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RESEARCH ARTICLE

Using life history traits to assess climate change vulnerability in understudied species

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Abstract
Climate change is a primary threat to biodiversity, but for many species, we still lack information required to assess their relative vulnerability to changes. Climate change vulnerability assessment (CCVA) is a widely used technique to rank relative vulnerability to climate change based on species characteristics, such as their distributions, habitat associations, environmental tolerances, and life-history traits. However, for species that we expect are vulnerable to climate change yet are understudied, like many amphibians, we often lack information required to construct CCVAs using existing methods. We used the CCVA framework to construct trait-based models based on life history theory, using empirical evidence of traits and distributions that reflected sensitivity of amphibians to environmental perturbation. We performed CCVAs for amphibians in 7 states in the north-central USA, focusing on 31 aquatic-breeding species listed as species of greatest conservation need by at least 1 state. Because detailed information on habitat requirements is unavailable for most amphibian species, we used species distributions and information on traits expected to influence vulnerability to a drying climate (e.g., clutch size and habitat breadth). We scored species vulnerability based on changes projected for mid-century (2040–2069) from 2 climate models representing "least-dry" and "most-dry" scenarios for the region. Species characteristics useful for discriminating vulnerability in our models included small range size, small clutch size, inflexible diel activity patterns, and smaller habitat breadth. When projected climate scenarios included a mix of drier and wetter conditions in the future, the exposure of a species to drying conditions was most important to relative rankings. When the scenario was universally drier, species characteristics were more important to relative rankings. Using information typically available even for understudied species and a range of climate projections, our results highlight the potential of using life history traits as indicators of relative climate vulnerability. The commonalities we identified provide a framework that can be used to assess other understudied species threatened by climate change.

KEYWORDS
amphibian, at-risk, climate change vulnerability assessment, climate models, scenario modeling, species of greatest conservation need, trait variation

Plain language summary
As climate change threatens plants and animals worldwide, it is important to understand which species are most at risk. Researchers know little about some species, such as many amphibians, which makes it difficult to assess climate change effects. We estimated the climate vulnerability of

31 amphibians, summarizing risk based on where they live and characteristics of the species that we do know. We estimated how vulnerable a species might be using two different climate scenarios: one where the study region will become drier, and one where the region will become drier in some places and wetter in others. We found that some species characteristics were more useful for estimating vulnerability, such as how many eggs they lay, whether they can avoid hot temperatures by being active at night, and how many different types of habitats they can live in. In the scenario where the whole region gets drier, species characteristics were more important to vulnerability estimates. Our work is an example of using characteristics that are generally known, even in understudied species, to estimate how at-risk they will be due to climate change, and how to best improve conservation outcomes.

1 | INTRODUCTION

Climate change is an ongoing threat to biodiversity worldwide (Arneth et al., 2020; Isbell et al., 2023; Parmesan et al., 2022). Our ability and funding to mitigate biodiversity losses are limited, so prioritizing conservation targets is essential (Martin et al., 2018; Mawdsley et al., 2009; Wintle et al., 2011). One way to identify conservation priorities is by estimating the vulnerability of species or populations to threats such as climate change. However, baseline data on species status and threats vary among taxonomic groups. Outside of birds and mammals, a large proportion of species are "understudied," meaning we know little about their current distribution, threats to persistence, or population trends (Haelewaters et al., 2024; McKinney, 1999). These species also tend to be at higher risk of extinction because of small ranges, endemism, or life history traits which make them especially vulnerable (Bland et al., 2015; Borgelt et al., 2022; Howard & Bickford, 2014). This presents a dilemma for conservation practitioners, as it may often be difficult to assess climate vulnerability of the species most in need of conservation action.

Climate change vulnerability assessment (CCVA) is a method used to estimate the relative vulnerabilities of populations, species, or ecosystems to future climate changes (Füssel & Klein, 2006). Three factors predict the relative vulnerability of a species to climate change: exposure, sensitivity, and adaptive capacity (Dawson et al., 2011). Exposure is the relative measure of climate change expected to be experienced by a species at a particular location and sensitivity is the degree to which a system or species is affected by climate change (IPCC, 2022). CCVAs usually treat intrinsic traits of organisms which make them more or less affected by climate change as an index of sensitivity, such as behaviors that limit exposure to climate changes (Tuberville et al., 2015), overlap between climate change exposure and affected life stages (Kingsolver et al., 2004), or the climatic range that a species typically occupies and is thought to be adapted to (Dickinson et al., 2014). Adaptive capacity is the ability of organisms to adjust or adapt to climate change (IUCN, 2021; Thurman et al., 2020), including plasticity in behaviors (Beever et al., 2017), physiological acclimatization (Leung et al., 2021), or rapid evolutionary change in expression of adaptive traits (Mills et al., 2018; Torda et al., 2017).

Trait-based CCVAs provide a tool for ranking species' climate vulnerability by overlaying spatially explicit climate change estimates onto current ranges, linking estimates of relative vulnerability to traits thought to influence how climate change will affect species in a particular location. While evaluating extinction risk from species traits has a long history (refer to McKinney, 1997 for a review), the availability of global climate models and spatially explicit projections of climate conditions allows researchers to combine projected climate conditions with species traits in CCVAs to provide insight into potential effects of climate change on different species. Focusing on basic life history traits that are linked to fitness (Foden et al., 2019; Pacifici et al., 2015; Pearson et al., 2014) allows leveraging

Practitioner points

- Lack of species information complicates understanding climate change vulnerability, but life history traits can be proxies for missing information.
- In the north-central United States, salamanders are generally more climate vulnerable than frogs and toads, and useful traits for discriminating vulnerability include range size, clutch size, diel activity patterns, and habitat breadth.
- Relative climate vulnerability depended greatly on the exposure of species to climate change projected in the future. Species traits are more useful for ranking vulnerability when exposure to climate change is spatially homogeneous across a group of species; otherwise, exposure to climate change is likely more indicative of vulnerability.

the limited available information to inform conservation and management goals, prioritizing allocation of resources, and directing future research (National Wildlife Federation, 2011).

