step 2).

We applied a mask removing any pixels with > 20% snow, ice, or cloud cover (Fig. 2 Step 3) prior to applying the SMA to estimate fractional abundance for each focal landcover class (water, shallow/murky water, meadow, trees, bare earth; Fig. 2 Step 4). SMA outputs were converted to a value of area, after which these values were used to calculate percent cover of each landcover class within each delineated wetland or watershed (henceforth area of interest). We then used this information to estimate surface water area of all wetlands or watersheds for each Landsat image over time (Fig. 2 Step 5).

Additionally, we quantified the percent of each area of interest that had Landsat pixel coverage on each date that a Landsat satellite passed over the area. We did this to ensure that surface water area estimates were not biased (i.e., underestimated) due to a lack of Landsat pixel coverage. We used the following formula to estimate Landsat pixel coverage:

eq. 1 $$pixel\ cover\ = \left(\frac{count\ of\ overlapping\ pixels\ x\ 900m^2}{wetland\ or\ watershed\ area\ (m^2)}\right) \text{ x } 100$$

where $900m^2$ represents the size of a Landsat pixel (30m x 30m). We eliminated any surface water area estimates derived from images with less than 60% pixel cover for wetlands and 40% pixel cover for watersheds to ensure surface area estimates were representative of the focal wetland or watershed (Fig. 2 Step 6). The lower threshold for watersheds reflected the challenges of achieving relatively high pixel coverage for each individual date across larger areas (i.e., watersheds) without severely reducing the dataset. Therefore, these thresholds were selected with the goal of balancing data quality with the need to retain sufficient imagery for analysis. Additional filtering was applied using the Root Mean Square Error (RMSE), which is a measure of the difference between observed and modeled values from the SMA. Lower RMSE values indicate a better fit. Highly variable RMSE could indicate 1) highly mixed or complex land cover types, which can be difficult to parse out and represent accurately, or 2) noise in the data as a result of shadows and other features that might obscure the spectral signal of what is truly happening on the ground. Thus, we filtered out surface water estimates with a RMSE of 0 (indicating a perfect fit, which is unlikely) or a RMSE greater than two standard deviations from the mean RMSE for each wetland (Fig. 2 Step 7). This post-processing was conducted in R (v4.2.1). Finally, monthly surface water area estimates were then generated by taking the median percent water value per month, for each area of interest (Fig. 2 Step 8).

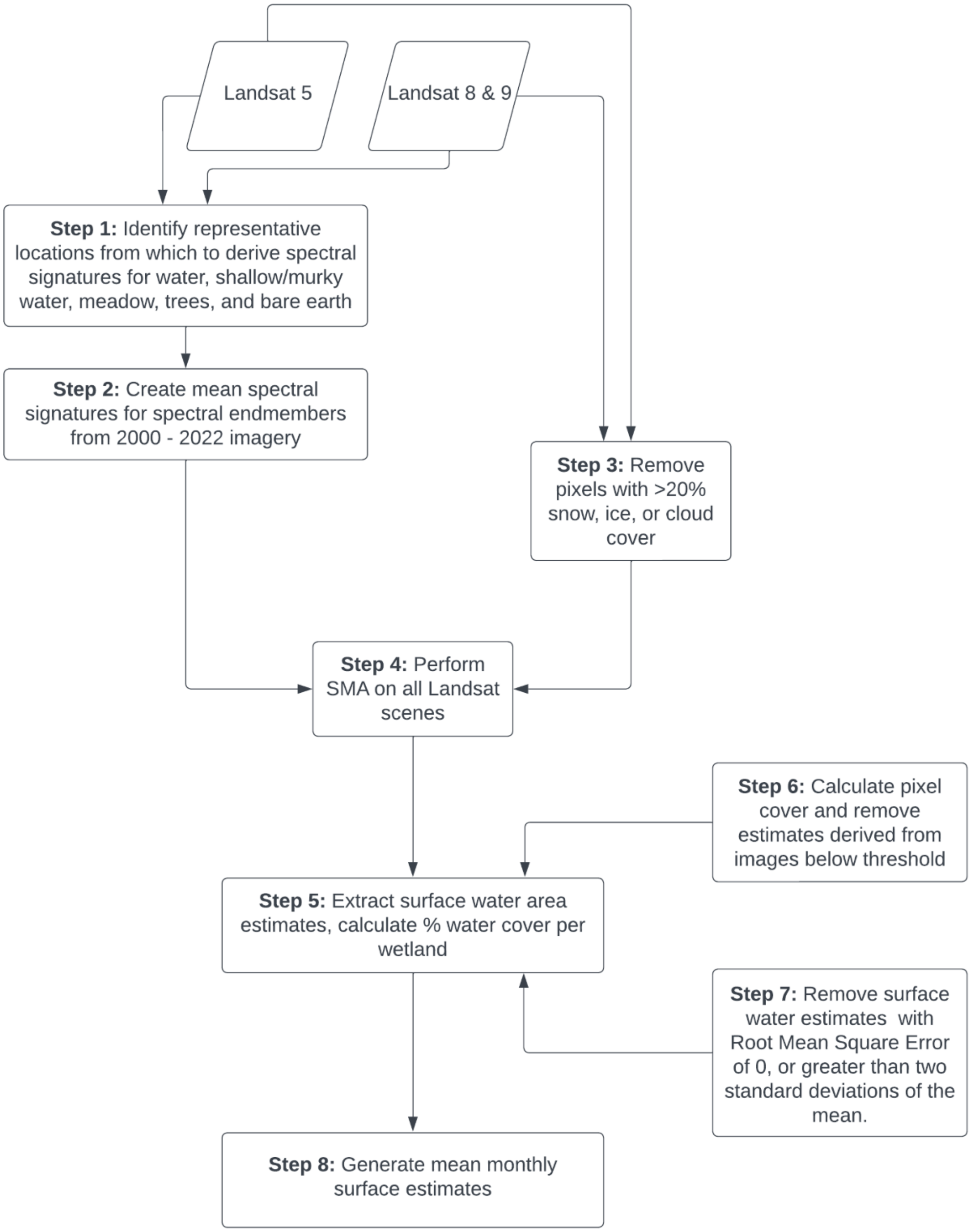


Figure 2. Spectral mixture analysis methods flowchart used to estimate surface water area at either the scale of the watershed or breeding site.

Boreal toad breeding wetlands SMA

We applied SMA to a study area of 159 wetlands spanning southern Wyoming to northern New Mexico (i.e., the southern Rocky Mountains, Fig. 1) that are current or historical boreal toad breeding sites. The goal of this analysis was to generate estimates of surface water cover through time at each historical boreal toad breeding site, which would serve as an input to subsequent hydroperiod models. Collating this spatial dataset of 159 breeding sites involved extensive engagement and iteration with managers and members of the BTCT to determine exact locations of breeding sites, as well as to delineate breeding site boundaries, which are crucial for the SMA. A 5-meter buffer was added to these wetlands for all subsequent analysis to account for the fact that wetlands may have filled beyond the delineated boundary at some point in time (Kissel et al. 2020). We considered wetlands that dropped below 15% of their maximum surface area within a year to have dried in that year (Kissel et al. 2020, refer to hydroperiod modeling section below).

Watershed level SMA for boreal toads

The purpose of the watershed level analysis for boreal toads was to provide a landscape-scale assessment of drying patterns across the SRMR, which could be used to identify refugia and potential boreal toad translocation sites. We used HUC12 watersheds (U.S. Geological Survey 2001, henceforth watersheds) to balance computational limitations with our landscape-level questions. To limit our analysis to viable boreal toad habitat, we identified the minimum elevation of all watersheds that contained boreal toad breeding sites. We applied this value (2,038 m [6,686 ft]) to select all watersheds within the SRMR with an elevation above this threshold. This resulted in 1,505 watersheds within the SRMR that could potentially contain suitable boreal toad breeding habitat. Within the watershed boundaries, we selected all ‘stream/river’ features from the National Hydrography Datasets (NHD, U.S. Geological Survey 2023) and buffered these features by 30m. Additionally, we extracted wetlands from the National Wetland Inventory (NWI) and removed any lakes and reservoirs with an area greater than the largest breeding wetland in our study area (greater than 143,770 m^2 [1,547,527 ft^2]), given that they are unlikely to be suitable for boreal toad breeding. Otherwise, these large bodies of water would likely bias surface water estimates within a watershed that may have a large amount of surface water overall, but a relatively small amount of which is truly suitable for toad breeding. All remaining NWI wetland features were buffered by 30 m. We applied the SMA to these features within each watershed between 1985 and 2022 for the months of June-August. For each watershed, we calculated the mean percent change in surface water area between two time periods (1985 – 1999 and 2000 – 2022) and used this to examine whether watersheds were getting wetter or drier through time.

Watershed level SMA for two additional threatened amphibians

We expanded our watershed analysis to two additional climate-sensitive amphibian species within the boundaries of the North Central region of the United States that are considered ‘data poor’: the wood frog and the Great Basin spadefoot (Hinderer et al. 2024). The goal of this analysis was to demonstrate the application of SMA in addressing data gaps for amphibian species that lack information on their biology, ecology, or status. The North Central Region is defined by the USGS Climate Adaptation Science Centers as the states of Colorado, Wyoming, Montana, North Dakota, South Dakota, Kansas, and Nebraska (https://www.usgs.gov/programs/climate-adaptation-science-centers/north-central-casc). We limited our analysis to watersheds within each species’ range and within the bounds of the

North Central Region. For wood frogs, we further limited our analysis to the relic population(s) in Wyoming and Colorado. Similarly to the watershed-level analysis for boreal toads, we then used the NHD and NWI datasets to delineate streams and watersheds (removing large lakes and reservoirs, see above) and buffered streams, rivers, and wetlands by 30m. We applied the SMA to these features within each watershed between 1985 and 2022 for the months of June-August. Similar to the boreal toad watershed analysis, we calculated the mean percent change in surface water area between two time periods (1985 – 1999 and 2000 – 2022) for each watershed and used this to determine whether watersheds were getting wetter or drier through time.

Data Extraction for Hydroperiod and Occupancy modeling

Climate

We aggregated climate data from multiple sources for use in the hydroperiod and occupancy modeling (see below). We downloaded historical (1985 – 2022) and future (2040 – 2069) 4 km resolution climate data for the extent of the boreal toad sites using packages *AOI* and *climateR* (Johnson 2023, 2024) in R v4.2.3 (R Core Team 2024). The historical climate dataset contained daily surface meteorological data (gridMET, https://www.climatologylab.org/gridmet.html) from 1979 to 2020 (Abatzoglou 2013). The future climate data used multivariate adaptative constructed analog datasets (MACA; https://climate.northwestknowledge.net/MACA/index.php) which downscale model outputs from general circulation models (GCMs) for two future Representative Concentration Pathways (RCPs) 4.5 and 8.5 (Abatzoglou & Brown 2012). We selected six GCMs (HadGEM2-ES365, CanESM2, IPSL-CM5A-LR, GFDL-ESM2M, inmcm4, and MIROC-ESM-CHEM) that represent a range of plausible futures in the SRMs (e.g., hot/wet winter, warm/dry winter, hot/wet spring, Steen 2017) for both RCPs (Table 1). For the historical and future climate data, we selected four variables for use in the hydroperiod modeling, precipitation (*pr*), minimum temperature (*tmin*), maximum temperature (*tmax*), and vapor pressure deficit (*vpd*) (Table 2). We then aggregated the daily data for each variable into a single (mean) monthly value for historical data (between 1985 and 2019), as well as a monthly mean value for each future GCM, and RCP scenario (between 2040 and 2069).

Table 1. Description of the six general circulation models representing different plausible future climate scenarios in the southern Rocky Mountains.

Model	Representative future	Change in Dec-Feb precip (in)	Change in Dec-Feb temp (°F)
CanESM2	Hot, wet winter	0.8	6.947
GFDL-ESM2M	Warm, wet winter	0.2	3.635
inmcm4	Warm, dry winter	0.3	3.722
IPSL-CM5A-LR	Hot, dry winter	0.2	4.886

Model	Representative future	Change in Mar-May precip (in)	Change in Mar-May temp (°F)

MIROC-ESM-CHEM	Hot, dry spring	1.7	8.396
HADGEM2-ES365	Hot, wet spring	-0.6	6.376

Table 2. Names and descriptions of variables used for hydroperiod modeling.

Variable group	Variable name	Variable description	Units	Data source	Resolution
Climate	*pr*	Mean precipitation	Millimeters	GridMET (historic) MACA (future)	4 km
	tmax	Mean maximum near-surface air temperature	Kelvin	GridMET (historic) MACA (future)	4 km
	tmin	Mean minimum near-surface air temperature	Kelvin	GridMET (historic) MACA (future)	4 km
	vpd	Mean vapor pressure deficit	Kilopascals	GridMET (historic) MACA (future)	4 km
Water balance	*snow*	Mean snow water equivalent	Millimeters	MWBM (historic and future)	4 km
	pet	Potential evapotranspiration	Millimeters	MWBM (historic and future)	4 km
	stor	Soil moisture storage	Millimeters	MWBM (historic and future)	4 km
CHILI	*CHILI*	Continuous heat-insolation load index	0 (very cool) – 255 (very warm)	Conservation Science Partners	10 m
Topographic	*aspect*	Aspect	Radians	NASA-SRTM	30 m
	altitude	Altitude	Meters	NASA-SRTM	30 m
	slope	Slope	Degrees	NASA-SRTM (derived)	30 m
	TRI	Topographic ruggedness index	<150 = low, 150-500 = moderate, >500 = high	NASA-SRTM (derived) - HUC12 and site levels	30 m
Wetlands	*emergent*	Emergent wetland	Square meters	US NWI – HUC12 level	Vector data
	forester	Forested wetland	Square meters	US NWI – HUC12 level	Vector data

Water balance

The historical and future water balance data were extracted from a 4 km resolution monthly water-balance model for 1950 to 2099 under RCP 4.5 and 8.5 (Alder and Hostetler 2021). We extracted data for three variables, mean snow water equivalent (*snow*), potential evapotranspiration (*pet*), and soil moisture storage (*stor*) (Table 2) for both our historical time period (1985 to 2020) and future climate scenarios between 2040 and 2069 (Table 1). Snowmelt is likely to drive water levels for wetlands in the SRMR (Mote et al. 2005), thus to estimate monthly probability of drying and surface water area, we used the *snow* data from the month prior as well as the total amount of *snow* of the preceding winter as covariates in our hydroperiod models.

Continuous heat-insolation load index

We extracted the mean continuous heat-insolation load index (CHILI; https://developers.google.com/earth-engine/datasets/catalog/CSP_ERGo_1_0_US_CHILI#description) for each of the HUC12 watersheds containing the boreal toad breeding sites. CHILI is an extension of the heat load index developed by McCune & Keon (2002) and a proxy for the effects of insolation and topographic shading on evapotranspiration (Theobald et al. 2015). CHILI values range from 0 (very cool) to 255 (very warm). We used this as a static covariate in our hydroperiod model, hypothesizing that breeding sites with a higher CHILI value are likely to dry at a faster rate.

Topography

We used the NASA Shuttle Radar Topography Mission (SRTM) 30 m resolution digital elevation model dataset (https://lpdaac.usgs.gov/products/srtmgl1v003/) to derive topography metrics. We extracted the elevation and calculated slope and aspect for each breeding site. We also derived the Topographic Ruggedness Index (TRI), which evaluates the amount of elevation difference between adjacent cells of a digital elevation model. We calculated mean TRI at the HUC12 watershed level and extracted the TRI value for each breeding site; TRI values below 150 represent terrain with low ruggedness, values between 150 and 500 represent moderately rugged terrain, and values >500 indicate highly rugged and topographically complex areas.

Wetlands

We used the U.S. National Wetland Inventory (NWI) (https://www.fws.gov/program/national-wetlands-inventory/wetlands-mapper) to extract the amount of wetland area and the proportion wetland area within HUC12 watersheds containing breeding sites. We used two categories of wetlands within the NWI dataset: 1) freshwater emergent wetland (NWI code PEM; Cowardin class = Palustrine Emergent), which includes herbaceous marsh, fen, swale and wet meadow wetland habitat, and 2) freshwater forested and shrub wetlands (NWI codes = PFO and PSS; Cowardin class = Palustrine forested and/or Palustrine shrub), which includes forested swamp, wetland shrub bog, and wetland habitat. We selected these two categories only, as they represented the majority of wetland habitat within any given HUC12 watershed and we hypothesized that the total area and proportion of wetland area within a watershed would be a good indicator for the capacity of the watershed to retain water, complementary to the soil moisture storage metric.

Hydroperiod modeling

The purpose of our hydroperiod models was to understand drying trends at breeding wetlands (sites) and identify potential hydroperiod shifts at breeding sites through time. We used a Bayesian modeling framework implemented in the package *brms* (Bürkner 2017, 2018) for program R v4.3.2 (R Core Team 2024). We used hurdle models to simultaneously estimate the probability of a wetland drying (logistic model with a logit link) and the total surface water area of the wetland (gamma distribution) in July of a given year (a critical month for boreal toad larval development) between 1985 and 2020. We used the surface area values generated from the SMA as the response variable, applying a threshold to classify the breeding site as dry (<15% of maximum surface area of the wetland) or not dry (>15% of maximum surface area of the wetland, Kissel et al. 2020). Four outlier sites (MI04, EA06, PI04, LR05) were removed from the analysis as they were large managed reservoirs and unlikely to be representative of natural hydroregimes.

