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Some of these are not like the others: Relative thermal sensitivity among anuran species of the Southeast United States

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Abstract

Estimating how close a species is to its upper thermal limits (i.e., warming tolerance, a thermal sensitivity index) and how that proximity changes across space enables spatially explicit identification of species with increased extinction risk as temperatures increase. Yet, thermal sensitivity is often difficult to calculate because it is the result of many traits. We aimed to synthesize multiple traits into a single estimate of relative terrestrial thermal sensitivity for 13 anuran species in the southeastern United States. We employed models that incorporate traits and microclimate variation to (1) estimate species warming tolerance (the difference between species critical thermal maximum and modeled operative temperature, an estimate of body temperature) and (2) investigate how warming tolerance varied with latitude (whereby latitude represents different temperature regimes and external drivers of thermal sensitivity). We ran mechanistic niche models across a 12° latitudinal gradient and 10 years to estimate individual operative temperature. We calculated the minimum, 25th percentile (hottest quarter), and median daily minimum warming tolerance. Estimates of minimum warming tolerance spanned −5 to 10°C (*Lithobates palustris* and *Gastrophryne carolinensis* respectively) and differed among species. For most species, modeled operative temperatures exceeded species' critical thermal maximum during extreme warm temperatures (i.e., heat waves) in part of their range, and warming tolerance increased with latitude. During heat waves, five species had lower warming tolerance at higher latitudes, and three species' warming tolerance did not change with latitude. We identified species that are approaching their thermal limits in the Southeast and characterized spatial patterns of warming tolerance. Increased temperatures could increase anuran extinction risk, posing an additional challenge for threatened anuran species. Spatial patterns of warming tolerance were not consistent among species in our study, highlighting that patterns

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identified at higher taxonomic categories could be inconsistent at lower taxonomic categories.

KEYWORDS
environmental stressors, mechanistic niche model, thermal ecology, vulnerability analysis, warming tolerance

INTRODUCTION

Interspecific thermal sensitivity affects species' vulnerability and estimated extinction risk due to increased temperatures, but thermal sensitivity is difficult to estimate due to the interaction of species ecology and geographic location. Thermal sensitivity is multidimensional and depends upon species' geographic range (Barria & Bacigalupe, 2017; Rohr et al., 2018), behavior (Díaz-Ricaurte et al., 2020; Sunday et al., 2014), and physiological limits that can change based on species' acclimation ability (Brattstrom & Lawrence, 1962; John-Alder et al., 1988). Each of these dimensions has a unique response to changes in temperature that can compound or mitigate the other dimensions of thermal sensitivity (Huey et al., 2012; Morley et al., 2019; Sunday et al., 2014). Incorporating estimates of how close species are to their thermal limits into assessments of species vulnerability remains a challenge because of these multiple dimensions and data disparities among species (DuBose et al., 2024; Huey et al., 2012), even though incorporating thermal sensitivity into assessments can improve assessment accuracy (Morin & Thuiller, 2009).

Taken alone, a single dimension of thermal sensitivity can belie a species' actual thermal sensitivity by missing context. Biophysical models such as mechanistic niche models (MNMs) synthesize multiple dimensions of thermal sensitivity by incorporating many traits in a process-based model, thus providing a more complete description of species thermal sensitivity than single traits alone. Specifically, MNMs translate microclimate radiation and temperature into estimated energy exchange between an individual and its environment based on thermodynamic theory (i.e., mass and heat budgets bounded by evaporative loss and radiative temperature gain) and a behavioral algorithm (Briscoe et al., 2023; Kearney & Porter, 2020). MNMs can be parameterized with empirical or observed thermal, size, metabolic, and behavioral trait values, which allows scientists to tailor MNMs to their question (Riddell et al., 2023). Summarizing multiple dimensions of thermal sensitivity with MNMs allows us to make direct comparisons between guilds and species, which can identify taxa at greater risk due to increased temperatures (Riddell et al., 2021).

Multidimensional summaries of thermal sensitivity reveal interspecific variation, intraspecific variation, and geographic variation in thermal sensitivity (Enriquez-Urzelai et al., 2020; Sunday et al., 2011), but rarely compare many species within the same taxonomic order. Although amphibians can use behavior to withstand increases in temperature (Sunday et al., 2014) and different populations within species may experience decreased occupancy due to higher temperatures (Enriquez-Urzelai et al., 2019; Riddell et al., 2021), interspecific comparisons of multidimensional thermal sensitivity are rare. One example of a comparison of thermal sensitivity between nine coexisting species found that species had unique responses to changes in precipitation and temperature (Muñoz et al., 2022). Investigating geographic variation in thermal sensitivity can generate hypotheses about the external drivers of thermal sensitivity (Deutsch et al., 2008) and further our understanding of order-level and within-species thermal sensitivity. Although midlatitude ectotherms as a group are sensitive to warmer temperatures (Comte & Olden, 2017; Murali et al., 2023; Pinsky et al., 2019), we expect external drivers of thermal sensitivity to differ among species because thermal resource use differences can drive speciation and foster coexistence (Paterson & Blouin-Demers, 2017). By investigating interspecific and geographic variation in thermal sensitivity at smaller taxonomic and spatial scales, we can identify species at higher extinction risk with increasing temperatures, examine whether external drivers of thermal sensitivity vary among species, and inform data needs for wildlife managers and conservation biologists (Griffis-Kyle, 2016; Muñoz et al., 2022).

Species' sensitivity to increased temperature can be quantified in multiple ways. For example, critical thermal maximum (CTmax or the maximum temperature at which coordinated movement is lost) can predict thermal stress induced mortality (Cicchino, Ghalambor, et al., 2023) but does not account for species exposure to thermal stress based on location. In contrast, warming tolerance describes the leeway that species have to changes in the thermal regime and is the difference between species' CTmax and its operative temperature, or estimated steady-state body temperature using a heat-balance model, at a location. The difference between species'

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CTmax and its operative temperature is sometimes called its thermal safety margin (Sunday et al., 2014), but historically that term refers to the difference between species optimal performance temperature and its operative temperature (Clusella-Trullas et al., 2021). We refer to the proximity of a species operative temperature to its CTmax as its warming tolerance. Species operating closer to their thermal limits and having lower warming tolerance often have suboptimal performance and thus reduced fitness (Huey et al., 2012). Sensitivity to increased temperature can also be estimated using the proportion of a species' range that remains inhabitable. Although vertebrates are predicted to lose a mean of 10% of their range with a 2°C rise in temperatures (Warren et al., 2018), species-specific estimates of range loss or expansion are often unknown. Understanding species warming tolerance and potential range loss due to increases to mean annual and extreme (heat wave) temperatures (Vose et al., 2017) quantifies species susceptibility to future temperature changes.