Amphibian species present unique challenges and opportunities for CCVAs. Amphibians are imperiled globally (Finn et al., 2023; Grant et al., 2016), due to climate change among other factors (Case et al., 2015; Miller et al., 2018). Evaluating the effects of climate change on amphibians is complicated by a lack of information about current and potential future population status. A large fraction of understudied amphibians are probably threatened with extinction (Borgelt et al., 2022; Howard & Bickford, 2014). We know little about physiology, specific habitat use, or population trends in large numbers of amphibians, all of which are potentially important to understanding climate vulnerability (Luedtke et al., 2023; Womack et al., 2022). However, better-known life history traits can be important correlates of population processes (Sæther et al., 1996). Though they are typically understudied, amphibians possess some traits which could be useful indicators of climate vulnerability, such as fossorial habits or the ability to shift activity times away from daytime to avoid the most detrimental effects of climate change (Tuberville et al., 2015). Some of these traits might be more useful in discriminating vulnerability between species than others. Previous CCVAs have assessed global patterns in amphibian vulnerability (e.g., Foden et al., 2013), but studies at that scale have limited potential for application to local or regional scales, where management activities are often prioritized (Griffith et al., 2009; LeDee et al., 2021). CCVAs which overlap with the scale of management can identify where species ranges overlap with the highest risk of climate change exposure, prioritizing conservation work in those areas. Though it remains uncertain how climate change will affect most amphibians, widely known life history traits might be useful indicators for understanding climate effects, especially traits that make species either especially vulnerable or resistant to change.

Because amphibians are relatively understudied, imperiled, and negatively affected by climate change, we sought to better understand their climate vulnerability on a management-relevant scale. We used spatially explicit, trait-based CCVAs for imperiled amphibians of the north-central USA, incorporating traits which are potential indicators of vulnerability specific to amphibians. The north-central USA region includes species of conservation concern and a broad range of environmental gradients. We also examined how vulnerability rankings changed between 2 climate scenarios that represented the broad range of variation in projections for the region, from relatively even drying across the region driven by increased summer temperatures and decreased precipitation, to mixed drying and wetting with moderate increases in summer temperatures. Using multiple climate projections to capture the range of uncertainty around potential climate futures allows comparison of species vulnerabilities within the context of our uncertain future. Despite calls to incorporate multi-scenario approaches into CCVAs (Huntley et al., 2016), common CCVA tools do not typically use this approach (Young et al., 2015). For this study, we ranked amphibians across 2 climate change scenarios to identify commonalities in traits linked with higher vulnerability rankings and to allow conservation practitioners to better identify and prioritize conservation targets for understudied and imperiled species.

2 | METHODS

2.1 | Species and location

In the United States, states maintain lists of species of greatest conservation need (AFWA, 2022). States in the north-central USA prioritize at-risk species based on many factors, including data scarcity, dependence on rare habitats, endemism, and in many cases the results of broad CCVAs (Szcodronski et al., 2022). We evaluated 31 aquatic-breeding amphibian species designated as species of greatest conservation need by at least 1 of 7 states in our study area (Montana, Wyoming, Colorado, North Dakota, South Dakota, Nebraska, and Kansas; https://www1.usgs.gov/csas/swap/). We chose the north-central USA for this analysis because of shared conservation planning among these states (Szcodronski et al., 2022), a number of amphibian species of greatest conservation need, and a wide range of habitat types. This region ranges from approximately 200 to 4400 m above sea level and is topographically diverse, including portions of the Rocky Mountains, Great Plains, and Colorado Plateau, and native ecosystems including prairie, woodlands, and alpine systems (U.S. EPA, 2013). We limited our analysis to species that breed in water because availability of surface waters can be a limiting resource that varies with weather and climate.

We limited our CCVA rankings to portions of species' ranges within our study area, even if a range extended outside the region. Species ranges were known-range polygons from the IUCN for each species in the study (IUCN, 2021). CCVAs are most useful as prioritization tools for a specific question and are sensitive to the limits of the study area and the chosen species assemblage (Harper et al., 2022; Huntley et al., 2016). In our case, we sought to prioritize species at the regional level (e.g., multiple states) where cross-state collaboration is possible and limited our analysis to species already deemed of conservation concern by 1 or more states. Because US states maintain their own lists of threatened species, which are often based on status within the state rather than across the entire species range, conclusions from regional assessments are often more applicable to state and local conservation planning than broad-scale assessments of climate change threats.

2.2 | Climate exposure metrics

We chose two projections that represent the variation of predicted climate changes from multiple global climate models (GCMs) for this region. We compared projections from 20 Coupled Model Intercomparison Project 5 (CMIP5) GCMs using the Climate Scatter Tool from Climate Toolbox (www.climatetoolbox.org). We only included model projections under representative concentration pathway (RCP) 8.5, which represents the more-likely climate scenario for the mid-21st century (Schwalm et al., 2020; but refer to Hausfather & Peters, 2020). To capture variation in climate projections we identified the 2 GCMs that illustrated a wide range of projected regional climate change: a "least-dry" model (GFDL-ESM2M under RCP 8.5) and a "most-dry" model (HadGEM2-ES365 under RCP 8.5; Appendix S1). The most-dry model predicted the greatest increase in mean summer temperature and second-greatest decrease in precipitation, while the least dry model predicted the second-lowest increase in mean summer temperature and second-greatest increase in precipitation across the region.