We used a similar parameterization for the logistic and gamma sub-models within the hurdle model. We first eliminated several variables with high (>|0.7|) Pearson correlations (retaining the most ecologically relevant variable), and retained the following variables for modeling: *areaSqMeters, monthly precipitation, monthly mean vpd, soil water storage, snow water equivalent in the previous winter, snow water equivalent in the previous month, watershed area, area of forested and shrub wetland, area of emergent wetland, TRI, aspect* and *CHILI.* We used two random effects for each sub-model: a *year* effect and *site* effect. The former accounts for latent variation in climate conditions within each year (i.e., coarse climate patterns), while the latter accounts for latent variation in conditions at each site across all years (i.e., site-specific hydroperiod conditions).

We tested several models containing parameters grouped by climate, water balance, topography, CHILI and wetland, along with several models with combinations of variables drawing from different groups (see Table 2). We compared models using leave-one-out (LOO) cross-validation. We used the best performing model based on LOO evaluation to predict the probability of drying and the area of surface water for the month of July for each breeding site between 1985-2022 and identify variables that affect hydroperiod in the study area. We evaluated model performance using conditional and marginal LOO-adjusted R^2 with compatibility interval (function *r2_loo* in package *performance* [Lüdecke et al. 2021]). We then used the best performing model based on LOO to forecast the probability of drying and surface water area for the future time horizon (2040-2069) under the six GCMs (Table 1) and two RCPs (4.5 and 8.5).

To assess potential hydroperiod shifts for the future time horizons, we classified ponds as *ephemeral, intermediate, perennial* and *permanent* (Lee et al. 2015) under current and future scenarios based on their likelihood to shrink in the future relative to the current estimated mean area. We used equation [*Area Reduction (AR) = 1 – (current area – predicted area)/current area*] and classified ponds as *ephemeral* (*AR* <= 0.03), *intermediate* (0.03 < *AR* <= 0.33), *perennial* (0.033 < AR <= 0.70) and *permanent* (*AR* >= 0.7) (Lee et al. 2015).

Occupancy model covariate development

We then developed occupancy models with the goal of understanding the role of climate and *Bd* on boreal toad occupancy dynamics. In a webinar held in January of 2022, we queried the signatories of the BTCT to identify important covariates and corresponding hypotheses for how covariates would affect the demographic parameters estimated by the occupancy model. Stemming from this webinar, we developed covariates related to three primary categories: 1) water availability, 2) temperature, and 3) phenology. Additionally, we explored the boreal toad and *Bd* literature to determine covariates that have been used in other demographic or distributional studies that had some explanatory power related to demographic rates of toads, or geographic presence or distribution of toads or *Bd*. Based on the webinar and literature, we developed three covariates related to toad demographics (*Active season length, May cold events,* and *Proportion of years wetland dried*) and two covariates related to *Bd* characteristics (*Bd growing degree days*, and *Proportion of years wetland dried*). We further hypothesized that because boreal toads are relatively long-lived and require multiple years to reach sexual maturity, occupancy rates are likely to be related to conditions over a longer time frame (i.e., multiple years) as opposed to interannual variation in conditions (i.e., changes from one year to the next). Thus, to capture long-term trends that may affect toad occupancy, we developed covariates that span fifteen years (approximately three toad generations). We chose this based on the available time series of covariate data (e.g., Landsat imagery is available from 1985 onward), and because we felt three generations were sufficient to capture a signal in occupancy dynamics while also allowing us to leverage the full extent of our occupancy data time series (19 years). We used temperature data (refer to Data Extraction methods above) to derive covariates for *Active season length*, *May cold events*, and *Bd growing degree days*, and output from the hydroperiod models (see Hydroperiod modeling methods section) to derive the *Proportion of years dried* for each wetland. We derived covariate data for each historical toad breeding site between 1985 and 2019, as well as for the six GCMs and two future RCP scenarios described above (refer to Climate Data Extraction section). Table 3 describes how each covariate was defined and derived.

Table 3. Description and definition of the covariates used in the occupancy model used to explore the effects of climate change on boreal toad persistence in the Southern Rocky Mountain Region of the United States. The first five covariates are dynamic and change through time, and were used to model extinction and colonization probabilities. The last two covariates were static and used to model the probability of initial occupancy. Bd = *Batrachochytrium dendrobatidis*

Covariate	Description
Active season length	We defined active season length for a single year as the deviation from average active season length described by the 35-year (1985 - 2019) climate norm. To derive this covariate, we calculated the cumulative number of days between the last day of -4.4°C temp in spring and first day of -4.4°C temp in autumn for each year between 1985 and 2019 and took the average for each site, which represents the 35-year climate norm. We then subtracted the climate norm for the site from the active season length for a given year. Thus, a negative value represents a shorter than average active season, and a positive value represents a longer than average growing season. We further calculated a rolling average of the 15 years prior to year *t* in our time

Covariate	Description
	series to represent long-term changes in active season length in our model. For example, 'active season length' in 2001 is the average deviation from the climate norm from 1985-2000, 'active season length' in 2002 is the average deviation from the climate norm from 1986 to 2001.
May cold events	For each year, we calculated the number of 'cold events' during the egg laying period (May). A 'cold event' is defined as a day with an average min temp at least 2 SD below the 30 year average minimum temperature for May. We then calculated the proportion of years with cold events for the 15 years prior to year *t*. For example, 'cold events' for 2001 is the proportion of years with cold events in May from 1985 to 2000.
Bd growing degree days	Cumulative number of days in a season with a minimum temperature above 17°C and a maximum temperature below 27°C. These values represent the thermal breadth of *Bd* from the literature (Piotrowski et al. 2004, Berger et al. 2004, Haver et al. 2022).
Proportion of years dried	The proportion of the last 15 years that the site was estimated to have dried from the hydrology models. This is a rolling value, such that the value for year *t* is derived from the probabilities of drying between years *t*-1 and *t*-15.
Presence of *Bd*	The probability of *Bd* occupying the site.

Occupancy model

We fitted a Bayesian multi-state dynamic co-occurrence occupancy model following the framework developed by Fidino et al. (2019). We chose this model because it directly accounts for the effects of *Batrachochytrium dendrobatidis* (*Bd*) on colonization and extinction rates of boreal toads at a site and can accommodate time-varying covariates. We used data from 75 sites across the historical breeding range that had detection/non-detection data for toads, or toads and *Bd*, between 2001 and 2019 (Colorado Parks and Wildlife 2024), and corresponding covariates. The model estimates the probability that each site is in one of four ‘states’: 1) occupied by toads only, 2) occupied by *Bd* and toads, 3) occupied by *Bd* only, or 4) unoccupied (refer to Fidino et al. 2019 for model derivation and Converse et al. 2017 for state definitions for this system). The initial occupancy probability (i.e., occupancy in 2001) is estimated directly, and in subsequent years extinction and colonization probabilities are estimated directly. The occupancy state of the site in years two through nineteen is derived via these rates. We modified the Fidino et al. (2018) model in three ways: 1) we included time-varying covariates, 2) we used an informed prior to constrain the probability of extinction of *Bd* because *Bd* extinction is rarely confirmed and extinction probability is low given it can persist in the environment (Johnson & Speare 2005), and 3) we did not model the effect of toad presence on colonization and extinction rates of *Bd* because we did not have *a priori* hypotheses on how the presence of toads would affect colonization or extinction probability of *Bd* and *Bd* data were sparse.

The collection process for detection/non-detection for boreal toads and *Bd* was different. Detection/non-detection data for toads were collected via visual surveys at sites on multiple occasions within a year. Following a standard occupancy modeling framework, we considered each year a ‘primary occasion’ between which the population was considered open (i.e., immigration, emigration, births, deaths can occur), and visits within a year were considered ‘secondary occasions’ between which the population is considered closed (Mackenzie et al. 2017). However, *Bd* data were collected via swabs of individual amphibians or water samples at sites and were reported as the number of samples (swab or water sample) taken, and proportion of positive samples from a PCR analysis in a given year (Colorado Parks and Wildlife 2024). Similar to the toad data, we considered years to be primary occasions for *Bd* data collection. However, we treated each *Bd* sample within a year as a secondary visit because associated sampling dates were not always available for *Bd*, and thus we could not associate detections and non-detections from swabs to a specific date (unlike the toad sampling data). We considered the number of positive samples as the number of detections and number of negatives as non-detections (Mosher et al. 2017, 2018b). Because the order in which *Bd* samples were taken was unknown, for each site and year we randomly assigned a ‘visit’ (i.e., sample) as a detection (i.e., positive for *Bd*) or non-detection (i.e., negative for *Bd*) based on the proportion of positive samples. For example, if 20 samples were collected from a site in a year and the *Bd* prevalence was reported as 0.25, we treated the site as having 20 secondary visits with *Bd* detections randomly assigned on five of those visits. We used this system to develop a *Bd* occupancy history for each site. However, the number of secondary visits was computationally expensive, thus, we collapsed the secondary visits into six occasions, and considered an occasion to have a positive *Bd* detection if one or more of the original secondary visits (i.e., samples) had a positive *Bd* detection.

We explored the effects of a suite of covariates described above on the probability of initial occupancy for both boreal toads and *Bd*, as well as the probability of colonization and extinction for boreal toads and *Bd*. Table 4 describes the covariates we included for each parameter and species and the associated *a priori* hypothesis.

Table 4. Hypotheses for each covariate as they relate to each species and parameter used to explore the effects of climate change on boreal toad persistence in the Southern Rocky Mountain Region of the United States. *Bd = Batrachochytrium dendrobatidis,* NA = not applicable.

Parameter	Species	Covariate	Hypothesis
Initial Occupancy Probability	toads	Proportion of years dried (1985 to 2000)	**Quadratic effect (convex curve)** - Toads generally breed at perennial or semi-permanent sites. Sites that dry too frequently prior to toad metamorphosis may result in sustained failed recruitment and a lower probability of occupancy. Thus, we hypothesize that initial occupancy will be low at sites with a high proportion of years dried (representing sites that dry too frequently to sustain toad populations) and occupancy will also be low at sites that rarely dry (representing permanent sites that never dry).
	Bd	Proportion of years dried (1985 to 2000)	**Negative effect** - *Bd* requires water to persist long-term, therefore sites with a higher proportion of years dried are less likely to be occupied by *Bd*.
		Mean annual *Bd* growing degree days (1985 to 2000)	**Positive effect** - A higher number of growing degree days represents more days when the temperature is in the ideal thermal range for *Bd* growth and persistence.
Colonization Probability	toads	Proportion of years dried	**Quadratic effect (convex curve)** - Toads generally breed at perennial or semi-permanent sites. Sites that dry too frequently prior to toad metamorphosis may result in sustained failed recruitment and a lower probability of occupancy. Thus, we hypothesize that colonization will be low at sites with a high proportion of years dried (representing sites that dry too frequently to sustain toads) and colonization will also be low at sites that rarely dry (representing permanent sites that never dry).
	Bd	Proportion of years dried	**Negative effect** - *Bd* requires water long-term to persist, therefore sites with a higher proportion of years dried are less likely to be occupied by *Bd*.
		Bd growing degree days	**Positive effect** - A higher number of growing degree days represents more days when the temperature is in the ideal thermal range for *Bd* growth and persistence.
		Presence of toads	**Positive effect** - Toads are a *Bd* host, therefore they facilitate colonization.

Parameter	Species	Covariate	Hypothesis
Extinction Probability	toads	Active season length	**Linear effect** - Very long active seasons may result in higher extinction probability because 1) potential phenological mismatch between foraging resources (i.e., food may not be available late in the season) and toad activity, and 2) increased desiccation risk for all life stages as snow-dependent (i.e., ephemeral) wetlands are more likely to dry before toads hibernate. Thus, we predict that sites with longer than average active seasons will have higher extinction probabilities.
		May cold events	**Positive effect** - As the proportion of years with cold days during the breeding season increases, breeding failure is more likely (temps are below the thermal tolerance of eggs and tadpoles) leading to local extinction.
		Proportion of years dried	**Quadratic effect (concave curve)** - Toads generally breed at perennial or semi-permanent sites. Sites that dry too frequently prior to toad metamorphosis may result in sustained failed recruitment and a lower probability of occupancy and higher local extinction. Thus, we hypothesize that extinction probability will be high at sites with a higher proportion of years dried (representing sites that dry too frequently to sustain toads) and extinction probability will also be high at sites that rarely dry (representing permanent sites that never dry).
		Presence of *Bd*	**Positive effect** - *Bd* reduces survival in toads in the southern Rocky Mountains. Therefore, we hypothesize that extinction probability will increase when *Bd* is present
	Bd	NA	We did not include covariates on extinction probability of *Bd* because we did not have a priori hypothesis of what may affect *Bd* extinction.

We predicted the site-specific occupancy states between 2001 and 2019 for 152 historical breeding sites. Of the original 161 breeding sites, covariate data were not available for 6 sites, and we excluded 3 sites that are large reservoirs (MI04, PI04, LR05) with hydroperiods managed by humans and thus, predictions at these sites are likely unreliable. We used 75 sites (sites with detection/non-detection data, see methods) of the total 152 sites to fit the model. Detection/non-detection data were not available for the remaining 77 sites, but covariate data were. For the 75 sites used to fit the model, we made predictions using the site-specific value for the intercept estimated by the model and site-specific covariates. For the remaining 77 sites, we used the mean estimated intercept from model (i.e., not site-specific) as well as site-specific covariates. Thus, the predictions for the 75 sites included in the model contain more site-specific information than the 77 sites not included in the model. We summarized occupancy results by mountain range, a biologically relevant management unit used by the BTCT.

Web Application

In consultation with the BTCT, we developed a web-based decision-support tool to provide managers an interface for visualizing and assessing boreal toad and *Bd* occupancy dynamics and hydrologic changes through time. The tool is intended to provide information to support decision making related to toad management, such as translocation or habitat restoration at relevant spatial scales (individual site, mountain range, and SRMR). We included mountain range as a spatial scale because a stated goal of the BTCT is to ensure that one or more sites within a mountain range are occupied by toads (Crockett 2023). The web-tool contains a map of breeding sites with relevant occupancy and hydroperiod information for each historical breeding site. Additionally, the map displays translocation sites identified by the BTCT, watershed drying patterns, and a spatial layer representing the mean watershed burn probability (Jaffe et al. 2024) for each watershed that contains a breeding site as a visual aid for managers. The tool was built using R Shiny v1.7.5 (Chang et al. 2024) in R v4.2.1 (R Core Team 2024), as well as the *leaflet* (Cheng et al. 2024) and *plotly* (Sievert 2020) packages to create interactive plots and enable dynamic exploration of all analysis results (i.e., outputs from hydroperiod and occupancy models).

Project Results, Analysis and Findings

Spectral Mixture Analysis

Boreal toad breeding wetlands SMA

The SMA of the breeding sites produced 29,131 estimates of surface water across all sites across 37 years (an average of 183 points per site). However, the number of points after removing observations with an RMSE > 2SD from the mean decreased by 7% to 27,078 points (Fig. 3). On average, 12 data points were removed for each site. The mean RMSE was highly correlated with the wetland polygon size, and larger wetlands had higher RMSE (e.g., large wetlands have greater absolute variability in surface water area, which translates to higher RMSE values, Fig. 4a). However, the maximum percent surface water estimated by the SMA for each site was not correlated with the mean RMSE, indicating the RMSE can be used as an unbiased metric for filtering potentially erroneous data points (i.e., sites with greater mean RMSE did not have surface water estimates that were consistently high or low, relative to the size of the wetland, Fig. 4b). This approach also resulted in detailed hydrographs for all breeding sites, which can be used to visualize long-term changes in surface water extent from 1985 to 2022 at each site (Fig. 5).

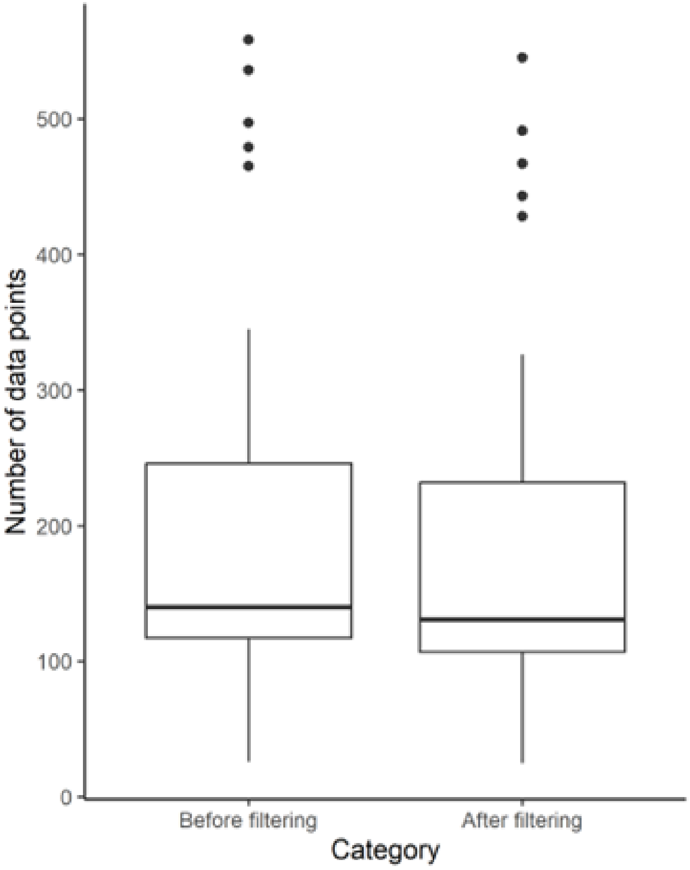


Figure 3. Boxplots comparing the number of data points prior to and after filtering out datapoints with a Root Mean Square Error (RMSE) greater than two standard deviations from the mean RMSE for the site-specific spectral mixture analysis (SMA) analysis. SMA was used to estimate surface water area at historical boreal toad breeding sites. Thick, black line represents the median value, lower and upper hinges represent the 25th and 75th quartile, respectively. Lower and upper whiskers represent 1.5 times the interquartile range of the hinge. Points represent outliers.