Here, we estimate relative interspecific, terrestrial thermal sensitivity for a regional suite of anurans in the southeastern United States using MNMs. We ask two key questions. First, how close are species to their upper thermal limits, and does proximity to upper thermal limits differ among species? We hypothesize that (1) some species are close to their upper thermal limits, (2) species differ in their thermal sensitivity, and (3) species closer to their upper thermal limits (i.e., have lower warming tolerance estimates) and with a larger proportion of their regional range with little to no warming tolerance are more vulnerable to warmer temperatures because of a reduced margin for increased temperatures (resiliency) and reduced redundancy in their range. Second, what is the relationship between species' warming tolerance and latitude, and does that relationship differ between species? We hypothesize anuran species will consistently show a positive relationship between warming tolerance and latitude because of higher mean air temperatures at lower latitudes. By investigating how close species are to their thermal limits and how sensitivity changes across a latitudinal gradient, we highlight how increased terrestrial temperatures could affect species and the possible drivers of their vulnerability.

METHODS

Study system

Taxa that are species-rich, have thermoregulation trait data available, and are differentially sensitive to increased temperatures are ideal for investigating interspecies and macroecological patterns in warming tolerances. Anurans (frogs and toads) meet these criteria. There are over 100 species of anurans within the United States (Lannoo et al., 2005), and anuran species are included in global and regional thermal trait datasets (Bennett et al., 2018; DuBose, Catalan, et al., 2023). Additionally, anuran species can be affected in different ways by changes in precipitation and temperature. For example, across 86 long-term study areas in the United States, *Dryophytes (Hyla) chrysoscelis* had lower occupancy in warmer summers, while *Pseudacris crucifer* had higher occupancy (Miller et al., 2018).

We used U.S. Geological Survey Hydrologic Unit Level 2 boundaries found in the U.S. Department of the Interior's southeast region as our study extent referenced to North American Datum 1983 and the Geodetic Reference System 1980 ellipsoid (U.S. Geological Survey, 2020). We focused on the southeastern United States because of its high anuran species richness (Lannoo et al., 2005), and because as a region, it is expected to experience increased temperatures (Vose et al., 2017). The southeastern United States is already experiencing warmer annual average temperatures; daily maximum temperatures are increasing in winter and spring, but are not increasing in summer and fall, potentially due to anthropogenic (e.g., land use change) or natural (e.g., atmospheric circulation) causes (Carter et al., 2018; Vose et al., 2017).

To investigate thermal sensitivity of anurans within the southeastern United States, we first identified species with sufficient thermoregulation trait data for the adult life stage available in a regional thermal trait database (TRAD: Thermal traits of anurans database for the southeastern United States; DuBose, Catalan, et al., 2023) as the focal species of our analysis. MNMs are more sensitive to some parameters than others (Peterman & Gade, 2017), and we limited our focal species to those with trait data for at least three of the four traits that influence MNMs: CTmax, critical thermal minimum (minimum temperature at which coordinated movement is possible), preferred temperature (Tpref or body temperature to which a species regulates and is often close to optimal performance temperatures), and retreat emergence temperature (temperature at which species are outside of underground burrows). Of the 37 species included in the TRAD database, 13 species met this criterion (Table 1).

Trait imputation

After identifying species with sufficient trait data, we used phylogenetically informed trait imputation to estimate missing continuous thermoregulation trait values

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TABLE 1 Area sampled (*N* points) and the percentage of that area where individuals are thermally sensitive (minimum daily warming tolerance [WT_d] < 0°C and minimum WT_d < 2°C) for 13 anuran species in the Southeast United States.

Common name	Species	*N* points	Minimum WT_d < 0°C (%)	Minimum WT_d < 2°C (%)
Blanchard's cricket frog	*Acris blanchardi*	1542	43.2	67.2
American toad	*Anaxyrus americanus*	7599	5.4	19.4
Fowler's toad	*Anaxyrus fowleri*	9751	7.6	28.1
Cope's gray treefrog	*Dryophytes chrysoscelis*	10,765	4.2	25.0
Gray treefrog	*Dryophytes versicolor*	737	64.2	79.2
Eastern narrow-mouthed toad	*Gastrophryne carolinensis*	12,519	0.0	0.0
Crawfish frog	*Lithobates areolatus*	50	100.0	100.0
American bullfrog	*Lithobates catesbeianus*	13,636	0.0	0.3
Green frog	*Lithobates clamitans*	13,447	79.6	84.2
Pickerel frog	*Lithobates palustris*	4007	99.6	100.0
Wood frog	*Lithobates sylvaticus*	1185	21.7	83.0
Spring peeper	*Pseudacris crucifer*	7421	87.4	89.9
Eastern spadefoot	*Scaphiopus holbrookii*	6869	0.0	0.0

for species' critical thermal limits, Tpref, retreat emergence temperature, basking temperature, foraging temperature limits, and mass. We subsetted the global anuran phylogeny (Jetz & Pyron, 2019) to 36 species that were native to the Southeast United States, were within the phylogeny (excludes *Lithobates kauffeldi*), and had thermoregulation trait data available (excludes *Pseudacris brimleyi*, *Pseudacris nigrita*, and *Pseudacris ocularis*). CTmax values were not imputed and represent literature-based values. When TRAD contained multiple trait values for a species, we removed trait values that were derived in states with centroids more than 1000 km away from states that form the northern edge of our study extent (Mississippi, Tennessee, or Virginia; Appendix S1: Figure S1) and recalculated the summarized interspecific trait values (e.g., recalculated the maximum CTmax values found within *c.* 1000 km of our study region) (Figure 1). By removing trait values measured outside of our study region, we hoped to replicate trait values found within the region and avoid misapplying trait values that exhibit geographic effects (e.g., larger frogs at higher latitudes (Olalla-Tárraga & Rodríguez, 2007) or acclimation in cooler environments). Using the Jetz and Pyron (2019) phylogeny, interspecific thermal trait values, and the rphylopars R package (Goolsby et al., 2021; R Core Team, 2021), we ran three trait imputation models to identify the most appropriate model of evolution (Brownian Motion, Ornstein-Uhlenbeck, and Pagel's λ) based on Akaike information criterion (AIC). We used the lowest AIC model to complete phylogenetically informed trait imputation on summarized interspecific trait values and fill in any missing trait data.