We used evapotranspiration deficit (ED) as the metric of climate change exposure because it reflects drying rather than simply precipitation or temperature (Huntley et al., 2016). Though we chose two GCM projections based on precipitation and temperature changes across the region, ED is an integrative measure of available moisture based on precipitation, temperature, soils, and other factors that more fully reflects conditions experienced by plants and animals (Roberts et al., 2019; Stephenson, 1998). Increased drying is linked to population declines and range reductions in amphibians (Beranek et al., 2022; Crawford et al., 2022; Hossack et al., 2013a), through mechanisms such as direct mortality of aquatic larvae or reduced population connectivity (Ray et al., 2016; Walls et al., 2013). We used a monthly water balance model of the continental United States to derive the exposure score of our CCVAs, based on climate changes projected across a spatially explicit area at 4 × 4–km resolution (Alder & Hostetler, 2021). We calculated ED change (in mm/month) for the most water-limited part of the year by averaging monthly ED values in late summer (July–September) during 1990–2019 (near past) and 2040–2069 (mid-century) and calculated the mean ED change projected between the two time periods. This resulted in two maps of ED change (between near past and mid-century) for each of two GCM projections (most-dry and least-dry; Figure 1).

2.3 | Species traits

We considered potential traits based on basic life history theory, habitat associations that often reflect sensitivity to disturbance (e.g., Stearns, 1992), previous amphibian CCVAs (e.g., Foden et al., 2013), or recent work highlighting limitations or expansions of CCVA studies (e.g., Thurman et al., 2020; Tuberville et al., 2015). Some of the traits proposed for CCVA analyses are unavailable for most amphibians (e.g., genetic diversity or dispersal ability), yet we were able to select useful traits based on published

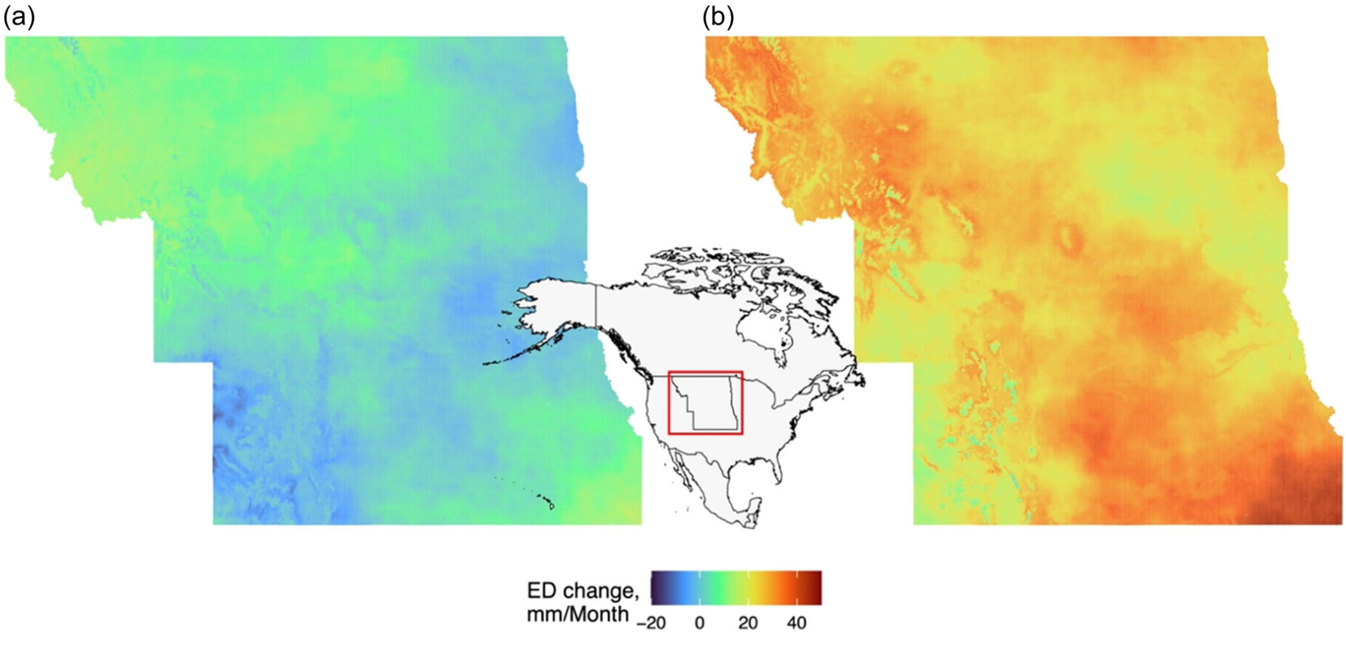

FIGURE 1 Projected changes in late summer (July–September) evapotranspiration deficit (ED) across the north-central United States. Change is the difference between mid-century (2040–2069) and near-past (1990–2019) late-summer ED averages from the (a) GFDL-ESM2M (least dry; mixed drying and wetting across the region) and (b) HadGEM2-ES365 (most dry; universally drying across the region) GCMs under RCP 8.5. The least dry model predicted the second-lowest increase in mean summer temperature and second-greatest increase in precipitation across the region, while the most dry model predicted the greatest increase in mean summer temperature and second-greatest decrease in precipitation.

links between vulnerability and drying conditions (Appendix S2). Some traits could potentially be categorized into either sensitivity or adaptive capacity; the separation between the two is treated differently in various studies (Thurman et al., 2020). We separated traits based on whether the trait would confer higher or lower vulnerability based on climate conditions (sensitivity) or would be advantageous regardless of climate (adaptive capacity; refer to model formulation below). Each trait was scored on a relative scale, where the trait's score is relative to the other values of species in the analysis. Trait values were from the literature (Petranka, 1998; Hammerson, 1999; Lannoo, 2005; Dodd Jr., 2013) or databases of organism traits (Oliveira et al., 2017; Moore et al., 2020; Appendix S3).

We chose 8 traits to indicate climate sensitivity and adaptive capacity (Table 1, Appendix S2). For example, in assessing climate sensitivity, fossorial or cave-dwelling species would generally be less exposed to hotter and drier conditions. Larger-bodied species have a lower surface area to volume ratio and could be less sensitive to evaporative water loss than smaller species, and species which can breed in multiple waterbody types (perennial or ephemeral water bodies) would have greater chance of finding appropriate breeding habitat as drying makes some perennial water sources ephemeral, and some ephemeral sources disappear (Table 1, Appendix S2).