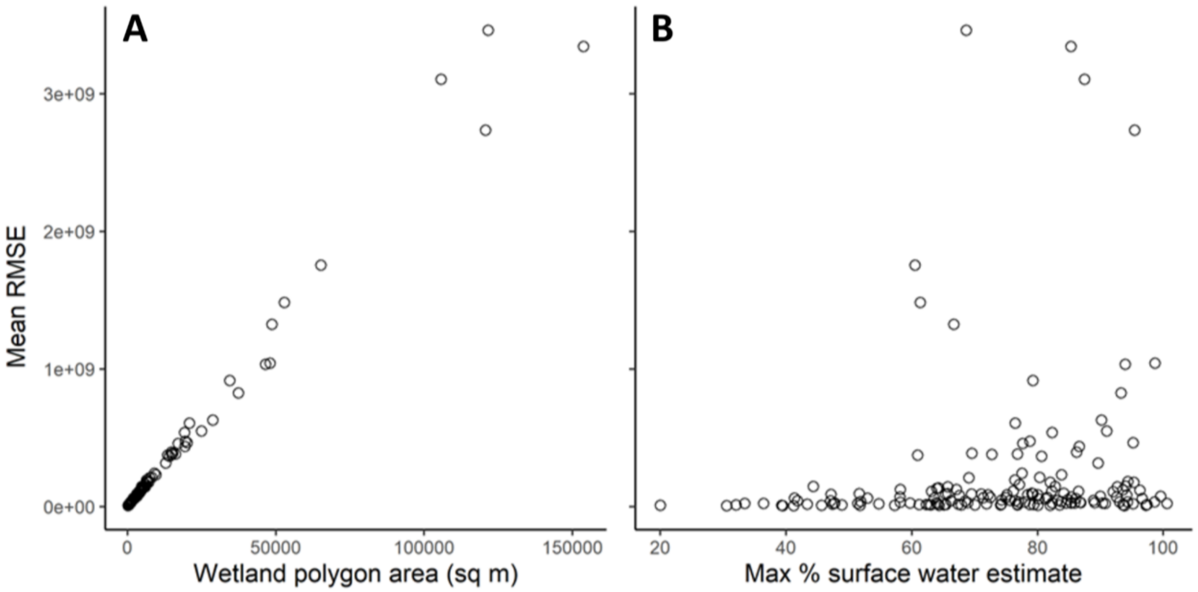


Figure 4. Correlation between the mean Root Mean Square Error (RMSE) and wetland polygon size of toad breeding sites (A) and maximum percent surface water cover as estimated by the spectral mixture analysis (B). Spectral mixture analysis was used to estimate surface area of historical boreal toad breeding sites.

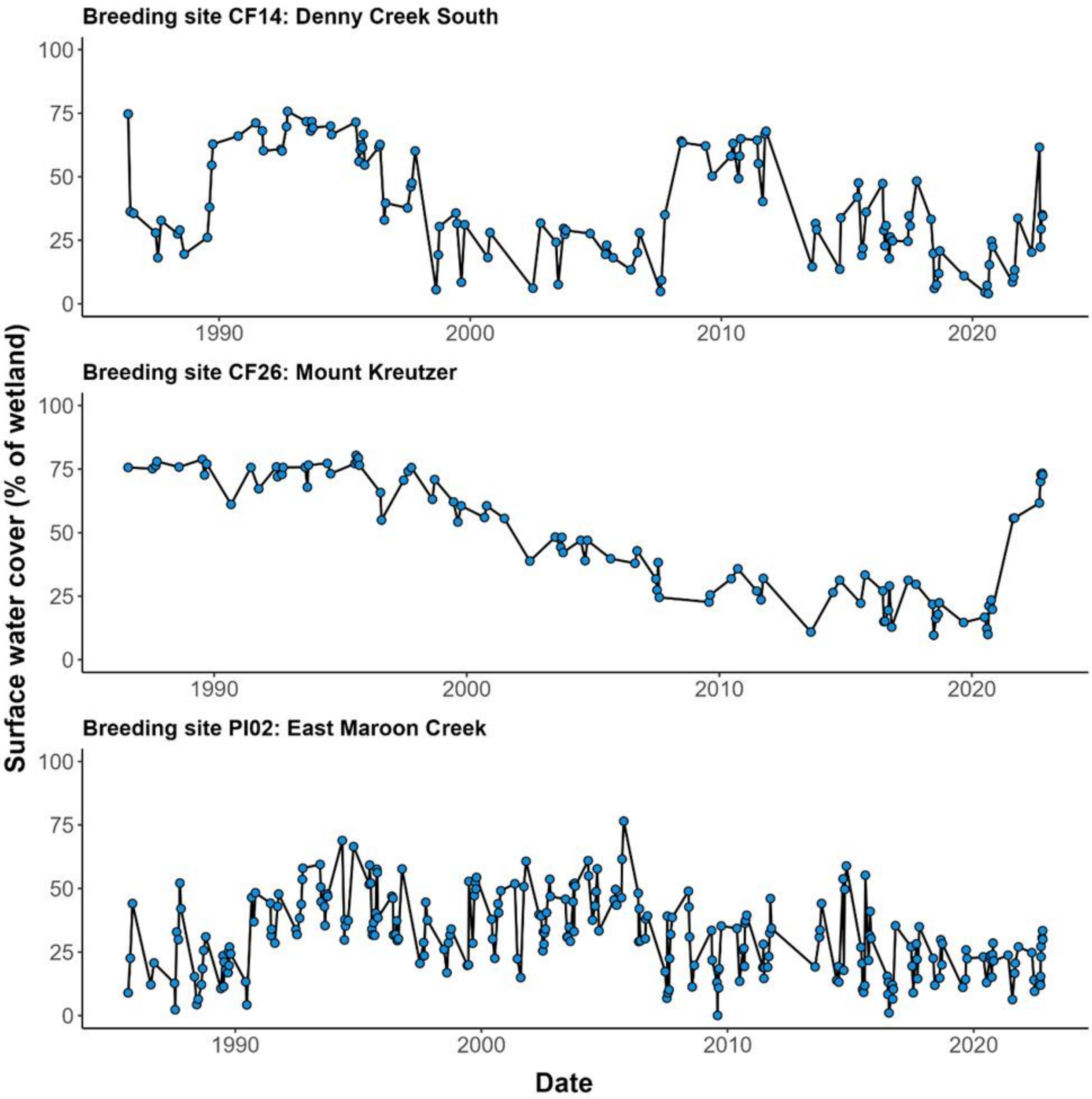


Figure 5. Hydrographs for three different breeding sites (top to bottom: CF14, CF26, and PI02) in the Southern Rocky Mountain Region study area, demonstrating variation in percent surface water cover through time from 1985 to 2022.

Watershed level SMA for boreal toads

The watershed-level SMA for boreal toads produced 319,292 estimates of surface water across 1,505 HUC12 watersheds over 37 years (an average of 212 observations per watershed). After removing observations with an RMSE > 2SD from the mean, the number of observations decreased by 25% to 239,395. On average, 53 data points were removed for each watershed

(Fig. 6). A greater proportion of observations were removed following this filtering approach for the watershed-level outputs as opposed to the breeding wetland outputs because there is greater noise in the data when applying the SMA over larger areas (i.e., boreal toad breeding sites ranged from 26 to 143,770 m^2 in area, while the total area analyzed within each watershed ranged from 13,927,043 to 474,531,774 m^2). Across these larger areas, there are more opportunities for additional noise created by shadows from trees or other features on the landscape, or greater variability or error during the unmixing process due to highly mixed or complex land cover types, which can result in more variation in RMSE values. Similarly to the breeding wetlands SMA, mean RMSE was highly correlated with the area of the NHD and NWI features within each watershed and the maximum percent surface water estimated by the SMA for each site was not correlated with the mean RMSE.

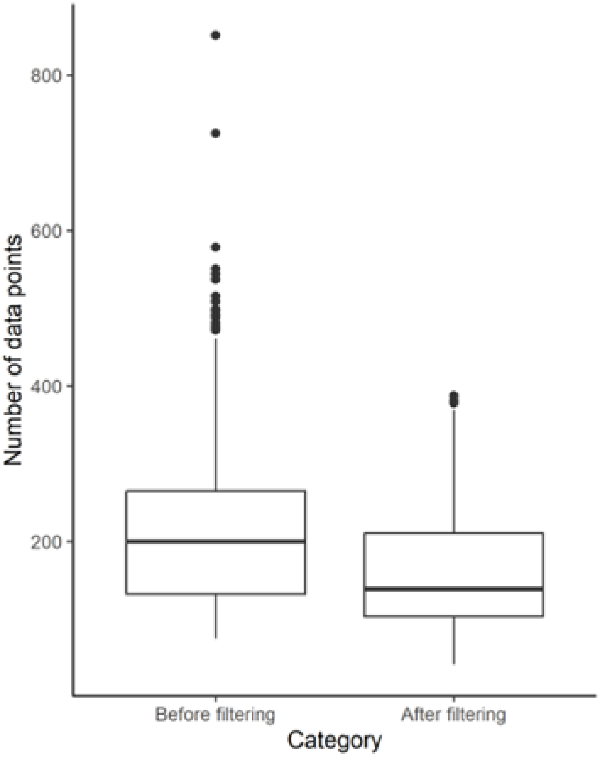
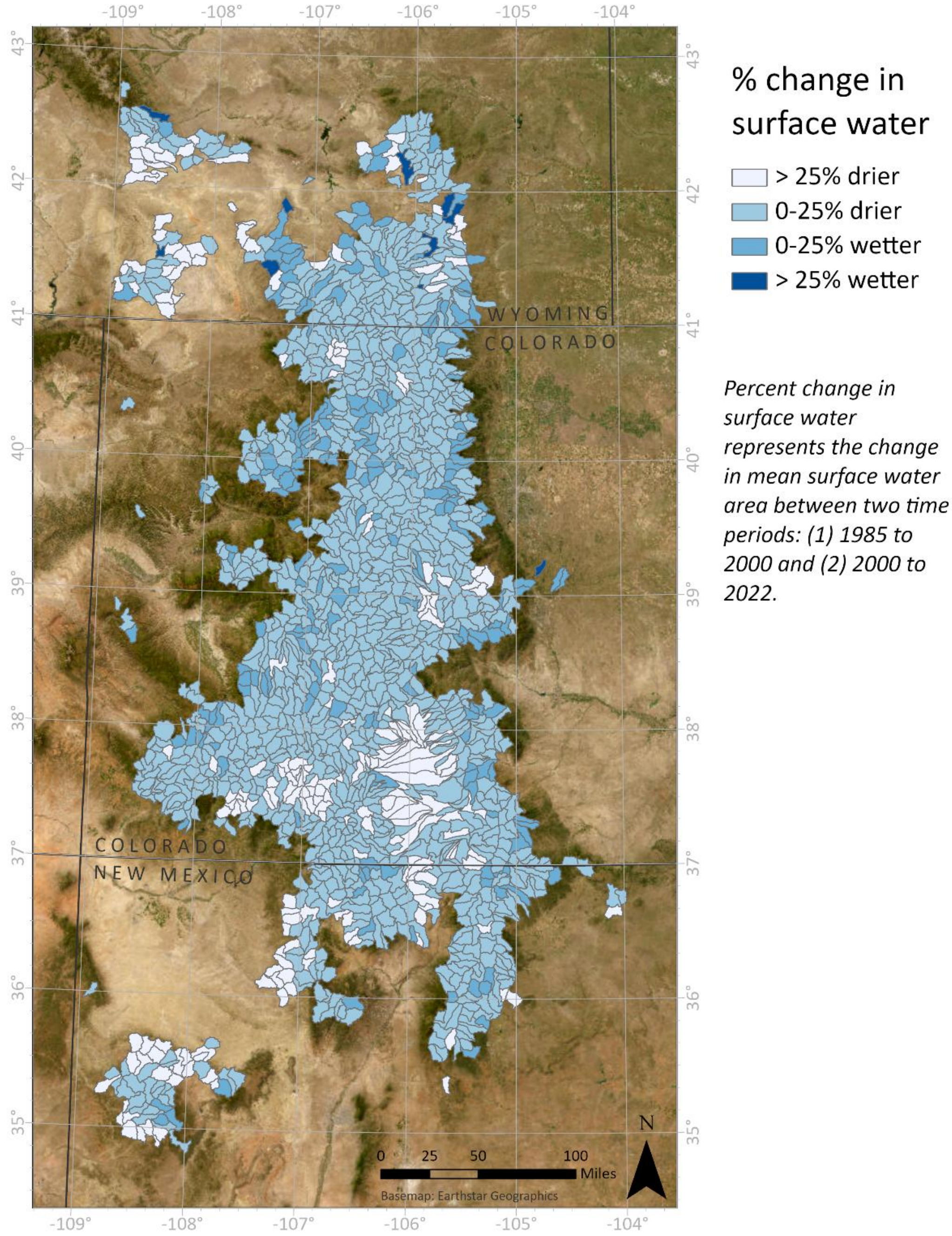


Figure 6. Boxplots comparing the number of data points prior to and after filtering out datapoints with a Root Mean Square Error (RMSE) greater than two standard deviations from the mean RMSE watersheds containing boreal toad in the Southern Rocky Mountain Region study area. Thick, black line represents the median value, lower and upper hinges represent the 25th and 75th quartile, respectively. Lower and upper whiskers represent 1.5 times the interquartile range of the hinge. Points represent outliers.

Based on our watershed-level drying metric (change in mean surface water between 1985 – 1999 and 2000 – 2022), we found that the majority of watersheds are drier in the latter half of the time series (i.e., a negative percent change in surface water area; Fig. 7).

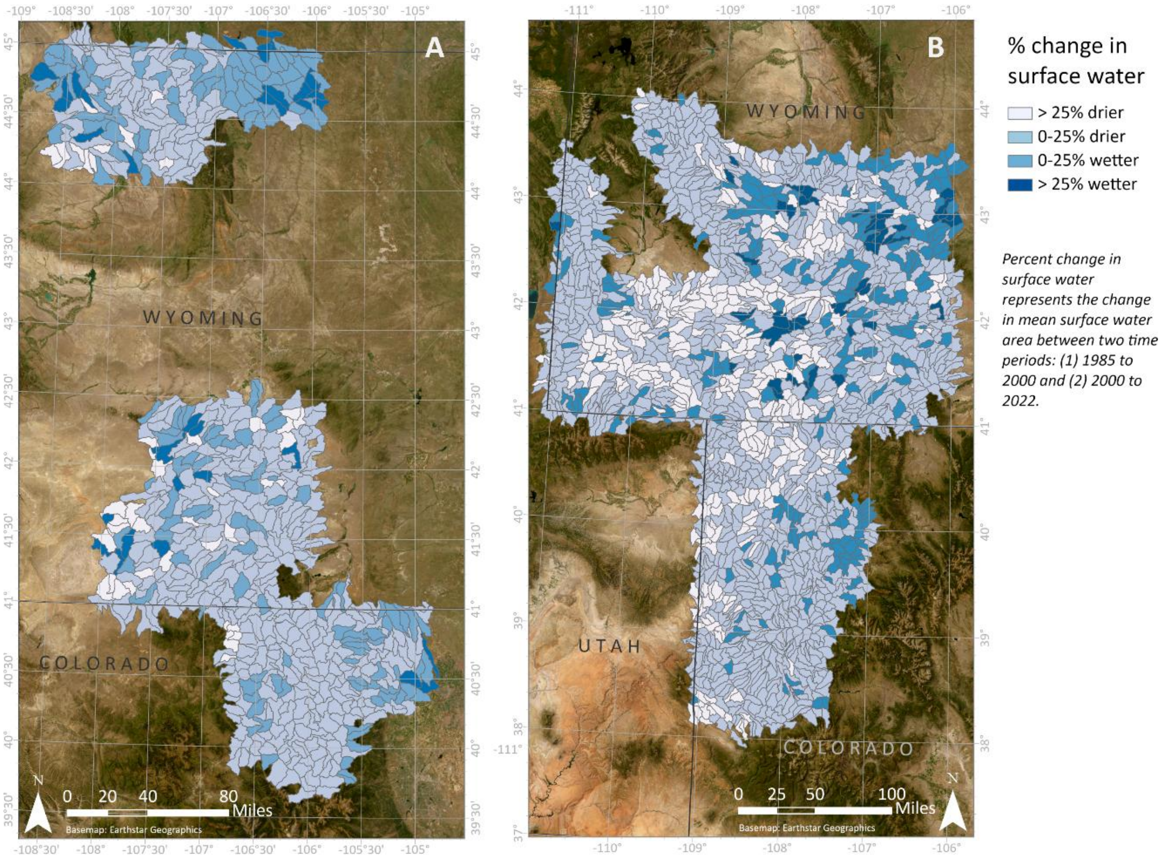


Percent change in surface water represents the change in mean surface water area between two time periods: (1) 1985 to 2000 and (2) 2000 to 2022.

Figure 7. Map of drying patterns for watersheds likely to be suitable for boreal toads in the Southern Rocky Mountain Region of the United States.