MNM construction

We used the NicheMapR package in R to build our MNMs (Kearney & Porter, 2020). MNMs pair microclimate models with heat-balance equations, and sometimes a behavioral algorithm, to estimate the operative temperature of a model organism at a specific time and place. Microclimate models translate mesoscale meteorological data, terrain aspects, and soil characteristics into weather estimates at a specific height (i.e., the height of a model animal) (Kearney et al., 2020). To capture daily extreme temperatures as precisely as possible, we used the NicheMapR function *micro_ncep* to generate microclimate estimates from January 1, 2011 to December 31, 2020 (Kearney et al., 2020; Kearney & Porter, 2017), which uses mesoscale climate data from the National Centers for Environmental Prediction at a 6-hourly time step and 200 km resolution and a 1000 m digital elevation model to estimate the temperatures at a 1-cm reference height and within a 200 cm deep soil profile. The micro_ncep model can perform similarly to microclimate models that use higher spatial resolution climate data (Kearney et al., 2020) and produced similar hourly historical observations for multiple points in our region (TPD, personal observation). We modeled shaded and unshaded temperatures on land; modeled frogs could not seek thermal refuge in water. We think this assumption is acceptable given the potentially greater thermal buffer offered by behavioral thermoregulation in terrestrial habitats (Ruthsatz et al., 2024).

Using the generated microclimate data and NicheMapR's *ectotherm* function, we use hydrothermal mass balance equations and a behavioral algorithm to

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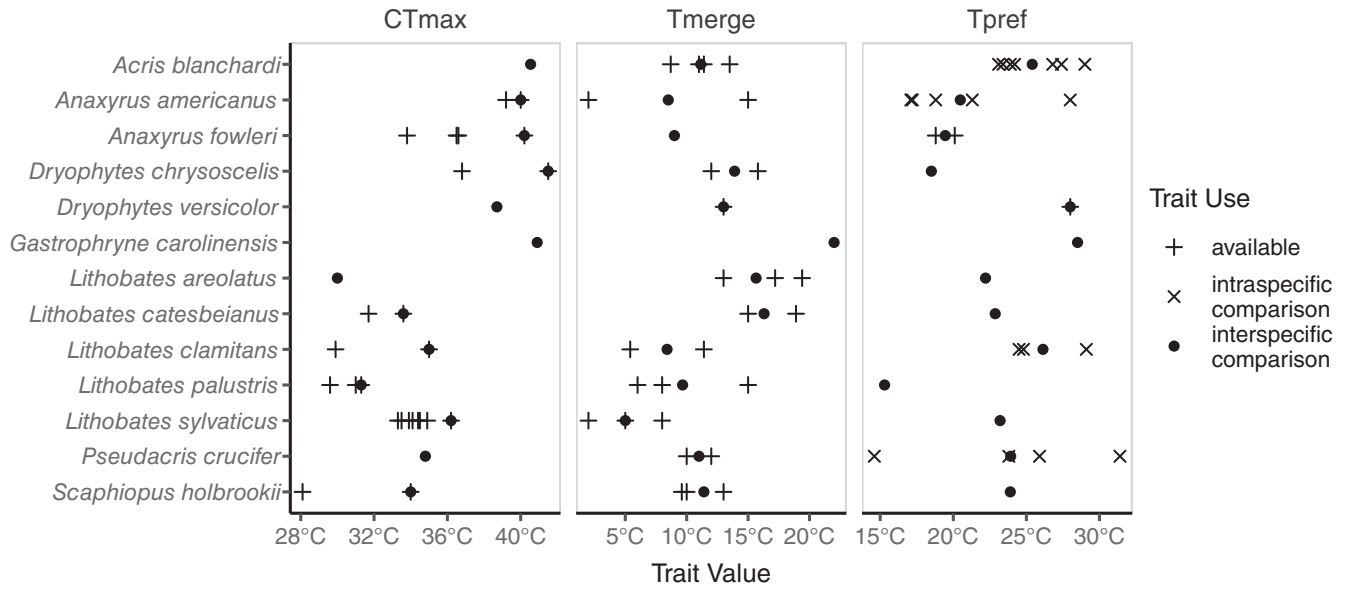


FIGURE 1 Critical thermal maximum (CTmax), emergence temperature (Tmerge), and preferred temperature (Tpref) variation among and within anuran species. Trait use refers to the availability of trait values near our study region within TRAD (Thermal traits of anurans database for the southeastern United States) or whether trait values were used in our intraspecific comparison analysis or interspecific comparison analysis.

estimate the operative temperature of an individual with a frog-like shape (an ellipsoid half as high as it is round). The hydrothermal mass balance equations translate estimated environmental temperature into operative temperature based on physical properties (e.g., mass and shape) of the modeled individual. The behavioral algorithm simulates behavioral thermoregulation by dictating where the individual is placed in the environment (e.g., in a tree, on the ground, or in a burrow) based on the input traits (e.g., refuge emergence temperature, arboreal and burial habit, and diurnal or nocturnal activity preference), minimization of thermal stress (i.e., avoiding its CTmax) and maximization of time at its Tpref. The behavioral algorithm switches the individual to shade on the ground or within a burrow to reduce operative temperatures below CTmax and maintain operative temperatures at Tpref if operative temperatures become too high in solar radiation. Trait parameterizations for all MNMs are included in DuBose et al. (2025) (U.S. Geological Survey data release). For more details, consult Kearney and Porter (2020).