We attempted to capture adaptive capacity through traits that may influence capacity to cope with drying and increased variation in breeding habitat availability. These traits included characteristics of behavior (diel flexibility), physiology (clutch size), and species range (habitat breadth). For example, species that are able to lay large clutches should have a greater potential for persisting through changes by laying more eggs during sporadic but favorable climatic conditions, while species limited to small clutches have less potential for capitalizing on favorable conditions (Cody, 1966; additional justification in Appendix S2). Ecoregions are areas of similar biotic, abiotic, and climatic conditions (McMahon et al., 2001). The number of ecoregions occupied by a species is considered a surrogate for the specificity of habitat requirements (Davidson et al., 2021). Species with wide habitat breadths (larger number of ecoregions occupied) may be better equipped to accommodate or adapt to changing conditions compared to species with narrow habitat breadths (Table 1, Appendix S2).

We did not incorporate a measure of genetic adaptive potential, which is important to climate change responses (Hoffmann & Sgró, 2011; DeMarche et al., 2019), because this information is generally lacking for many amphibians, including those in our study. Likewise, we did not control for covariation among life history traits, and we expected some traits to covary based on life history theory (e.g., maximum body size and maximum clutch size). We instead carefully chose traits for which we could obtain complete information across all 31 species and related to climate vulnerability. In this group of species, no traits we selected were strongly correlated (Pearson's $r < |0.5|$ for all pairwise comparisons).

TABLE 1 Traits included in the climate change vulnerability assessment of 31 amphibian species listed as species of greatest conservation need in at least 1 of 7 north-central United States. Traits were combined to calculate overall vulnerability scores. Justification for trait inclusion is in Appendix S2.

Species trait	Vulnerability category	Description	Relationship to vulnerability
Minimum age at maturity	Sensitivity	Minimum age at which the species may breed	Higher age at maturity = Higher sensitivity
Maximum body size	Sensitivity	Maximum body size (snout-vent length in Anura, total length in Caudata)	Larger body size = Lower sensitivity
Range size	Sensitivity	The size of the species' range in the assessment area	Larger range size = Lower Sensitivity
Adult habitat type	Sensitivity	Fossorial or cave dwelling, terrestrial, or aquatic	Typically use fossorial/cave habitats = Lower sensitivity
Breeding habitat specificity	Sensitivity	Ephemeral and/or perennial typical breeding habitat	Use perennial and ephemeral breeding habitat = Lower sensitivity
Maximum clutch size	Adaptive capacity	Largest recorded clutch size for the species; all species in the study typically lay one clutch per year (Oliveira et al., 2017)	Larger maximum clutch size = Higher adaptive capacity
Diel activity flexibility	Adaptive capacity	Diurnal, crepuscular, or nocturnal typical activity times	Greater number of potential diel activity times (1–3) = Higher adaptive capacity
Habitat breadth	Adaptive capacity	Number of EPA level–3 ecoregions (https://www.epa.gov/eco-research/ecoregions) occupied across species' range	Greater number of ecoregions occupied = Higher adaptive capacity

2.4 | Vulnerability model

Climate change vulnerability assessments can be scored many ways depending on how traits are weighted and whether exposure is assumed to be interactive or additive with sensitivity traits (Huntley et al., 2016). Because we lack information on which traits confer greater climate vulnerability in amphibians, we used the scoring system of Culp and others (2017) which weights all traits for sensitivity and adaptivity capacity equally. This approach requires the fewest assumptions about the relative importance of vulnerability elements, in the absence of strong reasoning for a weighting structure (Jamwal et al., 2022). The vulnerability score for each species was

$$\text{Vulnerability} = \frac{\sum_{ik}\left[(E_i \times S_{ik})^{1/2} - AC_{ik}\right]}{3}$$

where E_i is the exposure score for species i, S_{ik} is the value of each sensitivity trait k of species i, and AC_{ik} is the value of each adaptive capacity trait k of species i. We then ranked species by vulnerability score. We chose the Culp model, which calls for an interaction between sensitivity traits and exposure scores, as climate sensitive traits mean little to climate vulnerability in the absence of climate stress, whereas adaptable species are likely to have an advantage over others in any changing environment, regardless of climate change exposure.

We calculated exposure as the mean ED change (near past to mid-century) within the range of each species in the study area. To prevent some larger raw trait values from overwhelming influence on vulnerability scores, we converted all exposure, sensitivity, and adaptive capacity scores to a 1–100 scale, with the highest score being 100 and all other values scaled by their proportion of that highest value (e.g., Wade et al., 2017). We recalculated the scaled 1–100 values of exposure, sensitivity, and adaptive capacity for the CCVAs under each climate scenario. For example, the maximum recorded body size of any species in our study was the mudpuppy (*Necturus maculosus;* 486 mm total length), assigned a score of 100. We then assigned the western tiger salamander (*Ambystoma mavortium*; maximum 350 mm total length) a score of 350/486 = 72/100 for maximum body size (Appendix S3).

2.5 | Commonalities in vulnerability

After computing the vulnerability score for each species, we calculated Pearson's correlation coefficient (r) for the relationship between vulnerability scores and each trait's standardized value for the least-dry and most-dry scenario CCVAs. Correlation coefficients were from a linear regression of each species' vulnerability score and a trait value, calculated once for each trait. These correlation values allowed assessment of which traits were most strongly associated with vulnerability scores. Because they were weighted equally, traits with the largest variance among species generally had the greatest influence on relative rankings, moderated by a species' range on the continuum of climate change projections. Thus, correlation values provide a way to discriminate among potential traits indicating climate vulnerability.