Watershed level SMA for two additional threatened amphibians

The watershed-level SMA for the wood frog and the Great Basin spadefoot produced 144,661 estimates of surface water across 632 watersheds and 314,821 estimates of surface water across 1,629 watersheds, respectively. After removing observations with an RMSE > 2SD from the mean, the number of observations for the wood frog decreased by 25% to 109,071 and the number of observations for the Great Basin spadefoot decreased by 26% to 231,008. Similarly to the HUC12 level results for boreal toads, the majority of watersheds within the Wood frog and Great Basin spadefoot ranges are either drier or experienced little change in mean surface water between 1985-1999 and 2000-2022 (Fig. 8). We found that 83% of watersheds within the Great Basin spadefoot range and 71% of watersheds for the relic population of wood frogs were drier in the latter half of our time series (2000-2022).



Percent change in surface water represents the change in mean surface water area between two time periods: (1) 1985 to 2000 and (2) 2000 to 2022.

Figure 8. Map of drying patterns for watersheds within the (A) wood frog range and (B) Great Basin Spadefoot range in the North Central region of the United States. For the purpose of this analysis the range is truncated to the states in the North Central region (i.e., Colorado and Wyoming). We further limited the wood frog range to the relic populations in Colorado and Wyoming. Drying patterns were derived by comparing the mean percent change in surface water (estimated via spectral mixture analysis (SMA)) between 1985-1999 and 2000-2022.

Hydroperiod Modeling

Historical data model and predictions

The best performing hydroperiod model based on LOO was the global model, which included variables across all groups (Table 2). The global model LOO-adjusted conditional R^2 (accounting for both fixed and random effects) was 0.929 (95% CI [0.910, 0.946]), while the fixed effects-only model had a LOO-adjusted marginal R^2 of 0.440 (95% CI [0.299, 0.544]). Thus, more than half of the predictive power in the model was due to the random factors *year* and *site*. Random effect *year*, which accounts for latent variation in climate conditions within each year explained less variance in the data compared to random effect site which accounts for latent variation in conditions at each site (residual variance for *year* = 0.514 and for *site* = 0.865).

The probability of pond drying in July was greatest for smaller ponds (low wetland area) located in watersheds with higher area of emergent wetland and low terrain ruggedness; ponds were less likely to dry in July during years with greater snowfall during the preceding winter and during the month of June, particularly when overall humidity during July was greater (low vapor pressure deficit; Table 5, Fig. 9). July precipitation, CHILI, watershed area, soil water storage, aspect and the area of forested wetlands in a watershed were less important (Table 5, Fig. 9). The area of open and shallow water predicted by the model was positively associated with wetland area while the estimated coefficients of all other variables had credible intervals that overlapped zero (Table 5).

Table 5. Coefficient estimates for the top hurdle model predicting hydroperiod (probability of drying) and area of standing water in the Southern Rocky Mountain Region of the United States.

Variables	Mean Coefficient Estimate	Std. Error	Lower 95% Credible Interval	Upper 95% Credible Interval	R-hat	Effective Sample Size (posterior distribution)
Gamma submodel (water area)						
Intercept	6.75	0.04	6.67	6.82	1.00	1238
Wetland area	1.54	0.03	1.48	1.60	1.00	1257
Precipitation (*pr*)	-0.01	0.01	-0.03	0.02	1.00	1325
Vapor Pressure Deficit (*vpd*)	0.01	0.02	-0.03	0.06	1.00	1459
Water storage (*stor*)	0.04	0.03	-0.01	0.09	1.00	1595
Snow previous winter	-0.02	0.04	-0.11	0.06	1.00	1495
Snow previous month (June)	0.02	0.02	-0.02	0.06	1.00	1463
Watershed area	0.07	0.04	0.00	0.15	1.00	1361

Variables	Mean Coefficient Estimate	Std. Error	Lower 95% Credible Interval	Upper 95% Credible Interval	R-hat	Effective Sample Size (posterior distribution)
Forested wetland	-0.04	0.04	-0.11	0.03	1.01	1193
Emergent wetland	-0.02	0.04	-0.10	0.06	1.00	1183
TRI (ruggedness)	0.00	0.04	-0.07	0.07	1.00	1169
Aspect	0.01	0.03	-0.04	0.07	1.00	1077
CHILI	0.00	0.03	-0.06	0.07	1.00	1355
Logistic submodel (probability of drying)						
Intercept	-2.51	0.32	-3.21	-1.89	1.00	1476
Wetland area	-2.04	0.30	-2.65	-1.47	1.00	1493
Precipitation (*pr*)	0.29	0.12	0.05	0.51	1.00	1654
Vapor Pressure Deficit (*vpd*)	0.84	0.22	0.42	1.29	1.00	1534
Water storage (*stor*)	0.43	0.25	-0.04	0.94	1.00	1315
Snow previous winter	-0.48	0.38	-1.23	0.24	1.00	1427
Snow previous month (June)	-0.62	0.29	-1.18	-0.06	1.00	1508
Watershed area	0.31	0.31	-0.30	0.92	1.00	1496
Forested wetland	-0.06	0.28	-0.60	0.48	1.00	1432
Emergent wetland	0.74	0.35	0.06	1.44	1.00	1350
TRI (ruggedness)	-0.79	0.33	-1.45	-0.16	1.00	1599
Aspect	-0.05	0.25	-0.54	0.44	1.00	1240
CHILI	-0.02	0.25	-0.52	0.46	1.00	1325

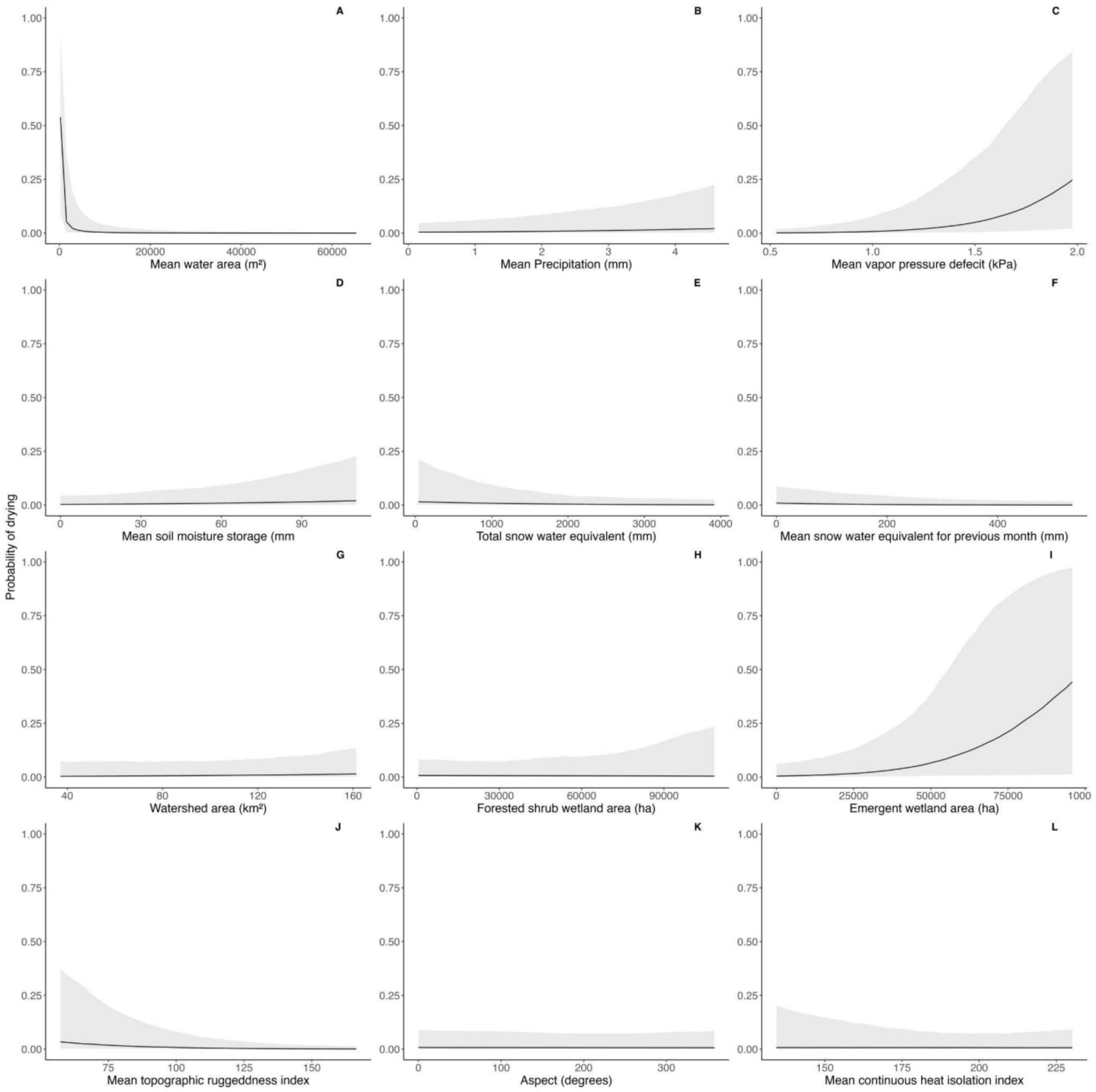


Figure 9. Marginal effects plots of coefficients included in the top hydroperiod model for the probability of drying for historical boreal toad breeding sites in the Southern Rocky Mountain Region of the United States.

Future hydroperiod predictions

Overall, we found that the probability of drying increased for the 2040-2069 horizon relative to the historical baseline, with higher drying under the RCP8.5 compared to RCP4.5 scenarios using the ensemble mean from all six GCMs (Figs. 10 and 11). Under the RCP8.5 scenario, the proportion of *ephemeral* ponds almost doubled, from 0.06 to 0.10, intermediate ponds increased slightly from 0.51 to 0.60, while the proportion of perennial and permanent ponds decreased from 0.35 to 0.25 and 0.08 to 0.05, respectively. The RCP4.5 scenario showed similar patterns, but the results were more moderate compared to RCP8.5.

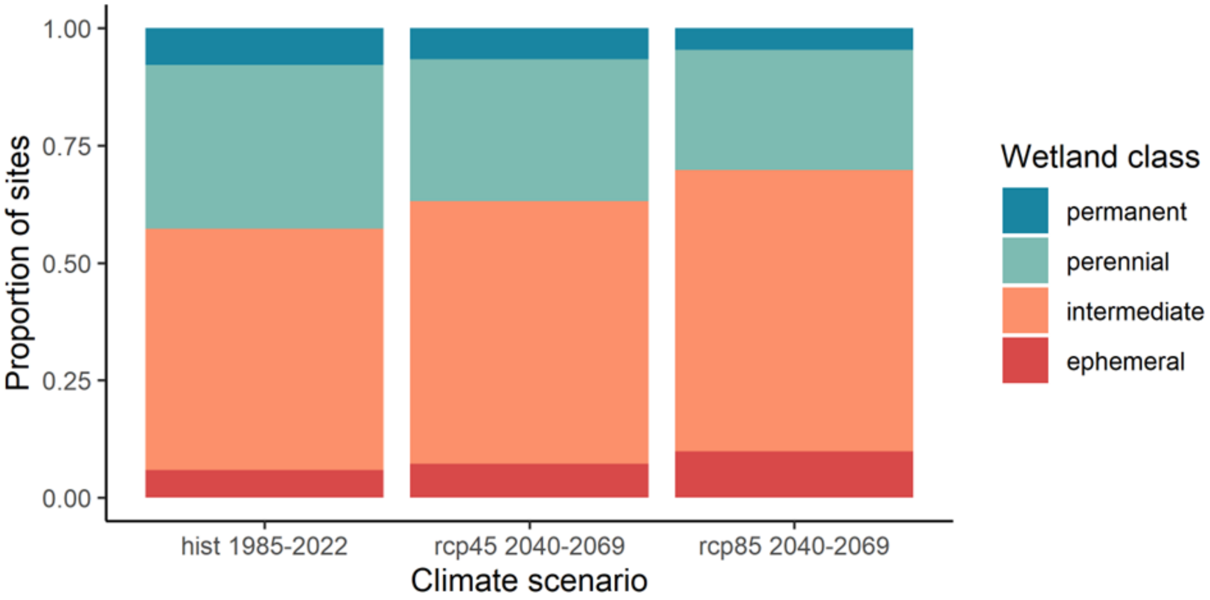


Figure 10. Shift in wetland hydroperiod class for historical boreal toad breeding sites under current (1985-2022) and future (2040-2069) climate scenarios (Representative Concentration Pathway 4.5 and 8.5, representing lower and higher emission scenarios, respectfully) in the Southern Rocky Mountain Region of the United States, using the ensemble mean from all six general circulation models.

The probability of pond drying in July increased under both RCPs relative to the historical drying regimes. However, there were differences in the future (2040-2069) hydroperiod predictions between the six GCMs, with the probability of drying being greatest under the IPSL.CM5A.LR model and lowest for the CanESM2 models under both RCP's relative to the historical (1985-2022) baseline (Fig. 11).

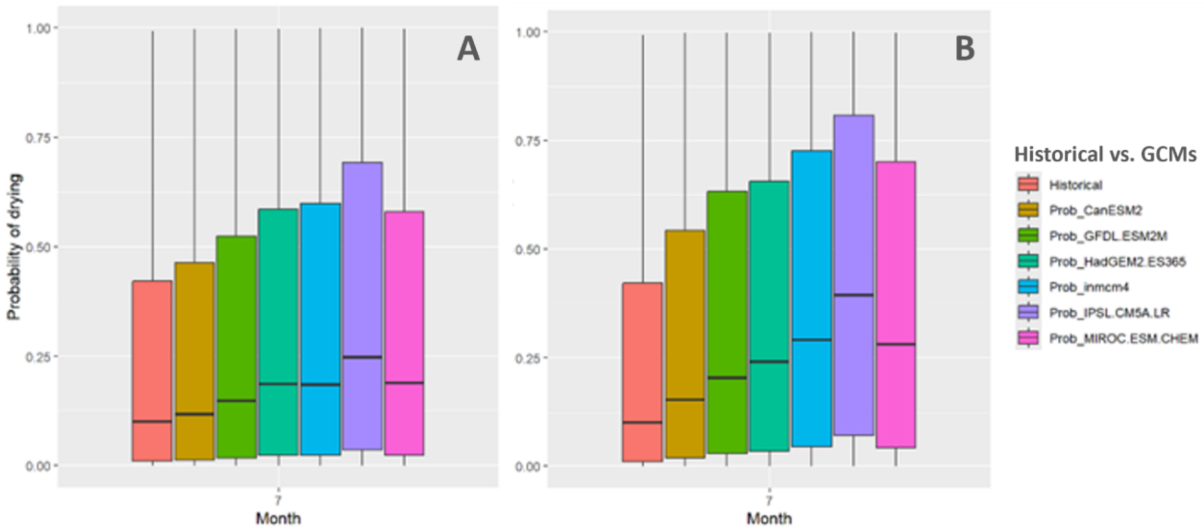


Figure 11. Probability of drying for historical boreal toad breeding sites in the Southern Rocky Mountain Region of the United States for current (1985-2022) and future (2040-2069) time periods under six Global Circulation Models and two Representative Circulation Pathways: (A) RCP4.5 and (B) RCP8.5

Comparison between pond-scale drying probabilities and hydroperiod class

We used the top hydroperiod model to calculate the proportion of years the ponds dried in July for the periods 1985 – 1999, 2000 – 2022 and 2040 – 2069 under the two RCPs (averaged across the six GCMs) and compared these proportions to the assigned hydroperiod classes described above. Drying probabilities and hydroperiod class predictions largely matched; the change in hydroperiod regime based on the AR metric (ephemeral, intermediate, perennial, permanent) between 1985-1999 and 2000-2022 periods was consistent with the proportion of years dried; ponds shifting from intermediate to ephemeral were predicted to dry each year (proportion of years drying 2001-2020 = 1), while changes from perennial to intermediate states occurred for ponds with no predicted drying. Ponds showing no change between the two historical time horizons had a large variation in proportion in years the site dried, but the median probability of drying was 0. The comparison under future scenarios showed higher uncertainty given that we averaged the proportion of years dried and the AR metric across the six GCMs. However, the trends are similar, with ponds switching between shorter hydroperiods (ephemeral to intermediate and *vice versa*) corresponding to a high proportion of years dried (Fig. 12).