For each MNM model, we input the species' mass, critical thermal limits, Tpref, foraging temperature limits, and basking temperature trait values within the ectotherm model. Individuals were allowed to be active based on species' activity behavior and could either climb or burrow based on species' fossorial or arboreal trait values (Moore et al., 2021). We substituted four trait values after the imputation process to supplement missing values that could not be imputed (activity) and adjust an extreme emergence temperature value within TRAD. We supplemented missing activity trait values for *Lithobates areolatus* based on results from Hoffman et al. (2010) and allowed *L. areolatus* to be active at all times. We also used the minimum emergence temperature (22°C) for *Gastrophryne carolinensis* reported in Loftus-Hills and Littlejohn (1992) instead of the mean (27°C) to model *G. carolinensis* individuals as on the landscape instead of in burrows for more hours of our study period. We did not change the body shape, solar absorptivity, percent of water exchange areas, percent of contact with surface, or tissue density of the model individual, all of which do vary intra- and interspecifically and contribute to differences in anuran thermal sensitivity (Riddell et al., 2023).

We investigated how intraspecific trait values affected operative temperature estimates for a subset of species with multiple Tpref trait values. We ran MNMs with different Tpref trait values instead of the interspecific mean value at 5000 random points, resulting in approximately 4% of each species' randomly sampled points in the populated grid described below. We also investigated the intraspecific bounds of estimated warming tolerance by running ectotherm models parameterized with trait suites we assume to be least and most sensitive to increased temperatures at the same subset of points above. For example, we ran MNMs representing the most sensitive *D. chrysoscelis* individuals using the lowest CTmax, adult mass, Tpref, and emergence temperature and higher

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critical thermal minima trait values to estimate a potential lower bound on the warming tolerance of *D. chrysoscelis*. Although these models estimate how intraspecific trait variability affects warming tolerance estimates, they do not account for local adaptation to environmental conditions (e.g., an elevational gradient in *Ascaphus montanus* CTmax associated with higher stream temperatures along that gradient; Cicchino, Shah, et al., 2023), which are evident in multiple amphibian species (Bodensteiner et al., 2021). The models above generated hourly estimates of microclimate variables and individual operative temperatures, which we used to estimate the warming tolerance of 13 anuran species as an estimate of thermal sensitivity.

Thermal sensitivity quantification

Most of the locations where CTmax values were determined are outside the southeastern United States (Appendix S2); accounting for acclimation by only modeling warming tolerance at those locations would not provide insight into thermal sensitivity in our region. Thus, we ran MNMs for populated 1 km × 1 km grid cells within our study region using occurrence data from GBIF and HerpMapper that was filtered to species' native range and expected realized climate niche breadth (DuBose, Moore, et al. 2023; GBIF.org, 2021a, 2021b) and the sf package (Pebesma, 2018). We created a 5-km radius circle centered at each point occurrence, merged areas that overlapped, and overlaid the resulting polygon on the 1 km × 1 km grid of our study region to identify populated grid cells. We used the centers of populated grid cells as the locational input into the MNMs, and hereafter refer to each unique location as a point. Points were referenced in the World Geodetic System 1984 datum and ellipsoid. At each point, we first ran a single microclimate model to control for differences in microclimate estimation and then ran an ectotherm model for each species whose 5-km buffered area of occurrence (AOO) intersected the grid cell. We subtracted the individual's hourly estimated operative temperature from the species' CTmax for hourly warming tolerance and calculated the daily minimum warming tolerance (hereafter referred to as WT_d).

To quantify species' relative thermal sensitivity, we calculated the minimum, 25th percentile, and median WT_d for each species (DuBose et al., 2025). Species with lower WT_d values are more sensitive to warmer temperatures. Minimum WT_d values described species' warming tolerance to extreme temperatures (the hottest day of 3298 daily minimums, which represent temperatures experienced during heat waves), 25th percentile WT_d described species' warming tolerance during hotter periods of the year (825 of 3298 daily minimums possible, hereafter referred to as the hottest quarter WT_d), and median WT_d describes species' median daily minimum warming tolerance across the entire 10-year time span. We identified differences among species WT_d using an ANOVA, with a Tukey's honestly significant difference (HSD) test to identify differences between species. We compared the congruence between species' rank thermal sensitivity based on minimum, hottest quarter, and median WT_d using a Spearman's rho correlation using the asymptotic t approximation. We conducted the Spearman's rho correlation with the alternative hypothesis that there is a positive correlation between rank WT_d. We calculated the percent of points (hereafter percent sampled distribution) where minimum WT_d is less than 0°C (indicating modeled operative temperature was higher than species' CTmax for at least 1 h of 1 day in 2011–2020) and 2°C (indicating the species could be at its thermal limits with 2.5°C warming; Vose et al., 2017). We assume species with higher proportions of their regional AOO below these thresholds are more sensitive to increased temperatures.

We investigated if and how species' thermal sensitivity changed across a latitudinal gradient using linear models that related minimum, hottest quarter, or median WT_d to point latitude by incorporating a species-specific intercept and the interaction of latitude and species. We investigated differences among the coefficients of the interaction between latitude and species using an ANOVA F test and alpha = 0.05. To determine the coefficient's 95% CI, we used the *emtrends* function in the R package emmeans and compared species' coefficients using the *pairs* function (Lenth, 2022). Species' latitudinal extent within our study area sometimes differed widely from species' latitudinal extent within their range (Appendix S1: Figure S2), which could affect our interpretation of these coefficients. For simplicity, median WT_d results are reported in Appendix S1. The results exploring how intraspecific variation (variation in Tpref, least sensitive, and most sensitive trait suites) could affect relative thermal sensitivity quantification are reported in Appendix S3, except for the relationship between hottest quarter WT_d and latitude for Tpref variance models.

RESULTS

Using mechanistic models that incorporate thermal traits, a behavioral algorithm, and microhabitat variables, we estimated the operative temperature of 13 anuran species across 17.5% of occupied points that spanned a latitudinal gradient of 25.1–37.8° N within the southeastern United States. To estimate species thermal traits, we removed redundant trait values from TRAD measured

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outside the southeastern United States and recalculated interspecific trait values (Appendix S1: Figure S1). Using the Ornstein-Uhlenbeck model of evolution (Appendix S1: Table S1), we imputed 38 missing trait values, 31 of which described basking and foraging behavior; imputed values were generally lower than or close to interspecific values according to the leave-one-out cross-validation analysis (Appendix S1: Table S2). As a result, we reduced available intraspecific trait values into interspecific thermal trait values we used to parameterize the MNMs (Figure 1). We identified intraspecific variation in Tpref trait values in *Acris blanchardi*, *Anaxyrus americanus*, *Lithobates clamitans*, and *P. crucifer* (Figure 1), built least and most sensitive trait suites for *An. americanus*, *L. clamitans*, *P. crucifer*, *D. chrysoscelis*, *L. palustris*, *Lithobates sylvaticus*, and ran MNMs with those intraspecific trait values at 5083 randomly sampled points (Appendix S3: Table S1). Of the 246,779 occupied grid cells, we ran models at 43,109 points (Table 1).