3 | RESULTS

3.1 | Species rankings

Relative vulnerability rankings of 31 amphibians of state-level greatest conservation need varied depending on the climate scenario used to calculate exposure. Species with smaller proportions of their range in the study area (range: 0.04% to 100%) were generally more vulnerable (Table 2 and 3; Figure 2), especially those listed as species of greatest conservation need in Kansas, where the greatest increases in ED are anticipated in both the least-dry and most-dry models (Figure 1 and 2). Salamanders (order Caudata) tended to be more highly ranked under both climate scenarios than frogs and toads (order Anura). In the least-dry model, the Pacific giant salamander (*Dicamptodon aterrimus*) was ranked as most vulnerable, whereas the grotto salamander (*Eurycea spelaea*) was highest-ranked under the most-dry climate model. The Great Plains toad (*Anaxyrus cognatus*) was the lowest-ranked species in both climate scenarios (Table 2 and 3).

3.2 | Traits linked to vulnerability

Because of the structure of vulnerability models, all traits contributed equally to vulnerability score, though only sensitivity traits interacted with exposure. However, some traits had a stronger relationship with relative vulnerability based on their underlying variability in this group of species. In the least-dry climate scenario, relative vulnerability had the strongest relationship with projected exposure (Table 4). In both climate scenarios, regional vulnerability was higher for species with small range sizes in the assessment area, small maximum clutch sizes, those with less-flexible daily active periods, and those with more specific habitat requirements (Table 4).

3.3 | Importance of climate scenario

The relative importance of exposure and traits to vulnerability depended upon the climate scenario evaluated. The correlation of exposure and vulnerability across all species was higher in the least-dry model that projected mixed drying and wetting across the region by mid-century and lower in the most-dry model that projected drying across the

TABLE 2 Ranked vulnerability of 31 amphibian species of greatest conservation need evaluated in a regional climate change vulnerability assessment across 7 United States under the least-dry climate scenario (GFDL-ESM2M).

Rank	Common name	Scientific name	States listed[a]	Range %[b]	Order
1	Idaho giant salamander	*Dicamptodon aterrimus*	MT	0.07	Caudata
2	Grotto salamander	*Eurycea spelaea*	KS	1.35	Caudata
3	Cave salamander	*Eurycea lucifuga*	KS	0.34	Caudata
4	Longtail salamander	*Eurycea longicauda*	KS	0.18	Caudata
5	Eastern narrowmouth toad	*Gastrophryne carolinensis*	KS	0.10	Anura
6	Strecker's chorus frog	*Pseudacris streckeri*	KS	0.92	Anura
7	Eastern newt	*Notophthalmus viridescens*	KS	0.13	Caudata
8	Smallmouth salamander	*Ambystoma texanum*	NE	4.64	Caudata
9	Spring peeper	*Pseudacris crucifer*	KS	0.14	Anura
10	Crawfish frog	*Lithobates areolatus*	KS	5.96	Anura
11	Wyoming toad	*Anaxyrus baxteri*	WY	100.00	Anura
12	Mudpuppy	*Necturus maculosus*	KS	3.48	Caudata
13	Green toad	*Anaxyrus debilis*	CO, KS	3.11	Anura
14	Columbia spotted frog	*Rana luteiventris*	WY	19.85	Anura
15	Green frog	*Lithobates clamitans*	KS	0.04	Anura
16	Cope's gray tree frog	*Hyla chrysoscelis*	SD	3.73	Anura
17	Blanchard's cricket frog	*Acris blanchardi*	CO, SD, NE	13.41	Anura
18	Great Basin spadefoot	*Spea intermontana*	WY, CO	14.75	Anura
19	Plains spadefoot	*Spea bombifrons*	WY, ND	45.17	Anura
20	Great Plains narrowmouth toad	*Gastrophryne olivacea*	CO, NE	11.29	Anura
21	Couch's spadefoot	*Scaphiopus couchii*	CO	1.90	Anura
22	Canadian toad	*Anaxyrus hemiophrys*	ND	19.15	Anura
23	Western tiger salamander	*Ambystoma mavortium*	WY, KS	42.31	Caudata
24	Plains leopard frog	*Lithobates blairi*	CO	32.90	Anura
25	Western toad	*Anaxyrus boreas*	MT, WY, CO	16.41	Anura
26	Wood frog	*Lithobates sylvaticus*	WY, CO	2.84	Anura
27	American toad	*Anaxyrus americanus*	NE	3.55	Anura
28	Red-spotted toad	*Anaxyrus punctatus*	KS	4.13	Anura
29	Northern leopard frog	*Lithobates pipiens*	MT, WY, CO, NE	23.40	Anura
30	Canyon tree frog	*Hyla arenicolor*	CO	6.76	Anura
31	Great Plains toad	*Anaxyrus cognatus*	MT, WY	37.17	Anura

[a]State abbreviations include Colorado (CO), Kansas (KS), Montana (MT), Nebraska (NE), North Dakota (ND), South Dakota (SD), and Wyoming (WY).
[b]Range % is the amount of that species' total range contained within the assessment area, displayed as a percentage for ease of interpretation.

entire region (Table 4). For sensitivity and adaptive capacity factors that were highly correlated with vulnerability (range size, maximum clutch size, diel activity pattern, and habitat breadth), their importance to vulnerability increased in the most-dry scenario as exposure become less important (Table 4). In the most-dry climate scenario, even though the magnitude of change was greater than the least-dry scenario, drying effects were more homogenous across the study area; thus, exposure became less important to relative rankings because all species were exposed to drying conditions. In the least-dry scenario, some species were more exposed (projected to experience drying), and others were less exposed (projected to experience wetting) to changes, increasing the importance of exposure to vulnerability scores.

4 | DISCUSSION

Prioritizing conservation actions for species threatened by climate change can improve outcomes, but prioritization is difficult when little is known

TABLE 3 Ranked vulnerability of 31 amphibian species of greatest conservation need evaluated in a regional climate change vulnerability assessment across 7 United States under the most-dry climate scenario (HadGEM2-ES365).