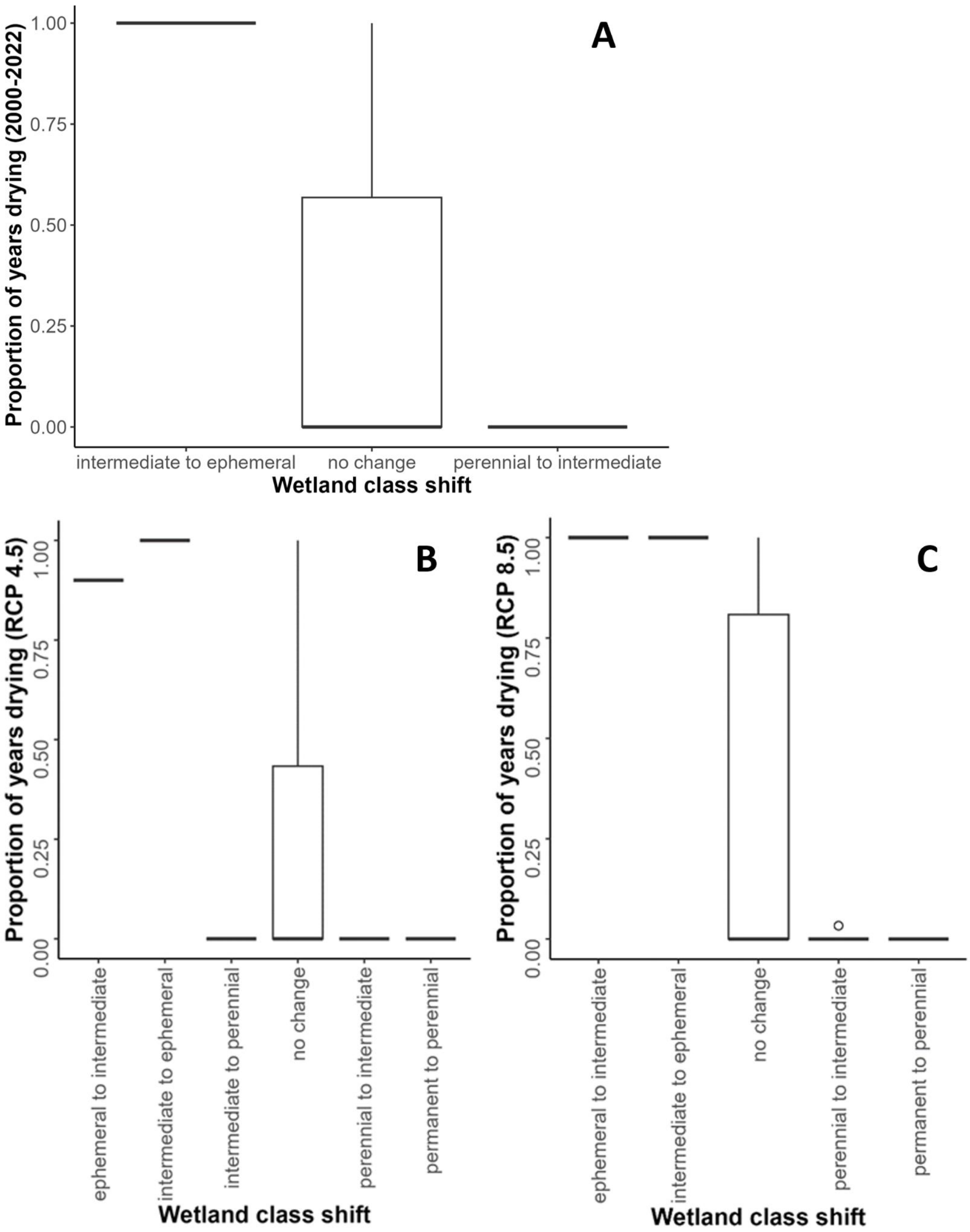


Figure 12. Change in hydroperiod type in the Southern Rocky Mountain Region of the United States between (A) 1985-1999 and 2000-2022, (B) 2000-2022 and 2040-2069 under Representative Circulation Pathway (RCP) 4.5 and (C) 2000-2022 and 2040-2069 under RCP 8.5 as a function of the proportion of years dried in each respective period. The hydroperiod type was determined using the Area Reduction metric (refer to Methods).

Occupancy modeling

Initial Occupancy - Toads

The posterior distribution of coefficient estimates for the linear term of *proportion of years dried* on the probability of initial occupancy of toads suggested a weakly negative relationship (indicated by 95% credible intervals that overlap zero), but the posterior distribution of coefficient estimates for the quadratic term suggested a weakly positive relationship (Fig. 13A). Contrary to our hypothesis, this resulted in a concave curve, where the probability of initial occupancy was lowest (mean: 0.48, 95% CI: 0.28-0.67) at sites that dried ~47% of the time (Fig. 13B).

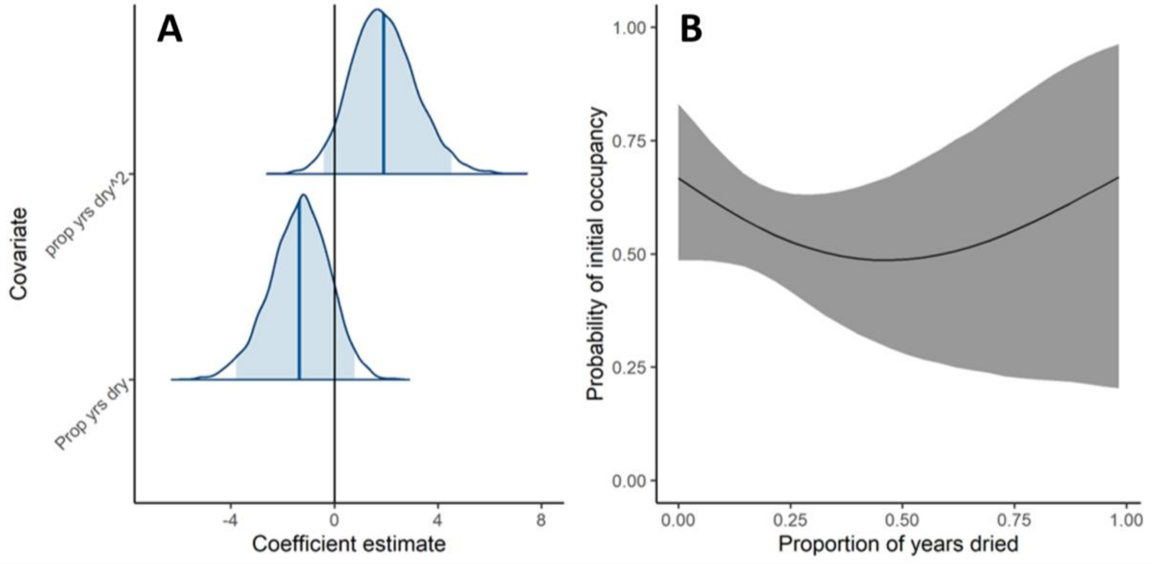


Figure 13. Plot of the posterior coefficient estimates for the effect of the quadratic term of the proportion of years dried on the probability of initial occupancy of toads at historical breeding sites in the Southern Rocky Mountain Region of the United States at a site (A) and associated marginal effects plot (B). In panel A, the thick blue line represents the median coefficient estimate and the shaded blue areas represent the 95% credible interval. In panel B, the solid black line represents the mean probability of occupancy for a range of values for the covariate and the shaded gray area represents the 95% credible interval.

Probability of Colonization - Toads

The posterior distribution of coefficient estimates for the linear term of *proportion of years dried* on the probability of colonization of toads was strongly positive (indicated by 95% credible intervals that do not overlap zero), but the posterior distribution of coefficient estimates for the quadratic term was strongly negative (Fig. 14A). This resulted in a convex curve which aligned with our hypothesis, and the probability of colonization was highest at sites that have dried ~43% of the time in the last 15 years (Fig. 14B).

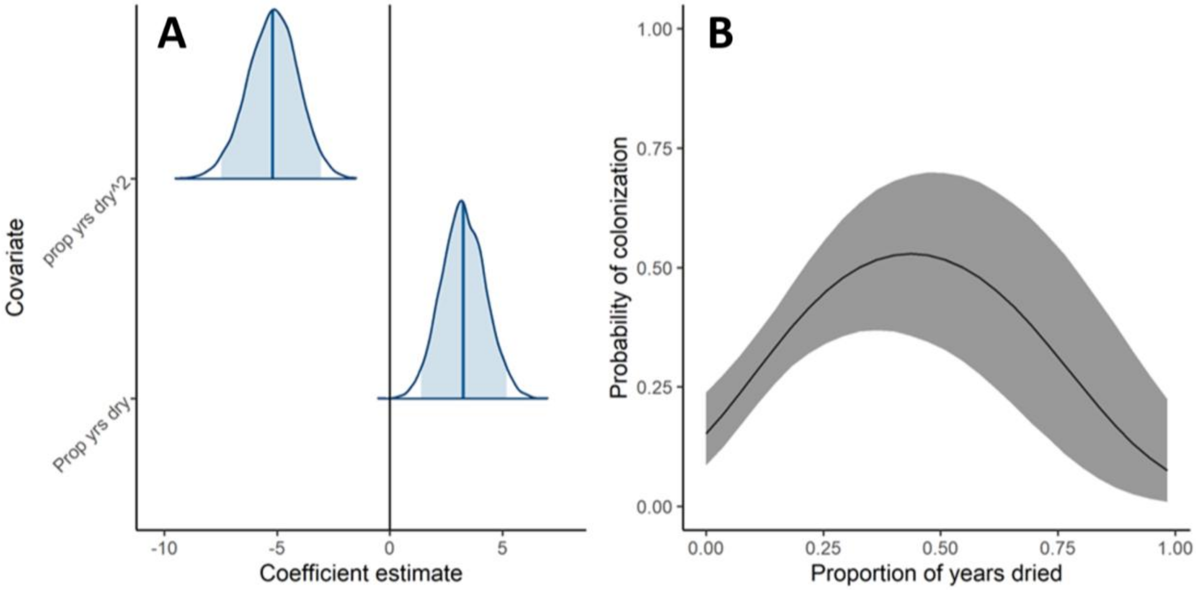


Figure 14. Plot of the posterior coefficient estimates for the effect of the quadratic term of the proportion of years dried on the probability of colonization of toads at historical breeding sites in the Southern Rocky Mountain Region of the United States at a site (A) and associated marginal effects plot (B). In panel A, the thick blue line represents the median coefficient estimate and the shaded blue areas represent the 95% credible interval. In panel B, the solid black line represents the mean probability of occupancy for a range of values for the covariate and the shaded gray area represents the 95% credible interval.

Probability of Extinction - Toads

The posterior distribution of coefficient estimates for the linear term of *proportion of years dried* on the probability of extinction of toads was strongly positive, but the posterior distribution of coefficient estimates for the quadratic term was strongly negative (Fig. 15A). Contrary to our hypothesis, this resulted in a convex curve, and the probability of extinction was highest at sites that have dried ~47% of the time in the last 15 years (Fig. 15B). Also contrary to our hypothesis, the posterior distribution of the coefficient estimates for the effect of the number of *May freeze events* was weakly negative (Fig. 15A,C), and extinction probability was highest (mean: 0.52, 95% CI 0.23-.80) when the proportion of years with freeze events was near zero. The posterior distribution of the coefficient estimates for the effect of *season length* was strongly positive (Fig. 15A, D), indicating that as season length increases, the probability of extinction increases as well, aligning with our hypothesis. Our model indicates extinction probability has a mean of 0.82 (95% CI 0.68-0.92) at sites with a *season length* that is 15 days greater than the 35-year climate average season length. Finally, the posterior distribution of the coefficient estimates for the effect of *Bd* presence on boreal toad extinction probability was weakly positive (mean probability = 0.12, 93% CI: -2.66 – 2.5), contrary to our hypothesis.

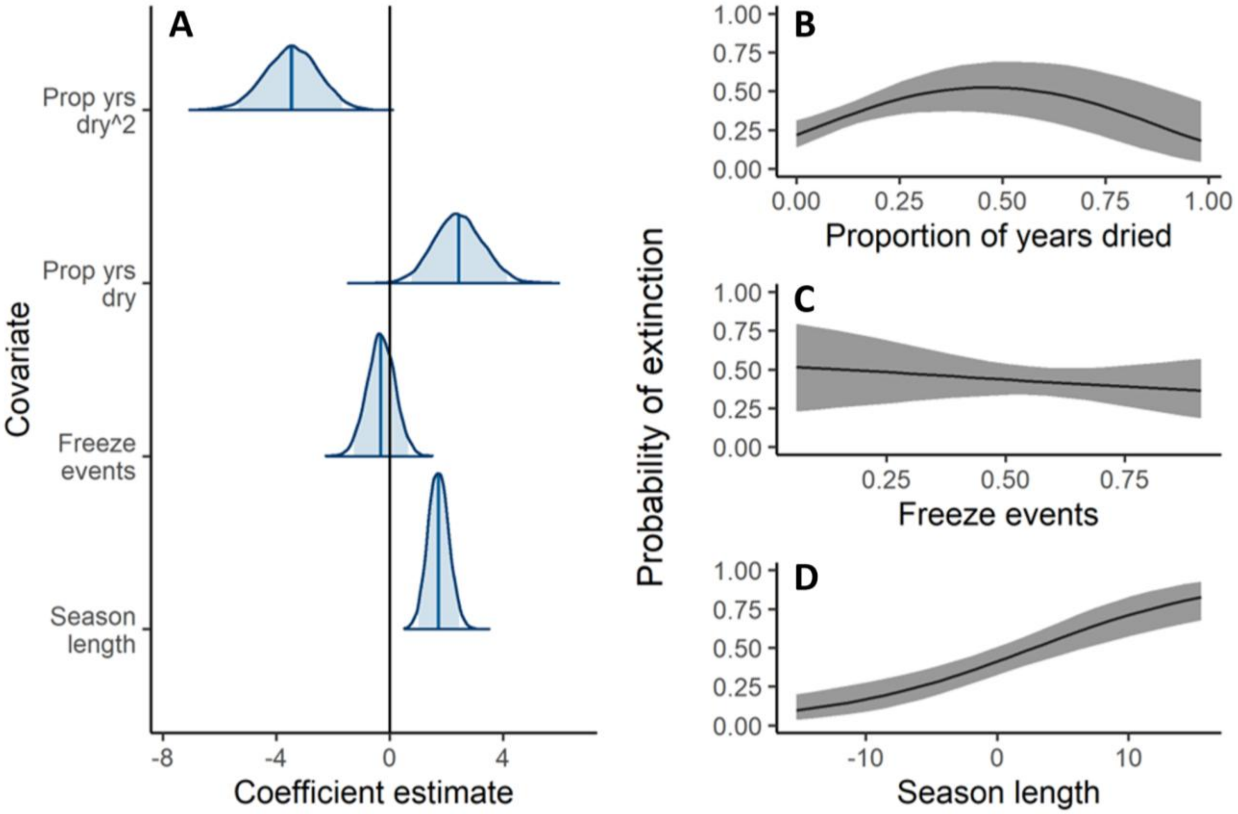


Figure 15. Plot of the posterior coefficient estimates for the effects of each covariate on the probability of extinction of toads at historical breeding sites in the Southern Rocky Mountain Region of the United States at a site (A) and associated marginal effects plot (B-D). In panel A, the thick blue line represents the median coefficient estimate and the shaded blue areas represent the 95% credible interval. In panels B-D, the solid black line represents the mean probability of occupancy for a range of values for the covariate and the shaded gray area represents the 95% credible interval.

Initial Occupancy - Bd

The posterior distribution of the coefficient estimates for *growing degree days* and *proportion of years dried* with respect to the probability of initial occupancy of *Bd* were both weakly positive (Fig. 16). The probability of initial occupancy of *Bd* ranged from a mean of 0.34 (CI: 0.22- 0.50) when the *proportion of years dried* was zero, to a mean of 0.52 (CI: 0.14- 0.89) when the *proportion of years dried* was 0.98. The probability of initial occupancy of *Bd* ranged from a mean of 0.04 (CI: 0.01- 0.11) when the average number of *growing degree days* in the last 15 years was 9.42, to a mean of 0.10 (CI: 0.03 – 0.24) when the average number of *growing degree days* in the last 15 years was 137.2.

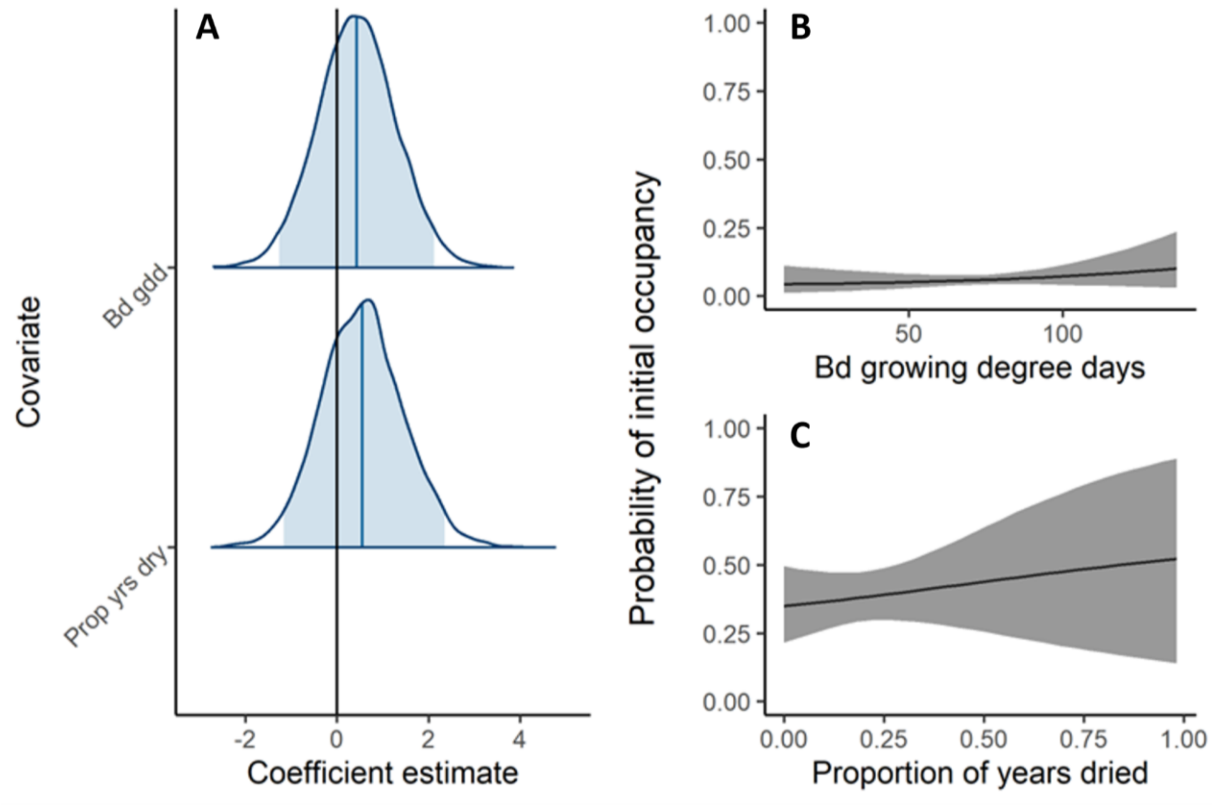


Figure 16. Plot of the posterior coefficient estimates for the effects of each covariate on the probability of initial occupancy of *Batrachochytrium dendrobatidis (Bd)* at historical breeding sites in the Southern Rocky Mountain Region of the United States at a site (A) and associated marginal effects plot (B, C). In panel A, the thick blue line represents the median coefficient estimate and the shaded blue areas represent the 95% credible interval. In panels B and C, the solid black line represents the mean probability of occupancy for a range of values for the covariate and the shaded gray area represents the 95% credible interval.