At 17,759 points (41.2% of total points) at least one species had a modeled operative temperature that was higher than its CTmax. Median WT_d across species was 11.2°C (range = 5.1–24.1°C). Species varied in their minimum WT_d ($F_{12,89,515} = 37{,}173$, $p < 0.001$), hottest quarter WT_d ($F_{12,89,515} = 57{,}686$, $p < 0.001$), and median WT_d ($F_{12,89,515} = 36{,}974$, $p < 0.001$; Figure 2). Almost all species had different WT_d (Tukey's HSD, $p < 0.05$; Appendix S1: Table S3), except for similar minimum WT_d between *Lithobates catesbeianus* and *Anaxyrus fowleri* ($p = 1.0$) and *L. areolatus* and *Dryophytes versicolor* ($p = 0.44$), and similar median WT_d between *D. chrysoscelis* and *An. americanus* ($p = 1.0$), *Scaphiopus holbrookii* and *L. clamitans* ($p = 0.99$), *L. palustris* and *D. versicolor* ($p = 0.20$), and *L. palustris* and *P. crucifer* ($p = 0.20$). Species' hottest quarter WT_d and median WT_d had the highest correlation ($\rho = 0.90$, $p < 0.001$). The correlations between minimum and hottest quarter WT_d and minimum and median WT_d were only moderate in strength ($\rho = 0.53$, $p = 0.03$ and $\rho = 0.45$, $p = 0.06$, respectively). Species that had lower WT_d typically had a smaller AOO and were unable to bury in the substrate to behaviorally thermoregulate (Figure 2).

For most species, at least a portion of the sampled distribution of their southeastern United States range had a negative minimum WT_d. Only three species had positive WT_d (CTmax values higher than their modeled operative

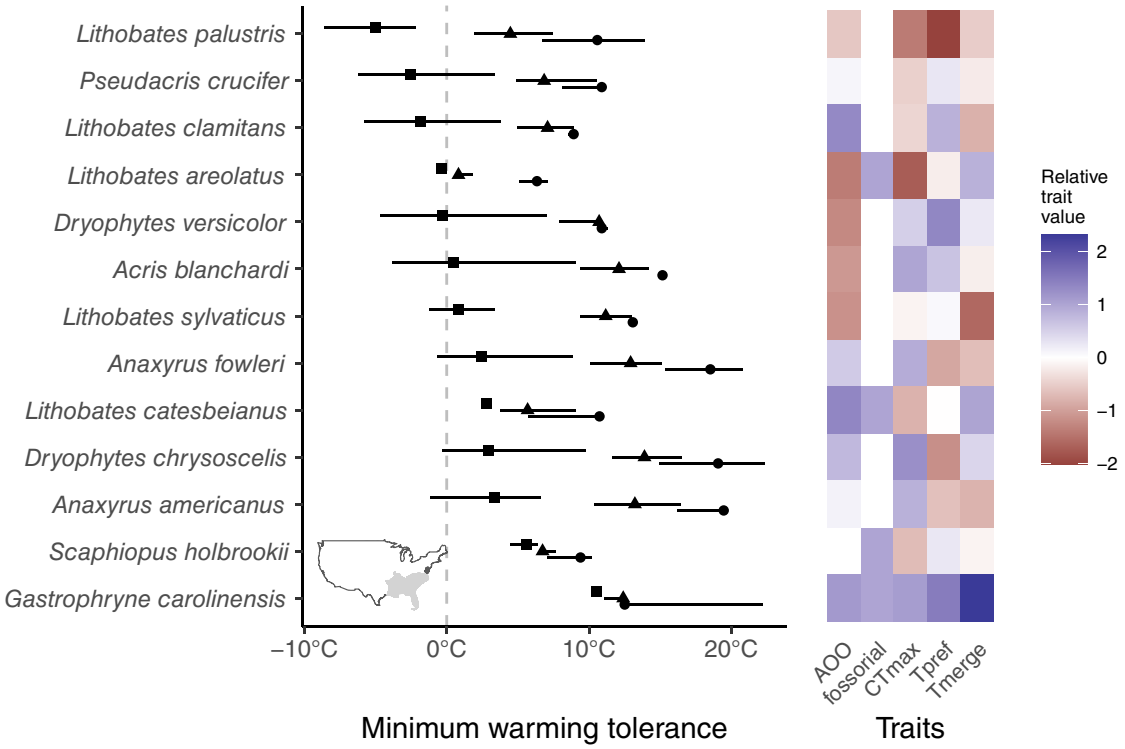


FIGURE 2 Species' median and 95% CIs of the minimum (square), hottest quarter (triangle), and median (circle) minimum warming tolerance across sampled occupied points within the southeastern United States (inset). Species are arranged top to bottom according to the lowest and highest minimum warming tolerance. Area of occupancy (AOO), fossorial, critical thermal maximum (CTmax), temperature preference (Tpref), and emergence temperature (Tmerge) are traits that aid in the interpretation of relative thermal sensitivity, with relative trait value reflecting the *z* score (mean centered and scaled by the SD) of the trait for this species list, except for the fossorial trait values representing species that can bury (1) and cannot bury (0). See Table 1 for the number of points sampled for each species.

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temperature) across the southeast: *G. carolinensis*, *S. holbrookii*, and *L. catesbeianus*. The median portion of species' sampled distribution with minimum $WT_d < 0°C$ was 39.4%, but variation in that proportion was high. For example, seven species had less than 25% of their sampled distribution with minimum $WT_d < 0°C$ (Table 1). *L. areolatus* had negative minimum WT_d across its entire sampled distribution, closely followed by *L. palustris* (99.5% of its sampled distribution).