Rank	Common name	Scientific name	States listed[a]	Range %[b]	Order
1	Grotto salamander	*Eurycea spelaea*	KS	1.35	Caudata
2	Idaho giant salamander	*Dicamptodon aterrimus*	MT	0.07	Caudata
3	Cave salamander	*Eurycea lucifuga*	KS	0.34	Caudata
4	Wyoming toad	*Anaxyrus baxteri*	WY	100.00	Anura
5	Longtail salamander	*Eurycea longicauda*	KS	0.18	Caudata
6	Strecker's chorus frog	*Pseudacris streckeri*	KS	0.92	Anura
7	Eastern narrowmouth toad	*Gastrophryne carolinensis*	KS	0.10	Anura
8	Green toad	*Anaxyrus debilis*	CO, KS	3.11	Anura
9	Smallmouth salamander	*Ambystoma texanum*	NE	4.64	Caudata
10	Eastern newt	*Notophthalmus viridescens*	KS	0.13	Caudata
11	Spring peeper	*Pseudacris crucifer*	KS	0.14	Anura
12	Mudpuppy	*Necturus maculosus*	KS	3.48	Caudata
13	Couch's spadefoot	*Scaphiopus couchii*	CO	1.90	Anura
14	Canyon tree frog	*Hyla arenicolor*	CO	6.76	Anura
15	Crawfish frog	*Lithobates areolatus*	KS	5.96	Anura
16	Cope's gray tree frog	*Hyla chrysoscelis*	SD	3.73	Anura
17	Blanchard's cricket frog	*Acris blanchardi*	CO, SD, NE	13.41	Anura
18	Great Basin spadefoot	*Spea intermontana*	WY, CO	14.75	Anura
19	Red-spotted toad	*Anaxyrus punctatus*	KS	4.13	Anura
20	Green frog	*Lithobates clamitans*	KS	0.04	Anura
21	Columbia spotted frog	*Rana luteiventris*	WY	19.85	Anura
22	Plains spadefoot	*Spea bombifrons*	WY, ND	45.17	Anura
23	Great Plains narrowmouth toad	*Gastrophryne olivacea*	CO, NE	11.29	Anura
24	Canadian toad	*Anaxyrus hemiophrys*	ND	19.15	Anura
25	Plains leopard frog	*Lithobates blairi*	CO	32.90	Anura
26	Western toad	*Anaxyrus boreas*	MT, WY, CO	16.41	Anura
27	American toad	*Anaxyrus americanus*	NE	3.55	Anura
28	Wood frog	*Lithobates sylvaticus*	WY, CO	2.84	Anura
29	Western tiger salamander	*Ambystoma mavortium*	WY, KS	42.31	Caudata
30	Northern leopard frog	*Lithobates pipiens*	MT, WY, CO, NE	23.40	Anura
31	Great Plains toad	*Anaxyrus cognatus*	MT, WY	37.17	Anura

[a]State abbreviations include Colorado (CO), Kansas (KS), Montana (MT), Nebraska (NE), North Dakota (ND), South Dakota (SD), and Wyoming (WY).

[b]Range % is the amount of that species' total range contained within the assessment area, displayed as a percentage for ease of interpretation.

about population status or how species might respond to climate change. By incorporating trait values for 31 species of amphibians and projections from 2 divergent climate change scenarios, we used the climate change vulnerability assessment (CCVA) framework to inform conservation prioritization even for understudied species, across a range of likely climate projections. The species ranked as most vulnerable regionally occurred in areas projected to experience the greatest increases in hotter and drier conditions. Species with small ranges within the study area, narrow habitat breadths (i.e., fewer ecoregions occupied across their range), that laid fewer eggs, or with inflexible diel activity times were ranked as the most vulnerable, with the relative importance of traits depending on future climate conditions.

We leveraged life history theory and known species traits to estimate vulnerability because of a general lack of information about amphibian responses to climate change. Traits advantageous for coping with perturbations, such as large clutch sizes which increase potential for rapid population recovery (Cody, 1966), are not unique to