Probability of Colonization - Bd

Similar to initial occupancy probability, the posterior distribution of the coefficient estimates for *growing degree days* on the probability of colonization of *Bd* was weakly positive (Fig. 17). However, the posterior distribution of the coefficient estimates for the *proportion of years dried* on the probability of colonization of *Bd* was centered on zero, suggesting no effect.

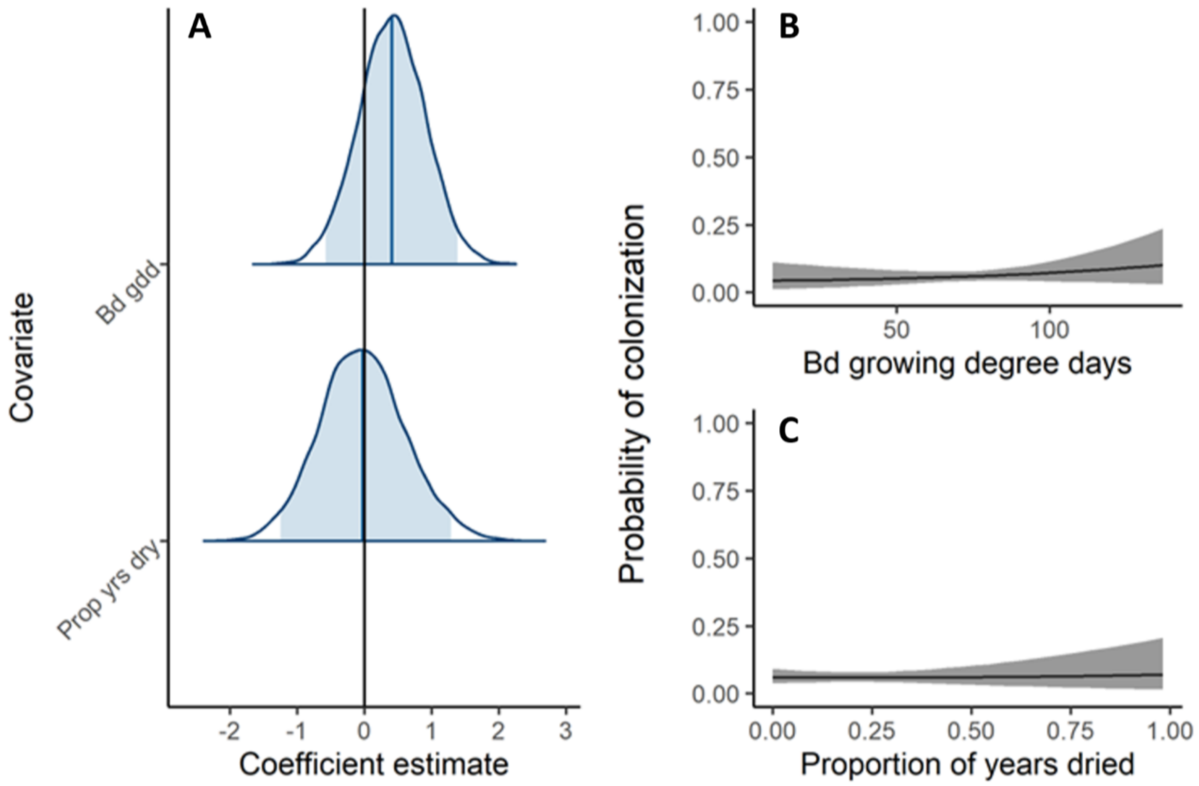


Figure 17. Plot of the posterior coefficient estimates for the effects of each covariate on the probability of colonization of *Batrachochytrium dendrobatidis (Bd)* at historical breeding sites in the Southern Rocky Mountain Region of the United States at a site (A) and associated marginal effects plot (B, C). In panel a, the thick blue line represents the median coefficient estimate and the shaded blue areas represent the 95% credible interval. In panels B and C, the solid black line represents the mean probability of occupancy for a range of values for the covariate and the shaded gray area represents the 95% credible interval.

Current and Future Occupancy States

The mean predicted probability that a site within the SRMR is occupied by boreal toads only (state 1) declined from 0.37 (95% CI: 0.11- 0.69) in 2001 to 0.21 (95% CI: 0.06 – 0.43) in 2022, a decline of 43.24% (Fig. 18a). The mean predicted probability that a site within the SRMR is occupied by boreal toads and *Bd* (state 2) declined from 0.15 (95% CI: 0.015 – 0.38) in 2001 to 0.08 (95% CI: 0.01 – 0.25) in 2022, concurrent to the decline in boreal toad occupancy. The overall mean occupancy probability of a site in the SRMR being occupied by ‘toads only’ under current climate conditions was 0.30 (95% CI: 0.08-0.57) (Fig. 18b). We used the ensemble mean of the 6 climate models (Table 1) to predict future occupancy, and we found that it declined to 0.16 (95% CI: 0.04 – 0.34) under the RCP 4.5 climate scenario and 0.14 (95% CI: 0.04 – 0.30) under the RCP 8.5 climate scenario (Fig. 18b).

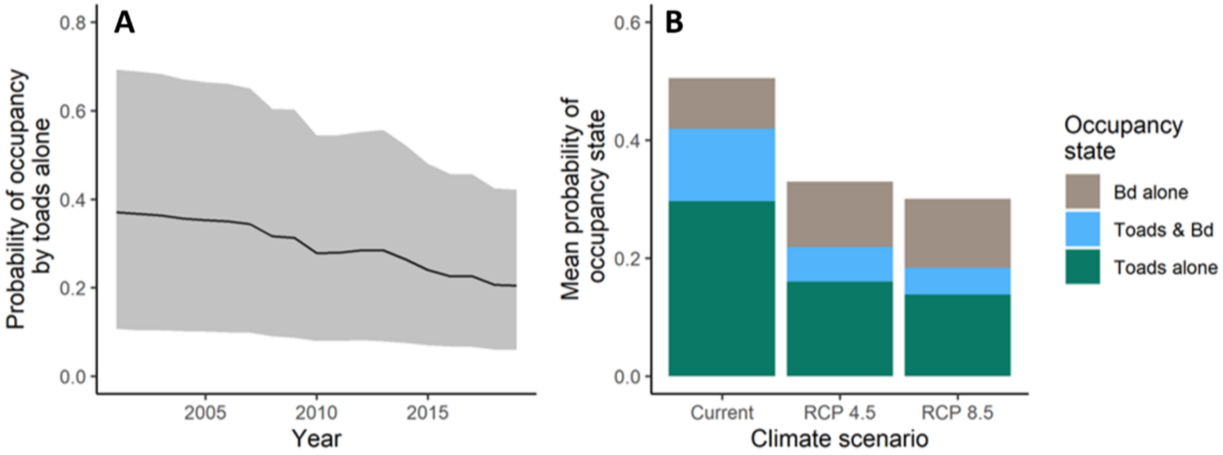


Figure 18. Probability of a historical boreal toad breeding site within the Southern Rocky Mountain Region (SRMR) being occupied by toads alone between 2001 and 2019 (grey shaded region represents 95% credible interval, panel A). Comparison of occupancy state probabilities between current and future climate scenarios (B). Representative Circulation Pathways (RCP) 4.5 and RCP8.5

The mean predicted probability of a site occupied by boreal toads only (state 1) within a mountain range under current conditions ranged from 0.19 (95% CI: 0.02 – 0.49) for the Elkhead Mountain Range (n = 3 sites) to 0.38 (95% CI: 0.11 – 0.66) for the Grand Mesa Mountain Range (n = 1 site, Fig. 19, Table 6). The mean probability of a site occupied by boreal toads and *Bd* (state 2) ranged from 0.07 (95% CI: 0.004 – 0.28) for Elkhead Mountain Range and 0.16 (95% CI 0.02 – 0.37, Fig. 19). Sawatch Mountain range and the Front Range contain over half of the 152 breeding sites for which we made predictions (n = 46 and n = 45 respectively). For the Sawatch Mountain Range, the mean probability that a site was occupied by boreal toads only (state 1) in 2001 was 0.39 (95% CI 0.11 – 0.74), which declined to 0.20 (95% CI: 0.06 – 0.41) by 2019. The mean probability of a site in the Sawatch Mountain Range being occupied by boreal toads and *Bd* (state 2) was 0.16 (95% CI: 0.01 – 0.39) in 2001 and 0.07 (95% CI: 0.1 – 0.23) in 2019. The overall mean probability of a site being occupied by toads only in the Sawatch Mountain Range was 0.30 (95% CI: 0.08 – 0.58; Fig. 19). Under future climate conditions using the ensemble mean of 6 GCMs (Table 6), the mean probability that boreal toads alone (state 1) occupied a site within the Sawatch Mountain Range was 0.16 (95% CI: 0.03 – 0.38) under the RCP 4.5 scenario, and 0.14 (95% CI: 0.03 – 0.33) under the RCP 8.5 scenario (Fig. 19). For the Front Range, the mean probability that boreal toads alone (state 1) occupy a site within that mountain range was 0.35 (95% CI 0.10 – 0.66) in 2001, and declined to 0.21 (95% CI: 0.06-0.43) in 2019. The overall mean probability of toads alone occupying a site within the Front Range was 0.29 (95% CI: 0.08 – 0.57). Under future climate conditions, the mean probability that boreal toads alone occupied a site within the Front Range was 0.16 (95% CI: 0.04 – 0.36) under the RCP 4.5 scenario, and 0.14 (95% CI: 0.03 – 0.31) under the RCP 8.5 scenario (Fig. 19).

The biggest decline in the mean probability of occupancy for state 1 (boreal toads only) under future climate change was in the Grand Mesa Mountain Range, from 0.38 under current conditions to 0.13 under the RCP 4.5 scenario and 0.11 under the RCP8.5 scenario; however, the Grand Mesa Mountain Range only consists of a single site (Table 6). The second biggest decline in boreal toad occupancy (state 1) under future climate change was the Medicine Bow Mountain Range (n = 3 sites), which declined from a mean of 0.35 under current climate conditions to 0.11 under the RCP 4.5 climate scenario and 0.10 under the RCP 8.5 climate scenarios (Table 6). The Elkhead Mountain Range had the lowest decline in occupancy under future conditions, declining from a mean of 0.19 under current conditions to 0.11 under the RCP 4.5 scenario and 0.09 under the RCP 8.5 scenario (Table 6).

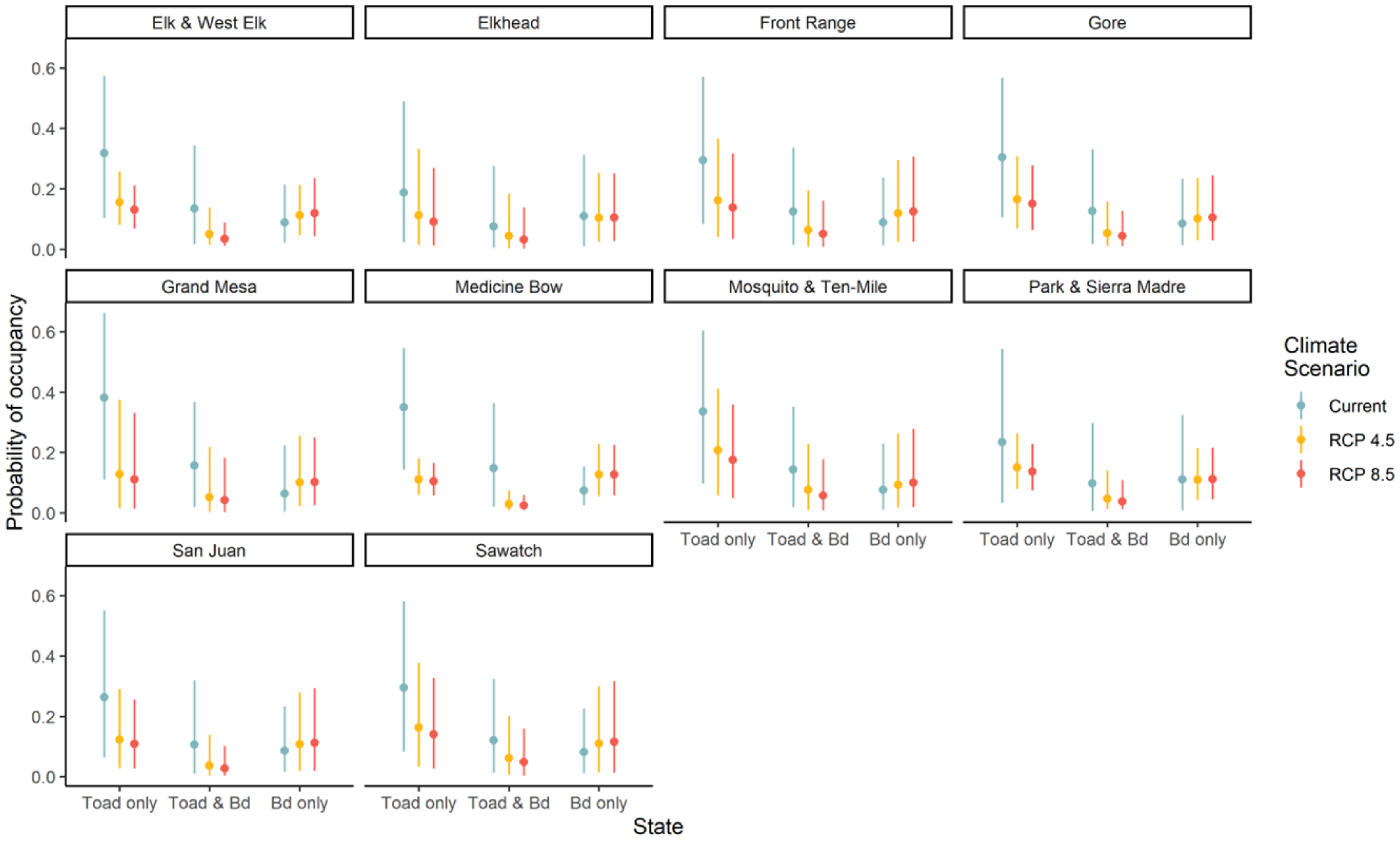


Figure 19. Probability of a historical boreal toad breeding site within a mountain range being in one of three states (occupied by toads only, occupied by toads and *Batrachochytrium dendrobatidis* (*Bd*), or occupied by *Bd* only) in the Southern Rocky Mountain Region of the United States under current climate conditions (blue) and the ensemble mean for the six general circulation models (GCMs) for two future climate

scenarios: representative concentration pathway (RCP) 4.5 (lower emissions, orange line) or 8.5 (higher emissions, red line). Points represent the mean value and vertical lines represent the 95% credible interval.

Table 6. Comparison of mean occupancy values for each state under current and future climate scenarios (using the ensemble mean for all six general circulation models (GCMs)) for each mountain range containing boreal toad breeding sites in the Southern Rocky Mountain Region. Representative concentration pathway = RCP. *Batrachochytrium dendrobatidis = Bd*

Mountain range	Number of sites	Occupancy state	Current	RCP 4.5	RCP 8.5
Elk & West Elk	20	Toad Only	0.32	0.15	0.13
		Toad & *Bd*	0.13	0.05	0.03
		Bd Only	0.09	0.11	0.12
Elkhead	3	Toad Only	0.19	0.11	0.09
		Toad & *Bd*	0.07	0.04	0.03
		Bd Only	0.11	0.10	0.10
Front Range	45	Toad Only	0.29	0.16	0.14
		Toad & *Bd*	0.12	0.06	0.05
		Bd Only	0.09	0.12	0.13
Gore	11	Toad Only	0.30	0.17	0.15
		Toad & *Bd*	0.13	0.05	0.04
		Bd Only	0.08	0.10	0.10
Grand Mesa	1	Toad Only	0.38	0.13	0.11
		Toad & *Bd*	0.16	0.05	0.04
		Bd Only	0.06	0.10	0.10
Medicine Bow	2	Toad Only	0.35	0.11	0.11
		Toad & *Bd*	0.15	0.03	0.02
		Bd Only	0.07	0.13	0.13
Mosquito & Ten-Mile	10	Toad Only	0.34	0.21	0.18
		Toad & *Bd*	0.14	0.08	0.06
		Bd Only	0.08	0.09	0.10

Park & Sierra Madre	6	Toad Only	0.23	0.15	0.14
		Toad & *Bd*	0.10	0.05	0.04
		Bd Only	0.11	0.11	0.11
San Juan	8	Toad Only	0.26	0.12	0.11
		Toad & *Bd*	0.11	0.04	0.03
		Bd Only	0.09	0.11	0.11
Sawatch	46	Toad Only	0.30	0.16	0.14
		Toad & *Bd*	0.12	0.06	0.05
		Bd Only	0.08	0.11	0.12

Discussion

Current and future occupancy

Our analysis indicates a >43% decline in the probability that boreal toads occupy a given breeding site occupancy across the SRMR, which aligns with empirical observations over the last 2 decades (Crockett 2023). While this decline has largely been attributed to *Bd*, we highlight the strong effect of increasing active season length on toad extinction probability (Fig. 15). While this result may seem counterintuitive given the short active season length relative to low elevation amphibians, this relationship may highlight a phenological mismatch, particularly in the fall, when food resources may be limited but toads are still active due to high temperatures (Church et al. 2007; Reading 2007; Williams et al. 2015). Additionally, the high elevation habitat for boreal toads in SRMR is a snow-dominated system, with relatively little precipitation falling during the active season (Mote et al. 2005). This may result in a drier landscape as the active season length is extended into the fall, increasing desiccation risk (Lertzman-Lepofsky et al. 2020; Greenberg & Palen 2021).