Hottest quarter WT_d increased with latitude, indicating species' thermal sensitivity was highest at lower latitudes (Figure 3A). Linear models that regressed WT_d to latitude explained at least 88% of the variance in WT_d (df = 26, 89,502, $F \geq 26{,}460$, adjusted $R^2 > 0.88$, $p < 0.001$) (Appendix S1: Table S3). Hottest quarter WT_d slopes differed among species and varied from 0.09°C/degree latitude (95% CI: 0.08, 0.1; *S. holbrookii*) to 0.64°C/degree latitude (0.62, 0.65; *An. americanus*) (Appendix S1: Table S3). The strength of the relationship between hottest quarter WT_d and latitude was affected by species Tpref trait value (Figure 3B) ($F_{38,27,029} = 80{,}860$, $p < 0.001$, adjusted $R^2 = 0.99$), but the relationship remained positive for all models except when *P. crucifer*'s Tpref was highest (Appendix S1: Table S4). For the relationship between minimum WT_d and latitude, five species had negative relationships (more sensitive at higher latitudes), three species had no relationship (sensitivity did not vary across latitude), and five species had positive relationships (more sensitive at lower latitudes; Figure 4; Appendix S1: Table S3). Almost all species had positive relationships between median WT_d and latitude, and only *L. sylvaticus* had no relationship between median WT_d and latitude (0.01°C/degree latitude [−0.06, 0.09]) (Appendix S1: Figure S4, Table S3).

DISCUSSION

Thermal sensitivity varied among 13 anuran species in the Southeast United States, with some species

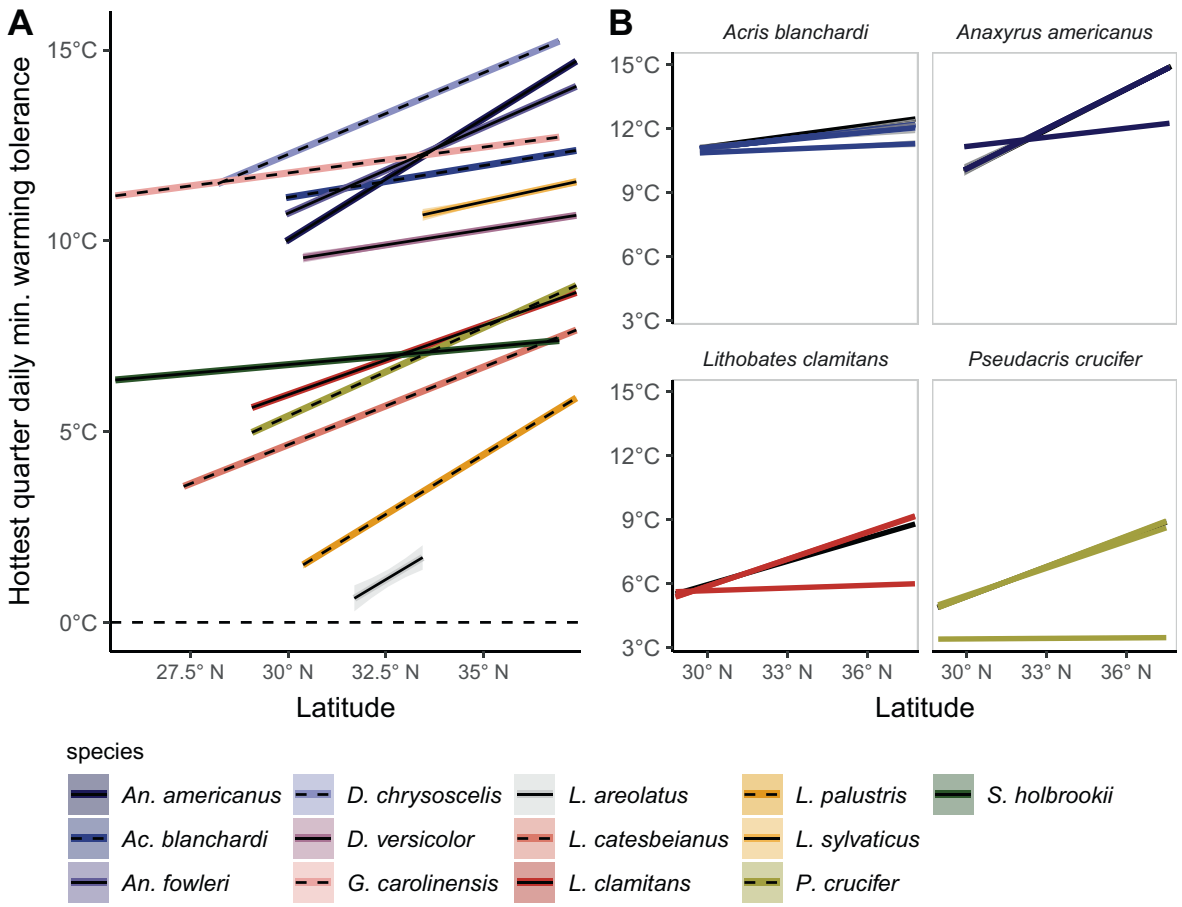


FIGURE 3 (A) Interspecific and (B) intraspecific differences in the predicted relationship between hottest quarter WT_d (25th percentile of daily minimum warming tolerance) and latitude. Intraspecific differences determined by varying the thermal preference trait value input into the mechanistic niche models. The line is the median and the ribbon is the 95% CI of the predicted linear relationship using a species-specific (interspecific) or model-specific (intraspecific) intercept and slope; in (B), black lines are the interspecific predicted relationship and 95% CIs are negligible.