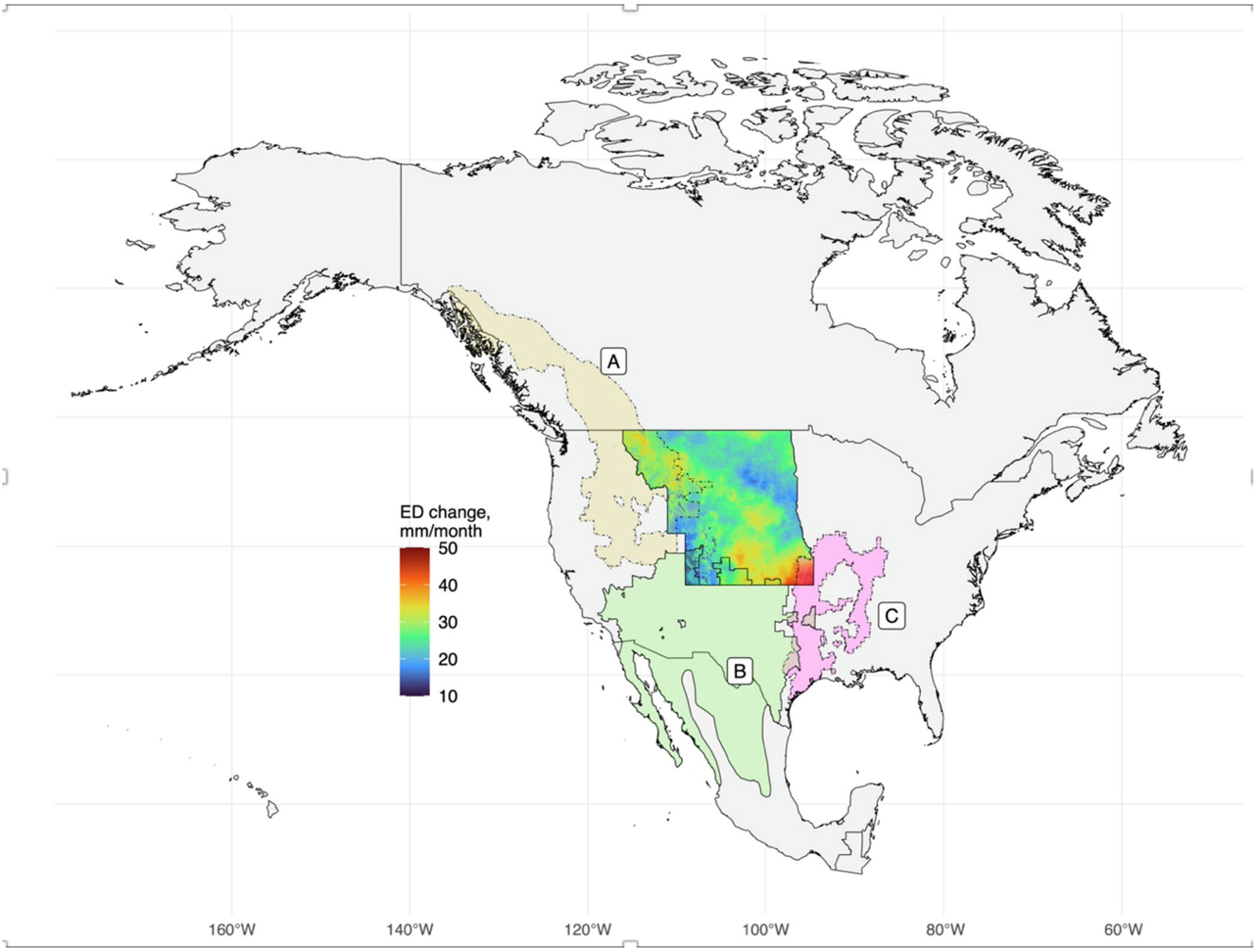

FIGURE 2 Projected changes in evapotranspiration deficit (ED) in our study region under the most-dry climate scenario and the range of 3 species assessed in the climate change vulnerability assessment. These 3 species have large ranges outside the study area and are projected to experience widely varying levels of ED within the region. Species ranges are (A) Columbia spotted frog, (B) red-spotted toad, and (C) crawfish frog. Change is the difference between projected mid-century (2040–2069) and near-past (1990–2019) late-summer ED averages from the HadGEM2-ES365 (most dry) GCM under RCP 8.5. Note that ED scale is adjusted from Figure 1 for clarity.

amphibians. Variation, plasticity, or data scarcity in any of these traits can influence our ability to estimate vulnerability, but variation or plasticity are themselves part of a species' response to climate. For example, clutch size can vary with elevation locally (Pettus & Angleton, 1967) or can be highly conserved across continental ranges (Davenport and Hossack, 2016). However, there is often little or no information about variation in trait expression for species across geographic regions, including for amphibians in our study area. For example, we found only 1 reported clutch size for cave salamanders (*Eurycea spelaea;* Brandon, 1971). We also assumed that the species in our study lay eggs every year, which may be unlikely in organisms with especially slow life histories, such as cave salamanders and Idaho giant salamanders (*Dicamptodon atterrimus*). Better understanding of the variation in traits or performance locally and across species' ranges, as well as the links between traits and climate, will help improve understanding of climate vulnerability. Where there is information on intraspecific differences in physiological tolerances (Hossack et al., 2013b) or on traits that vary predictably with local climate (Cayuela et al., 2021), this information can be incorporated into targeted CCVAs. Many life history traits, and their association with climate change vulnerability, are linked with organism phylogeny. In our study, salamanders (order Caudata) were generally ranked as more vulnerable to climate change than frogs and toads (order Anura; Table 2 and 3), which matches previous predictions that salamanders are more vulnerable when considering cumulative global threats (Luedtke et al., 2023). While in some regions limitations in dispersal ability may hinder the ability of frogs and toads to reach refuge and new breeding habitats, increasing their vulnerability to climate change (Inman et al., 2023), salamanders tend to lay fewer eggs and have smaller ranges and more specialized habitat requirements than frogs and toads, resulting in higher vulnerability scores in our study area (Appendix S3). Because there was large variation in these traits among species, these

TABLE 4 Pearson's correlation coefficient (r) of vulnerability elements (climate exposure or species traits) to overall vulnerability scores for the least- and most-dry climate scenarios.

Vulnerability element	r least dry[a]	r most dry[a]
Exposure		
Evapotranspiration deficit	0.79	0.60
Sensitivity		
Minimum age at maturity	−0.20	−0.18
Maximum body size	0.16	0.00
Range size in assessment area	−0.55	−0.73
Adult habitat type	−0.10	−0.10
Breeding habitat type	0.42	0.43
Adaptive Capacity		
Maximum clutch size	−0.56	−0.66
Diel activity pattern	−0.55	−0.67
Habitat breadth	−0.52	−0.64

[a]Exposure is from the GFDL-ESM2M (least dry) and HadGEM2-ES365 (most dry) GCMs under RCP 8.5.

values became more important to relative vulnerability in both climate scenarios. Trait variation linked with phylogeny may help provide an effective rule-of-thumb for understanding climate change impacts across species, if species can be generally categorized into risk categories based on their shared evolutionary history. When there is little information available about current population status or trajectory, we recommend leveraging all available information, including phylogenetic patterns, when considering relative vulnerabilities to climate change.

Though the spatial extent and severity of future climate change is uncertain, methods like CCVA can account for the range of projected changes in precipitation and temperature and how they interact with the landscape. Ensemble methods, which average climate projections from multiple global climate models, are commonly used because they ease interpretation of results, but they also obscure important uncertainties (Huntley et al., 2016; Rangwala et al., 2021). Although we are aware of few other CCVAs which explicitly incorporate variation in climate projections (e.g., Steel et al., 2011; Liebezeit et al., 2012), the choice of climate scenario strongly affected relative rankings and changed the relative importance of life history traits in determining vulnerability scores in our CCVAs. In the scenario where changes in climate stress were relatively uniform across a region, differences in life history traits then became important indicators of vulnerability. However, in cases of widely varying climate conditions, the effect of a species' range position relative to the direction and magnitude of change can overwhelm the effect of life history traits, as we found (Table 4; Figure 2). This is a strength of spatially explicit CCVA, as it can incorporate not only traits thought to influence vulnerability, but also species ranges, which indicate likely climate exposure. Performing CCVAs under a wide range of climate scenarios can also help explicitly consider uncertainties (Deser et al., 2012; Her et al., 2019), effectively bookending the range of plausible futures.