Additionally, our results indicate that the probability of initial occupancy is lowest for sites that dry about half the time (within the prior 15 years), and that the probability of colonization and extinction of toads is highest for these wetlands as well. This highlights the importance of perennial and intermediate wetlands for boreal toads, as these variable wetlands support the majority of boreal toad breeding (Fig. 11) but are also the most likely to have highly dynamic occupancy patterns (e.g., high rates of extinction and re-colonization, Fig. 15 and Fig. 14). Under future climate scenarios, our hydroperiod models predict that some sites will shift from more permanent to more ephemeral (Fig. 11), which is likely to exacerbate declines in toad occupancy if current relationships between toad occupancy and wetland drying remain the same (Fig. 19).

Our model suggests a weak negative relationship between the proportion of years with freezing events in the month of May and toad extinction probability, indicating that the probability of extinction declines as the proportion of years with freeze events in May increases. While this is contrary to our hypothesis, the pattern is consistent with our findings for active season length. These covariates were not highly correlated, and thus are both included in the model. However, as temperatures warm and the active season length increases the number of freeze events is likely to decrease as well. Thus, while we hypothesized that May freeze events could increase mortality at the egg stage due to freezing, our results indicate that the demographic effect of this is unlikely to be greater than the effect of warmer and longer active seasons on the probability of toad extinction.

Overall, we find that the decline in occupancy in the SRMR is predicted to be exacerbated by climate change. The mean probability of occupancy of toads in the SRMR declines by an additional ~47% (from 0.30 to 0.16) under the RCP4.5 scenario and ~53% (from 0.30 to 0.14) under the RCP8.5 scenario. The declines observed between 2001 and 2019, coupled with the predictions of further declines in the future due to the combined effect of changing hydroperiod and *Bd*, indicate a bleak picture for toads in the SRMR. However, the BTCT has developed a suite of conservation actions, and a decision-support tool that quantifies the probability of success of several conservation actions (Gerber et al. 2018). Importantly, related work indicates that this decision framework (Gerber et al. 2018) is robust to unknown or highly uncertain *Bd* dynamics (Mosher et al. 2018a; Gerber et al. 2024). We build on these decision-support tools by elucidating spatiotemporal trends in occupancy patterns with respect to climate covariates. The output from our analyses are easily accessible to the BTCT via a web tool developed with input from boreal toad managers (described below). The tool provides 1) background information on our modeling approaches, 2) geographic context for the analysis in the form of an interactive map visualizing boreal toad breeding and translocation sites (identified in collaboration with Colorado Parks and Wildlife), watershed drying patterns, and 3) summary statistics and time series plots of current and future estimates of boreal toad and *Bd* occupancy at different management levels (individual site, mountain range, and all sites combined). For additional context at the site level, we also included plots of boreal toad colonization and extinction, as well the 15-year probability of drying (the covariate used in the model). Each page on the tool is accompanied by a ‘How to’ guide to inform users of the many ways they can interact with the tool.

Spectral Mixture Analysis

In addition to current and future occupancy predictions we also applied a remote sensing method, SMA, to generate estimates of surface water area for historical breeding sites and relevant watersheds. The estimates of surface water area were used to parameterize hydroperiod models, and the watershed analyses were used to assess landscape-scale drying patterns for multiple amphibian species within the North Central region (boreal toads, Great Basin spadefoot toads, wood frogs). While the boreal toad is a relatively data-rich species (i.e., long-term monitoring across the region with fine-scale occupancy data), both the Great Basin spadefoot toad and wood frog lack annual monitoring programs, and little is known about their status and ecology within the region (Hinderer et al. 2024). We demonstrate the ability to generate critical hydrology and hydroregime data for these data poor species; data that can inform management decisions in the absence of fine-scale biological data. For example, we found that 83% of watersheds within the Great Basin spadefoot range and 71% of watersheds for the relic population of wood frogs were drier in the latter half of our time series (2000-2022) than the prior 15 years (1985-1999).

While SMA is a valuable tool for filling data gaps in wetland dynamics for aquatic or semi-aquatic species, there are also inherent sources of error in the SMA that must be considered when applying it to different landscapes and geographic areas. SMA can have difficulty distinguishing between surface water and shadows created by trees or other landscape features, making densely forested areas particularly challenging for the application of this method. Caution should also be used when working at larger scales such as HUC12 watersheds, given that applying the SMA to larger study areas likely introduces more noise and potential for error in the outputs. In the case of this study, the bias is likely to be consistent across our area of interest, and thus the results of the watershed-level SMA remain useful for comparing surface water presence and drying patterns relative to other watersheds, or within watersheds over time. Additional ground-truthing of these results is necessary to rely on absolute surface water area values generated from this analysis.

Hydroperiod modelling

We demonstrate the utility of the SMA output, coupled with large, publicly available long-term climate and climate-derived datasets (i.e., water balance) to develop predictive models of boreal toad breeding pond hydroperiods in the SRMR and to quantify hydroperiod shift under several GCMs and RCPs for 2040-2069. The SMA predictions and the long-term daily historical gridMET data (1985-2022), and the water balance data derived via multivariate adaptive constructed analog (MACA), provided the opportunity for fine-temporal scale predictions of surface water area and the probability of drying under past and current conditions, and future forecasts.

The hydroperiod predictions (probability of drying in July, the most sensitive month for boreal toad larval development) were driven largely by pond size and water balance and climate covariates (Table 5). In particular, the amount of snow in the previous winter was negatively associated with pond drying, which was expected given that ponds in this alpine system are fed largely via snowmelt. The snowpack across the SRMR can vary regionally, and it can fall for 6+ months of the year, including June. Other water availability related variables, such as precipitation and soil water storage had a lower-than-expected effect on pond drying. Another important driver of pond drying was the vapor pressure deficit, which is a measure of how much moisture the air can hold compared to how much is actually in the air. This moisture-related metric is temperature-dependent, so that at a similar air humidity value, the vapor pressure deficit is greater under warmer temperatures, thus leading to greater potential for evaporation. Overall, the results of the hydroperiod models are intuitive as they suggest that smaller ponds are at greater risk of drying when snowpack during the previous winter (and in June) is lower and overall July temperatures are higher, contributing to higher water pressure deficit and increased evaporation. Interestingly, we also found a positive association between the probability of drying and the amount of emergent wetland in a watershed and an inverse relationship with topographic ruggedness. A potential explanation for these results is that less rugged watersheds can accommodate larger areas of emergent wetlands, but they may also be shallower and more susceptible to evaporation, thus drying faster.

The hydroperiod predictions for the 2040-2069 horizon follow our hypothesis that the likelihood of drying will increase, particularly under the higher emissions RCP8.5 scenario. While there was high variability in hydroperiod predictions between GCMs, the proportion of ponds switching to less permanent and more ephemeral states increases overall (Fig. 10). The most extreme GCM was the IPSL.CM5A.LR model, which predicts warmer, drier winters (Steen 2017). During warmer and drier winters, precipitation is more likely to be rain, rather than snow, and periodic warm spells can lead to snowmelt, thus lower snowpack. The amount of snow in the previous winter (assuming colder temperatures that ensure consistent snowpack) was one of the main predictors for pond drying, thus greater drying rates under this particular model are expected.

We found shifts in hydroperiod type towards more drying (from intermediate to ephemeral and perennial to intermediate) between the 1985-2000 and 2011-2022 horizons. These results are consistent with the broader watershed SMA-derived drying predictions. Changes in hydroperiod type for the future (2040-69) horizon are more uncertain, with ponds switching in both directions (e.g., ephemeral to intermediate and *vice versa*); this could likely be due to spatial variability in predictions under various GCM's.

Conclusions

This project leveraged long-term, empirical data collected by a collaborative team (BTCT) with novel remotely sensed data to produce a decision-support tool for managing an imperiled amphibian species now and in the future. Our framework demonstrates the importance of long-term monitoring by multi-agency collaborations, particularly of long-lived species, to generate critical data for making informed decisions. While the boreal toad and *Bd* data have contributed to several other informative analyses (Muths et al. 2003, 2017; Converse et al. 2017; Gerber et al. 2018; Mosher et al. 2018a, 2018b; Crockett et al. 2020; Cayuela et al. 2021b) this analysis is the first to elucidate the demographic effects of climate change and explore spatial patterns in a hierarchical manner (i.e., individual sites, mountain ranges, SRMR). The supporting web tool allows managers from different jurisdictions to focus on site-specific estimates and future predictions to inform management of individual sites, while information at the level of 'mountain ranges' can help inform broader conservation efforts. For example, one goal of the BTCT is to maintain at least one occupied breeding site in each mountain range across the SRMR (Crockett 2023). Our analysis allows managers to look at trends and future predictions across mountain ranges to guide decisions targeting this goal.

Acknowledgements

We thank Jami Brislan for working with boreal toad managers to update the boreal toad breeding site locations and digitize breeding wetlands. We thank Brian Gerber, Brittany

Mosher, and Larissa Bailey for modeling guidance. We also thank Larissa Bailey and Andy Treble for assisting with collating detection/non-detection data for boreal toads and *Bd*. We thank Harry Crockett and Jenn Logan for iterative feedback on the direction of the project over time, as well as members of the BTCT for being available to brainstorm hypotheses, provide data and answer general questions about the data, and Jenn Logan, Boyd Wright, Alex Jouney, Matt Haworth, Daniel Cammack, and Tyler Swarr for exploring prototypes of the web tool and providing feedback. We thank Charles Labuzzetta, Ross Hinderer, Elizabeth Krone, and Blake Hossack for helpful reviews of the report. This is contribution #938 of the USGS Amphibian Research and Monitoring Initiative. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Data Availability

The data that support the decision support tool are available in a U.S. Geological Survey data release: Kissel, A.M., Lacey, L.M., Popescu, V.D., Dyck, M.A., Bailey, L., and Muths, E., 2025, Current and future hydrology and occupancy predictions for boreal toads (Anaxyrus boreas boreas) in the Southern Rocky Mountains: U.S. Geological Survey data release, https://doi.org/10.5066/P1VF3ZX4.

Conclusions and Recommendations

While we originally envisioned updating the structured decision analysis developed by Gerber et al. (2018), this process would have required a commitment from members of the BTCT that most did not have capacity for. Thus, we developed an alternative decision-support tool. While it does not incorporate alternative management strategies, it provides managers with critical predictions of occupancy at multiple landscape scales, in addition to other important landscape scale patterns (watershed drying patterns, burn probabilities for each watershed) which has not been available before in a single, user-friendly platform. We also addressed pressing questions posed by the team regarding the effects of a suite of climate covariates on toad occupancy dynamics. Given the strong patterns we observed between increasing active season length and toad extinction, a next step could be to understand the mechanisms behind this pattern. Designing studies to explore potential phenological mismatches between boreal toads and food availability during extended active seasons, particularly at the beginning and end of the active season, would be a logical extension of our project. Quantifying desiccation risk that may increase at the end of an active season due to higher-than-average temperatures and drier landscapes would be informative as well.

Outreach and Products

Articles in preparation, under review, accepted, or published in peer reviewed journals and non-peer reviewed journals

1. Kissel AM, Muths E, Bailey L, Lacey M, Halabisky M, Dyck M, Popescu V. *In prep*. A framework for guiding management decisions for amphibians in an uncertain future.
2. Lacey M, Halabisky M, Popescu V, Dyck M, Muths E, Kissel AM. *in Prep*. Using remotely sensed data to assess changes in hydrology in the Southern Rocky Mountains.
3. Hinderer RK, Hossack BR, Eby LA. 2024. Using life history traits to assess climate change vulnerability in understudied species. Integrative Conservation. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/inc3.77

Conference presentations, seminars, webinars, workshops

1. Kissel AM, Muths E, Bailey L, Lacey M, Halabisky M, Dyck M, Popescu V. 2024. A framework for guiding management decisions for amphibians in an uncertain future. Society for Conservation GIS. Shepherdstown, West Virginia. September 4-6, 2024.
2. Kissel AM, Muths E, Yackel Adams, AA. Two sides of the conservation coin: applying quantitative tools to manage invasive reptiles and native amphibians. FORT Seminar Series, Fort Collins, CO. May 1, 2024

Communications with decision-makers

1. Meeting with BTCT signatories and collaborators on January 5, 2022 to identify relevant climate covariates for modeling. Discussion facilitation by Amanda Kissel. In attendance: Harry Crockett (Colorado Parks and Wildlife), Leland Pierce (New Mexico Department of Game and Fish), Esther Nelson (U.S. Forest Service), Wendy Estes-Zumpf, (Wyoming Game and Fish Department), Larissa Bailey (Colorado State University), Erin Muths (U.S. Geological Survey)
2. Communications with BTCT:
    - Attended the annual BTCT meeting on March 4th, 2022. There were >20 stakeholders from various agencies that work across the species range. Amanda Kissel gave an update on the project and put out a data request for any additional data on chytrid, boreal toad presence/absence data, and breeding site locations/polygons.
    - Virtually attended the annual BTCT meeting in March, 2023. There were >20 stakeholders from various agencies that work across the species range. Amanda Kissel gave an update on the project and requested breeding site locations information from managers via a shared google sheet.
    - Multiple conversations with several Team members that also serve as decision makers during the spring of 2023 via email and phone to refine breeding point locations and develop spatial polygons that reflected the extent of the breeding areas.
3. Meetings with decision makers at Colorado Parks and Wildlife took place over multiple months, including an initial discussion on July 24, 2024 regarding management strategy priorities and other decision-support needs with Jenn Logan, Native Aquatic Species Manager, and Boyd Wright, Native Aquatic Species Coordinator. We then met again on September 13, 2024 to walk decision makers (Jenn Logan, Boyd Wright, Alex Jouney,

Matt Haworth, Daniel Cammack, and Tyler Swarr) through a beta version of our decision-support tool. We also shared a link to the tool and an accompanying user testing survey to gather feedback on tool appearance and functionality. The current version of the decision-support tool was then deployed on September 16, 2024.

Websites created for the project

The decision support web application created for this project has limited availability owing to the sensitive nature of the boreal toad breeding site spatial data it contains. Contact Amanda Kissel or Mae Lacey for more information.

Data or databases

The following data are available at https://doi.org/10.5066/P1VF3ZX4.:

1. SMA outputs for historical breeding sites and watersheds
2. Hydrology modeling outputs for current and future climate scenarios
3. Occupancy modeling outputs for current and future climate scenarios

Additionally, we will provide the Boreal toad team with an updated spatial database of historical breeding points and polygons and associated excel file with notes and communications from managers (not released due to the sensitive nature of the location data.

References

Abatzoglou JT. 2013. Development of gridded surface meteorological data for ecological applications and modelling. International Journal of Climatology **33**:121–131. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/joc.3413 (accessed November 15, 2024).

Abatzoglou JT, Brown TJ. 2012. A comparison of statistical downscaling methods suited for wildfire applications. International Journal of Climatology **32**:772–780. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/joc.2312 (accessed November 15, 2024).

Adams JB, Gillespie AR. 2018. Remote Sensing of Landscapes with Spectral Images: A Physical Modeling Approach. Cambridge University Press.

Adams JB, Smith MO, Johnson PE. 1986. Spectral mixture modeling: A new analysis of rock and soil types at the Viking Lander 1 Site. Journal of Geophysical Research: Solid Earth **91**:8098–8112. John Wiley & Sons, Ltd. Available from https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/JB091iB08p08098 (accessed December 17, 2024).

Adams MJ et al. 2013. Trends in Amphibian Occupancy in the United States. PLOS ONE **8**:e64347. Public Library of Science. Available from https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0064347 (accessed December 17, 2024).

Alder JR, Hostetler SW. 2021. CMIP5 MACAv2-METDATA monthly water balance model projections 1950-2099 for the contiguous United States. U.S. Geological Survey data release.

Berger L et al. 2004. Effect of season and temperature on mortality in amphibians due to chytridiomycosis. Australian Veterinary Journal **82**:434–439. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1751-0813.2004.tb11137.x (accessed March 10, 2025).

Bosch J, Fernández-Beaskoetxea S, Garner TWJ, Carrascal LM. 2018. Long-term monitoring of an amphibian community after a climate change- and infectious disease-driven species extirpation. Global Change Biology **24**:2622–2632. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.14092 (accessed December 13, 2024).