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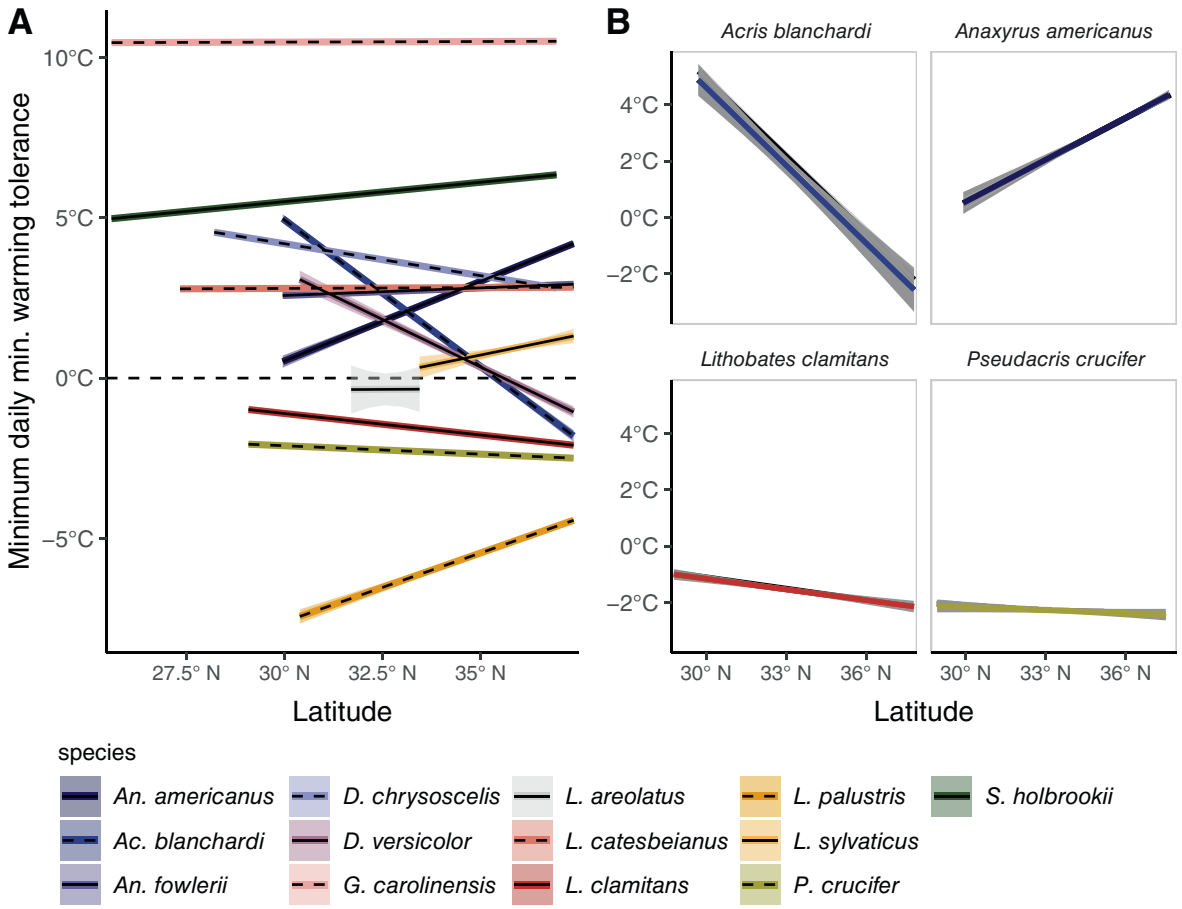


FIGURE 4 (A) Interspecific and (B) intraspecific differences in the relationship between minimum daily minimum warming tolerance and latitude. Intraspecific differences determined by varying the thermal preference trait value input into the mechanistic niche model. The line is the median and the ribbon is the 95% CI of the predicted linear relationship using a species-specific (interspecific) or model-specific (intraspecific) intercept and slope; in the intraspecific panel (B), black lines are the interspecific predicted relationship and 95% CIs are negligible.

approaching their thermal limits during the warmest quarter of the year and many species close to their thermal limits during heat waves. Thus, anurans join the growing list of taxa with some species living near their thermal limits: tropical lizards (Huey et al., 2009), North American freshwater fish (Matthews & Zimmerman, 1990; Troia, 2023), and freshwater mussels (Pandolfo et al., 2024), among others. Rising temperatures and prevalent low warming tolerance portend future biodiversity loss (Román-Palacios & Wiens, 2020). We found support for our hypothesis that anuran thermal sensitivity decreased with latitude (higher warming tolerance at higher latitudes), but the strength, and sometimes direction, of the relationship between latitude and warming tolerance differed among species. Species' warming tolerance typically increased with latitude, supporting results from investigations focused on higher taxonomic categories (Sunday et al., 2014). The latitudinal increase in warming tolerance could be confounded with the presence of higher elevation in the northern part of our study extent, which could act as a thermal refuge; however, anuran physiological adaptation to higher elevation varies among species and is under-explained by upper physiological limits and thermal performance curves (Cicchino, Shah, et al., 2023; Pintanel et al., 2024). A positive relationship between warming tolerance and latitude is thus likely due to higher mean annual temperatures at lower latitudes (Deutsch et al., 2008). Yet, the relationship between species' minimum WT_d and latitude was not consistent. Contrary to the latitudinal gradient of thermal sensitivity for terrestrial ectotherms (Pinsky et al., 2019), species' sensitivity to extreme temperatures did not always decrease toward the poles. Some species had lower warming tolerance at higher latitudes, which may exacerbate those species' vulnerability given higher exposure to extreme events at higher latitudes in the future (Murali et al., 2023).

Anuran species differ in their thermal sensitivity and characteristics that mitigate or compound their threat of extinction. Both *L. palustris* and *L. areolatus*

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(both of which are listed as Species of Greatest Conservation Need; Wellman et al., 2024) are likely already close to their thermal limits, adding to the threats they face based on the potential loss of their microhabitats (wetlands and crawfish burrows, respectively). In contrast, fossorial species like *G. carolinensis* can bury to reduce their operative temperature, increasing their WT_d and thus reducing their thermal sensitivity (Huey et al., 2012; Sunday et al., 2014). Using trait-rich mechanistic models allowed us to identify which species in this trait-diverse group are living closest to their thermal limits.

Our estimates of thermal sensitivity are relative and require many assumptions, but they provide clues to the regional and state-specific declines of some anuran species. Although *P. crucifer*'s occupancy has increased from 1998 to 2013 across the Southeast (Villena et al., 2016), its declining occupancy in Tennessee could be related to lower warming tolerance there. Based on our results, *G. carolinensis*'s occupancy decline across the Southeast (Villena et al., 2016) could be due to habitat loss and fragmentation instead of thermal stress (Lannoo et al., 2005). Our warming tolerance estimates could be used to identify species with potentially increased thermal threat with unknown population trends (e.g., *L. palustris*). However, our results provide insights on anuran thermal sensitivity specific to the southeastern United States and should not be extrapolated to other portions of species ranges (Appendix S1: Figure S2).