At finer scales, identifying refugia that buffer against the effects of climate change could improve projections of climate change effects on species (Nowakowski et al., 2018). Reliable climate data are typically limited to relatively coarse scales, including in our analysis (4 × 4–km), but amphibians often select habitat at very fine spatial scales (Bartelt et al., 2010; Hinderer et al., 2021; Brown et al., 2021). Though microhabitat-scale information is seldom available, some landscape characteristics such as riparian and landform features are important predictors of suitable microhabitat and can be incorporated into climate scenario modeling (Szcodronski et al., 2024). Adding information about areas which provide important microclimates and increase adaptive capacity can focus management on improving or preserving important landscape features.

The scale of climate change vulnerability assessments is important both for study design and for applying study results. In our CCVAs, species whose ranges barely overlapped the study region tended to be ranked highly (Table 2 and 3). While we assessed vulnerability at the regional scale, not across a species' entire range, decision-makers can consider the total range of a species when considering conservation actions. Broadly distributed species with a tiny portion of their total distribution within a state or other political boundary may have local importance but be at low risk of extirpation overall (e.g., the red-spotted toad [*Anaxyrus punctatus*] is listed only in Kansas yet ranges well into Mexico; Figure 2). Species designated as conservation priorities across several jurisdictions (e.g., the crawfish frog [*Lithobates areolatus*] is a priority in 10 states, across most of its distribution; Figure 2) could provide opportunities for collaborative management. CCVAs done for only a portion of a species' range can help identify local vulnerabilities and prioritize conservation actions at the scale appropriate for management. The wolverine (*Gulo gulo*), sockeye salmon (*Oncorhynchus nerka*), and Swainson's hawk (*Buteo swainsoni*) are analogous cases — they are protected in U.S. jurisdictions but are of least concern on the global-scale IUCN Red List (IUCN, 2024). The scale of interest or the scale of potential management action can be incorporated at the planning stage of a CCVA, so that results are the most useful for conservation practitioners.

Our regional rankings also highlight differences between global species status and local and regional conservation priorities. Global conservation ratings, such as the IUCN Red List, are often based on current status and threats rather than susceptibility to future threats, even for species considered highly vulnerable to climate changes (Harper et al., 2022). In our study, all species except the federally endangered Wyoming toad (*Anaxyrus baxteri*) are least concern on the Red List (IUCN, 2024). The Wyoming toad was not in the top

3 of most vulnerable species for either climate scenario we evaluated. Though somewhat counterintuitive, the species most vulnerable to extinction due to current threats may not be the most at-risk due to future climate change, a limitation of CCVA that has been pointed out previously (Young et al., 2015). It is important to consider that CCVA only assesses the risks to a species with respect to climate change, and not other, perhaps more pressing threats such as habitat loss, invasive predators, disease, or extremely small population sizes (Young et al., 2015; Case et al., 2015; Caro et al., 2022). However, the scale of climate change's effects makes it particularly important to conservation decisions, and CCVAs can be integrated into a broad threat assessment framework that includes other stressors, including the potential to incorporate projected land-use changes into CCVAs (e.g., U.S. Environmental Protection Agency, 2017). Climate change will likely interact with other stressors, such as by increasing disease outbreaks or mediating the effect of invasive species on native biodiversity (Hossack et al., 2017; Price et al., 2019). Continued research into climate change's complex effects on biodiversity will be essential to best characterize the most effective outcomes for understudied species of conservation concern.

Climate change vulnerability assessment is an extremely flexible tool, which presents opportunities for practitioners to tailor models and produce useful results. We chose to focus our amphibian CCVA on a regional scale rather than global, to use empirically measured characteristics of species rather than the typical time-intensive expert elicitation process, and carefully chose characteristics from the literature, rather than using a more general suite of characteristics which may be unimportant or unknown in this group (e.g., Foden et al., 2013; Young et al., 2015; Harper et al., 2022). For example, genetic diversity may indicate adaptive capacity (e.g., Wade et al., 2017). However, local measures of genetic diversity are rarely available for under-studied species, and genetic diversity may not be a reliable indicator of conservation status without more information about phenotypic expression and ecological relationships (Teixeira & Huber, 2021). In our model, a species with high sensitivity or low adaptive capacity could have the same overall vulnerability score. However, by estimating the relative effect of each trait on vulnerability scores, CCVA users can identify which traits potentially influence vulnerability more and help target management actions (Thurman et al., 2020). For example, the southeast corner of the study area (Kansas) is a potentially high-risk area for increasing evapotranspiration deficit, regardless of global climate model (Figure 2). This area could be a high priority for programs aimed at conserving or constructing aquatic habitats to benefit amphibians and other priority wildlife under a warmer, drier future.

Planning for the future during unprecedented environmental change complicates efforts to halt or reverse biodiversity losses (Finn et al., 2023), a problem compounded by the lack of information for many species expected to be highly vulnerable to climate changes. By overlaying life history information and climate projections to better understand how climate change could affect under-studied animals, traits like clutch size, range size, and habitat breadth can be used as indicators of relative vulnerability in the absence of other information. The commonalities we identified including specific traits and the relative contribution of different climate scenarios to vulnerability also provide a framework that can be applied to under-studied species more generally.

AUTHOR CONTRIBUTIONS

Ross K. Hinderer: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; writing—original draft; writing—review and editing. **Blake R. Hossack**: Conceptualization; funding acquisition; project administration; resources; supervision; writing—review and editing. **Lisa A. Eby**: Conceptualization; funding acquisition; project administration; resources; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data from this study can be found at Hinderer (2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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