Brannelly LA, Ohmer MEB, Saenz V, Richards-Zawacki CL. 2019. Effects of hydroperiod on growth, development, survival and immune defences in a temperate amphibian. Functional Ecology **33**:1952–1961. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/1365-2435.13419 (accessed December 13, 2024).

Bürkner P-C. 2017. brms: An R Package for Bayesian Multilevel Models Using Stan. Journal of Statistical Software **80**:1–28. Available from https://doi.org/10.18637/jss.v080.i01 (accessed November 15, 2024).

Bürkner P-C. 2018. Advanced Bayesian Multilevel Modeling with the R Package brms. The R Journal **10**:395–411. Available from https://journal.r-project.org/archive/2018/RJ-2018-017/index.html (accessed November 15, 2024).

Cartwright J, Morelli TL, Grant EHC. 2022. Identifying climate-resistant vernal pools: Hydrologic refugia for amphibian reproduction under droughts and climate change. Ecohydrology **15**:e2354. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/eco.2354 (accessed December 13, 2024).

Cayuela H et al. 2021a. Thermal conditions predict intraspecific variation in senescence rate in frogs and toads. Proceedings of the National Academy of Sciences **118**:e2112235118. Proceedings of the National Academy of Sciences. Available from https://www.pnas.org/doi/abs/10.1073/pnas.2112235118 (accessed December 14, 2023).

Cayuela H et al. 2021b. Thermal conditions predict intraspecific variation in senescence rate in frogs and toads. Proceedings of the National Academy of Sciences **118**:e2112235118. Proceedings of the National Academy of Sciences. Available from https://www.pnas.org/doi/abs/10.1073/pnas.2112235118 (accessed December 17, 2024).

Chang W, Cheng J, Allaire J, Sievert C, Schloerke B, Xie Y, Allen J, McPherson J, Dipert A, Borges B. 2024. shiny: Web Application Framework for R. R package version 1.10.0. Available from https://github.com/rstudio/shiny, https://shiny.posit.co/.

Cheng J, Schloerke B, Karambelkar B, Xie Y. 2024. leaflet: Create interactive web maps with JavaScript "Leaflet" Library. R package version 2.2.2.9000. Available from https://github.com/rstudio/leaflet, https://rstudio.github.io/leaflet/.

Church DR, Bailey LL, Wilbur HM, Kendall WL, Hines JE. 2007. Iteroparity in the Variable Environment of the Salamander Ambystoma Tigrinum. Ecology **88**:891–903. Available from https://onlinelibrary.wiley.com/doi/abs/10.1890/06-0896 (accessed December 17, 2024).

Colorado Parks and Wildlife. 2024. Boreal toad breeding and translocation site monitoring database. CPS Aquatic Research Unit, Fort Collins, Colorado.

Converse SJ, Bailey LL, Mosher BA, Funk WC, Gerber BD, Muths E. 2017. A Model to Inform Management Actions as a Response to Chytridiomycosis-Associated Decline. EcoHealth **14**:144–155. Available from https://doi.org/10.1007/s10393-016-1117-9 (accessed December 10, 2024).

Crockett H, editor. 2023. Conservation plan for the boreal toad (*Anaxyrus boreas boreas*) in the southern Rocky Mountains. Boreal Toad Recovery Team.:84 p. + appendices. Available from https://cpw.state.co.us/species/boreal-toad.

Crockett JG, Bailey LL, Muths E. 2020. Highly variable rates of survival to metamorphosis in wild boreal toads (*Anaxyrus boreas boreas*). Population Ecology **62**:258–268. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/1438-390X.12044 (accessed December 14, 2023).

Fidino M, Simonis JL, Magle SB. 2019. A multistate dynamic occupancy model to estimate local colonization–extinction rates and patterns of co-occurrence between two or more interacting species. Methods in Ecology and Evolution **10**:233–244. John Wiley & Sons, Ltd. Available from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/2041-210X.13117 (accessed December 17, 2024).

Gerber BD, Converse SJ, Muths E, Crockett HJ, Mosher BA, Bailey LL. 2018. Identifying Species Conservation Strategies to Reduce Disease-Associated Declines. Conservation Letters **11**:e12393. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/conl.12393 (accessed December 17, 2024).

Gerber BD, Mosher BA, Bailey LL, Muths E, Crockett HJ, Converse SJ. 2024. Optimal management decisions are robust to unknown dynamics in an amphibian metapopulation plagued by disease. Animal Conservation **27**:65–77. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/acv.12877 (accessed December 17, 2024).

Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment **202**:18–27. Available from https://www.sciencedirect.com/science/article/pii/S0034425717302900 (accessed November 15, 2024).

Grant EHC et al. 2016. Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. Scientific reports **6**. Available from http://www.scopus.com/inward/record.url?scp=84971321287&partnerID=8YFLogxK (accessed December 14, 2023).

Green DM. 2017. Amphibian breeding phenology trends under climate change: predicting the past to forecast the future. Global Change Biology **23**:646–656. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13390 (accessed December 13, 2024).

Greenberg CH, Zarnoch SJ, Austin JD. 2017. Weather, hydroregime, and breeding effort influence juvenile recruitment of anurans: implications for climate change. Ecosphere **8**:e01789. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/ecs2.1789 (accessed December 13, 2024).

Greenberg DA, Palen WJ. 2021. Hydrothermal physiology and climate vulnerability in amphibians. Proceedings of the Royal Society B: Biological Sciences **288**:20202273. Royal Society. Available from https://royalsocietypublishing.org/doi/full/10.1098/rspb.2020.2273 (accessed December 13, 2024).

Halabisky M, Moskal LM, Gillespie A, Hannam M. 2016. Reconstructing semi-arid wetland surface water dynamics through spectral mixture analysis of a time series of Landsat satellite images (1984–2011). Remote Sensing of Environment **177**:171–183. Available from https://www.sciencedirect.com/science/article/pii/S0034425716300682 (accessed December 17, 2024).

Haver M, Le Roux G, Friesen J, Loyau A, Vredenburg VT, Schmeller DS. 2022. The role of abiotic variables in an emerging global amphibian fungal disease in mountains. Science of The Total Environment **815**:152735. Available from https://www.sciencedirect.com/science/article/pii/S0048969721078141 (accessed March 10, 2025).

Hinderer RK, Hossack BR, Eby LA. 2024. Using life history traits to assess climate change vulnerability in understudied species. Integrative Conservation **n/a**. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/inc3.77 (accessed December 13, 2024).

Hof C, Araújo MB, Jetz W, Rahbek C. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature **480**:516–519. Nature Publishing Group. Available from https://www.nature.com/articles/nature10650 (accessed December 13, 2024).

Hoffmann EP, Cavanough KL, Mitchell NJ. 2021. Low desiccation and thermal tolerance constrains a terrestrial amphibian to a rare and disappearing microclimate niche. Conservation Physiology **9**:coab027. Available from https://doi.org/10.1093/conphys/coab027 (accessed December 13, 2024).

Hoffmann M et al. 2010. The Impact of Conservation on the Status of the World’s Vertebrates. Science **330**:1503–1509. American Association for the Advancement of Science. Available from https://www.science.org/doi/full/10.1126/science.1194442 (accessed December 13, 2024).

Jaffe MR, Scott JH, Callahan MN, Dillon GK, Karau EC, Lazarz MT. 2024. Wildfire Risk to Communities: Spatial datasets of wildfire risk for populated areas in the United States. 2nd Edition. Updated 10 September 2024. Fort Collins, CO: Forest Service Research Data Archive.

Johnson M. 2023. AOI: Area of interest. Available from https://github.com/mikejohnson51/AOI/.

Johnson M. 2024. climateR: climateR. Available from https://github.com/mikejohnson51/climateR.

Johnson ML, Speare R. 2005. Possible modes of dissemination of the amphibian chytrid *Batrachochytrium dendrobatidis* in the environment. Diseases of Aquatic Organisms **65**:181–186. Available from https://www.int-res.com/abstracts/dao/v65/n3/p181-186/ (accessed December 10, 2024).

Kissel AM, Halabisky M, Scherer RD, Ryan ME, Hansen EC. 2020. Expanding wetland hydroperiod data via satellite imagery for ecological applications. Frontiers in Ecology and the Environment **18**:432–438. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/fee.2233 (accessed December 13, 2024).

Kissel, A.M., Lacey, L.M., Popescu, V.D., Dyck, M.A., Bailey, L., and Muths, E., 2025, Current and future hydrology and occupancy predictions for boreal toads (*Anaxyrus boreas boreas*) in the Southern Rocky Mountains: U.S. Geological Survey data release, https://doi.org/10.5066/P1VF3ZX4.

Lee S-Y, Ryan ME, Hamlet AF, Palen WJ, Lawler JJ, Halabisky M. 2015. Projecting the Hydrologic Impacts of Climate Change on Montane Wetlands. PLOS ONE **10**:e0136385. Public Library of Science. Available from https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0136385 (accessed December 18, 2024).

Lertzman-Lepofsky GF, Kissel AM, Sinervo B, Palen WJ. 2020. Water loss and temperature interact to compound amphibian vulnerability to climate change. Global Change Biology **26**:4868–4879. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.15231 (accessed January 26, 2024).

Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D. 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software **6**:3139. Available from https://joss.theoj.org/papers/10.21105/joss.03139 (accessed December 13, 2024).

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey L, Hines JE. 2017. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier.

Mantyka-Pringle CS, Martin TG, Rhodes JR. 2012. Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. Global Change Biology **18**:1239–1252. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-2486.2011.02593.x (accessed December 13, 2024).

McCune B, Keon D. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science **13**:603–606. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1654-1103.2002.tb02087.x (accessed December 12, 2024).

Miller DAW et al. 2018. Quantifying climate sensitivity and climate-driven change in North American amphibian communities. Nature Communications **9**:3926. Nature Publishing Group. Available from https://www.nature.com/articles/s41467-018-06157-6 (accessed December 14, 2023).

Miller DAW, Grant EHC. 2015. Estimating occupancy dynamics for large-scale monitoring networks: amphibian breeding occupancy across protected areas in the northeast United States. Ecology and Evolution **5**:4735–4746. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.1679 (accessed December 13, 2024).

Mims MC, Drake JC, Lawler JJ, Olden JD. 2023. Simulating the response of a threatened amphibian to climate-induced reductions in breeding habitat. Landscape Ecology **38**:1051–1068. Available from https://doi.org/10.1007/s10980-023-01599-w (accessed December 13, 2024).

Mosher BA, Bailey LL, Hubbard BA, Huyvaert KP. 2018a. Inferential biases linked to unobservable states in complex occupancy models. Ecography **41**:32–39. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.02849 (accessed December 17, 2024).

Mosher BA, Bailey LL, Muths E, Huyvaert KP. 2018b. Host–pathogen metapopulation dynamics suggest high elevation refugia for boreal toads. Ecological Applications **28**:926–937. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/eap.1699 (accessed December 17, 2024).

Mosher BA, Huyvaert KP, Chestnut T, Kerby JL, Madison JD, Bailey LL. 2017. Design- and model-based recommendations for detecting and quantifying an amphibian pathogen in environmental samples. Ecology and Evolution **7**:10952–10962. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.3616 (accessed December 17, 2024).

Mote PW, Hamlet AF, Clark MP, Lettenmaier DP. 2005. DECLINING MOUNTAIN SNOWPACK IN WESTERN NORTH AMERICA*DOI: 10.1175/BAMS-86-1-39. Available from https://journals.ametsoc.org/view/journals/bams/86/1/bams-86-1-39.xml (accessed December 17, 2024).

Murphy PJ, St-Hilaire S, Corn PS. 2011. Temperature, hydric environment, and prior pathogen exposure alter the experimental severity of chytridiomycosis in boreal toads. Diseases of Aquatic Organisms **95**:31–42. Available from https://www.int-res.com/abstracts/dao/v95/n1/p31-42/ (accessed December 17, 2024).

Muths E et al. 2017. Heterogeneous responses of temperate-zone amphibian populations to climate change complicates conservation planning. Scientific Reports **7**:17102. Nature Publishing Group. Available from https://www.nature.com/articles/s41598-017-17105-7 (accessed December 14, 2023).

Muths E, Hossack BR, Campbell Grant EH, Pilliod DS, Mosher BA. 2020. Effects of Snowpack, Temperature, and Disease on Demography in a Wild Population of Amphibians. Herpetologica **76**:132–143. Available from https://doi.org/10.1655/0018-0831-76.2.132 (accessed December 17, 2024).

Muths E, Stephen Corn P, Pessier AP, Earl Green D. 2003. Evidence for disease-related amphibian decline in Colorado. Biological Conservation **110**:357–365. Available from https://www.sciencedirect.com/science/article/pii/S0006320702002392 (accessed December 14, 2023).

Nagel LD, McNulty SA, Schlesinger MD, Gibbs JP. 2021. Breeding Effort and Hydroperiod Indicate Habitat Quality of Small, Isolated Wetlands for Amphibians Under Climate Extremes. Wetlands **41**:22. Available from https://doi.org/10.1007/s13157-021-01404-x (accessed December 13, 2024).

Petrovan SO, Schmidt BR. 2016. Volunteer Conservation Action Data Reveals Large-Scale and Long-Term Negative Population Trends of a Widespread Amphibian, the Common Toad (Bufo bufo). PLOS ONE **11**:e0161943. Public Library of Science. Available from https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0161943 (accessed December 13, 2024).

Pilliod DS, Arkle RS, Robertson JM, Murphy MA, Funk WC. 2015. Effects of changing climate on aquatic habitat and connectivity for remnant populations of a wide-ranging frog species in an arid landscape. Ecology and Evolution **5**:3979–3994. Available from https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.1634 (accessed December 13, 2024).

Pilliod DS, Muths E, Scherer RD, BarTELt PE, Corn PS, Hossack BR, Lambert BA, Mccaffery R, Gaughan C. 2010. Effects of Amphibian Chytrid Fungus on Individual Survival Probability in Wild Boreal Toads. Conservation Biology **24**:1259–1267. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1523-1739.2010.01506.x (accessed December 17, 2024).

Piotrowski JS, Annis SL, Longcore JE. 2004. Physiology of Batrachochytrium dendrobatidis, a chytrid pathogen of amphibians. Mycologia. Taylor & Francis. Available from https://www.tandfonline.com/doi/abs/10.1080/15572536.2005.11832990 (accessed December 10, 2024).

R Core Team. 2024. R: A language and environment for statistical computing. Vienna, Austria.

Reading CJ. 2007. Linking global warming to amphibian declines through its effects on female body condition and survivorship. Oecologia **151**:125–131. Available from https://doi.org/10.1007/s00442-006-0558-1 (accessed December 17, 2024).

Russell RE et al. 2019. Effect of amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) on apparent survival of frogs and toads in the western USA. Biological Conservation **236**:296–304. Available from https://www.sciencedirect.com/science/article/pii/S0006320719303003 (accessed December 17, 2024).

Ryan ME, Palen WJ, Adams MJ, Rochefort RM. 2014. Amphibians in the climate vise: loss and restoration of resilience of montane wetland ecosystems in the western US. Frontiers in Ecology and the Environment **12**:232–240. Available from https://onlinelibrary.wiley.com/doi/abs/10.1890/130145 (accessed December 13, 2024).

Sievert C. 2020. Interactive web-based data visualization with R, plotly, and shiny. Chapman and Hall/CRC. Available from https://plotly-r.com.

Steen V. 2017. Projected Change in Climatically Relevant Variables for Boreal ToadDOI: 10.5063/F1R78C42. Knowledge Network for Biocomplexity. Available from https://knb.ecoinformatics.org/view/doi:10.5063/F1R78C42 (accessed December 12, 2024).

Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, Waller RW. 2004. Status and Trends of Amphibian Declines and Extinctions Worldwide. Science **306**:1783–1786. American Association for the Advancement of Science. Available from https://www.science.org/doi/full/10.1126/science.1103538 (accessed December 13, 2024).

Theobald DM, Harrison-Atlas D, Monahan WB, Albano CM. 2015. Ecologically-Relevant Maps of Landforms and Physiographic Diversity for Climate Adaptation Planning. PLOS ONE **10**:e0143619. Public Library of Science. Available from https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0143619 (accessed November 15, 2024).

Thompson BK, Olden JD, Converse SJ. 2021. Mechanistic invasive species management models and their application in conservation. Conservation Science and Practice **3**:e533. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/csp2.533 (accessed May 24, 2024).

Todd BD, Scott DE, Pechmann JHK, Gibbons JW. 2010. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. Proceedings of the Royal Society B: Biological Sciences **278**:2191–2197. Royal Society. Available from https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2010.1768 (accessed December 13, 2024).

U.S. Geological Survey. 2001. National Hydrography Dataset (NHD). Reston, VA. Available from 10.3133/70046927.

U.S. Geological Survey. 2023. National Hydrography Dataset (NHD). Reston, VA. Available from https://doi.org/10.5066/P933X6VB.

Watling JI, Braga L. 2015. Desiccation resistance explains amphibian distributions in a fragmented tropical forest landscape. Landscape Ecology **30**:1449–1459. Available from https://doi.org/10.1007/s10980-015-0198-0 (accessed December 13, 2024).

Wilbur HM. 1980. Complex Life Cycles. Annual Review of Ecology and Systematics **11**:67–93. Annual Reviews. Available from https://www.jstor.org/stable/2096903 (accessed December 13, 2024).

Williams CM, Henry HAL, Sinclair BJ. 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. Biological Reviews **90**:214–235. Available from https://onlinelibrary.wiley.com/doi/abs/10.1111/brv.12105 (accessed December 17, 2024).