By incorporating interspecific differences in mass, behavior, and other traits, MNMs reflect the complexity of species adaptations to thermal stress better than single trait values. This complexity allows us to avoid underestimating species rank sensitivity based on a single trait. For example, *P. crucifer* was the second most thermally sensitive species based on warming tolerance estimates but the fifth most thermally sensitive based on CTmax value. Incorporating foraging time into thermal sensitivity estimates revealed reduced estimates of habitat loss due to precipitation and temperature changes for montane salamanders and lizards (Lyons & Kozak, 2020; Muñoz et al., 2022). In mammals, inclusion of morphological traits affected estimates of thermal neutral zone boundaries and thus thermal sensitivity (Mathewson et al., 2020). Future studies incorporating foraging behavior differences, morphological differences, or life-stage specific thermal tolerances could reveal differences in thermal sensitivity among species by incorporating more biological reality into MNMs (Briscoe et al., 2023).

Our models did not incorporate interspecific differences in water loss rate, which differ between arboreal and non-arboreal species (Wygoda, 1984) and may become important in a drier future (Sunday et al., 2014). Interspecific differences in performance and behavior at different temperatures and hydration levels, driven by differences in evaporative water loss rates, increase species extinction risk in a drier future (Greenberg & Palen, 2021; Lertzman-Lepofsky et al., 2020). Future research on interspecific differences in water loss rates and water conservation behavior could identify species sensitive to shifts in both temperature and water availability.

The heat waves modeled in this manuscript are predicted to become summer norms, increasing animals' thermal stress and potentially resulting in species' range loss in the absence of dispersal (Stillman, 2019). Our results suggest that during heat waves, most of the species we evaluated ($n = 9$ out of 13 species, amounting to almost a quarter of the anuran species in the Southeast United States) experience temperatures above their CTmax, which potentially limits their ability to forage and disperse and could lead to the inability to persist throughout their current range. In areas that become thermally untenable, species disperse to areas that match their thermal tolerance, with conventional wisdom suggesting poleward dispersal. However, evidence suggests directional differences between temperate and tropical species (VanDerWal et al., 2013). Based on our results, poleward dispersal for four hylids (*Ac. blanchardi*, *D. chrysoscelis*, *D. versicolor* and *P. crucifer*) and *L. clamitans* would bring them closer to their thermal limits during heat waves, increasing their thermal stress and extinction risk. Inconsistent latitudinal relationships between hottest quarter WT_d and minimum WT_d in our species pool highlight that species will need to respond to both increases in mean annual temperature and daily extreme temperatures to thermoregulate in the future (Kingsolver et al., 2013).

Within MNMs, uncertainty within the microclimate model propagates to uncertainty in modeled operative temperatures (Briscoe et al., 2023; Bütikofer et al., 2020). Even though NicheMapR microclimate models have been extensively tested (Kearney et al., 2020; Kearney & Porter, 2017), microclimate model outputs do not perfectly model species-specific microhabitats (e.g., large boulders in forested ecosystems; Newman et al., 2022). For example, we modeled terrestrial habitats, but species of *Lithobates* typically stay in water which can buffer estimated temperatures in ways our models do not capture. Terrestrial WT_d likely mediates dispersal ability for juveniles and adults of *Lithobates*, which reduces their ability to cope with increased temperatures (Araújo et al., 2006). Although future research incorporating specific habitat preferences could improve estimates of thermal sensitivity, we were able to quantify and compare thermal sensitivity among species by modeling the common environment among a habitat-diverse species pool.

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Thermal sensitivity comparisons can be influenced by intraspecific trait variation, temporal scale, and spatial scale (Clusella-Trullas et al., 2021). Thermal trait plasticity and acclimation ability affect estimates of vulnerability among and within species (Bennett et al., 2019). For example, the least thermally sensitive species among *L. palustris*, *L. clamitans*, and *L. catesbeianus* depends upon whether acclimation ability or warming tolerance is used to assess sensitivity (Bodensteiner et al., 2021; Brattstrom, 1968). Although acclimatization and plasticity in thermal traits can reduce the effect of increased temperatures, they are unlikely to completely compensate for predicted precipitation and temperature changes (Gunderson et al., 2017; Gunderson & Stillman, 2015; Morley et al., 2019). Mechanistic models that incorporate acclimatization would provide more accurate descriptions of intraspecific and interspecific thermal sensitivity (Cocciardi & Ohmer, 2024). Our methodology would also be appropriate for taxa with potentially minimal acclimation ability, such as freshwater mussels (Fogelman et al., 2023).

CONCLUSION

Estimating how close species are to their thermal limits and how that proximity shifts across a latitudinal gradient provides insight into (1) which species are the most vulnerable to increased temperatures, (2) where species tend to be most sensitive, and (3) possible external drivers of species thermal sensitivity. As such, our results can inform conservation planning efforts, like the Southeast Blueprint or State Wildlife Action Plans, by identifying areas or species with increased vulnerability to warmer temperatures. By using process-based models that incorporate multiple traits, we found that species varied in their warming tolerance and that many anuran species are living close to their thermal limits. By exploring the relationship between warming tolerance and latitude, we found that species generally are less thermally sensitive at higher latitudes. However, some species are more sensitive to extreme temperatures at higher latitudes. Differences in warming tolerance across a latitudinal gradient highlight species-specific drivers of thermal sensitivity (i.e., mean annual temperature or heat wave intensity) and show that patterns at higher taxonomic groups can be inconsistent at lower taxonomic groups. In all, increased mean annual temperature and temperature extremes (e.g., heat waves) could increase anuran extinction risk through reduced access to terrestrial habitats and potentially contribute to species loss in a North American biodiversity hotspot.

AUTHOR CONTRIBUTIONS

Traci P. DuBose and Meryl C. Mims conceptualized the manuscript with contributions from Abigail L. Benson, William A. Hopkins, and Sam Silknetter. Traci P. DuBose, Chloe E. Moore, Vincent R. Farallo, and Abigail L. Benson designed methodology. Traci P. DuBose conducted the analysis and wrote the original draft. All authors reviewed and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (DuBose et al., 2025) are available from the U.S. Geological Survey ScienceBase-Catalog: https://doi.org/10.5066/P13ZYSXP. Code (DuBose, 2025) is available from Zenodo: https://doi.org/10.5281/zenodo.15064988.

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