Vulnerability of amphibians to global warming

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Abstract

Amphibians are the most threatened vertebrates, yet their resilience to rising temperatures remains poorly understood. This is primarily because knowledge of thermal tolerance is taxonomically and geographically biased, compromising global climate vulnerability assessments. Here, we employed a novel data imputation approach to predict the heat tolerance of 60% of amphibian species and assessed their vulnerability to daily temperature variation in thermal refugia. We found that 198 out of 5203 species are currently exposed to overheating events in shaded terrestrial conditions. Despite accounting for heat tolerance plasticity, a 4°C global temperature increase would create a step-change in impact severity, pushing 9.4% of species beyond their physiological limits. In the Southern Hemisphere, tropical species encounter disproportionally more overheating events, while in the Northern Hemisphere, non-tropical species are more susceptible. Our findings challenge evidence for latitudinal gradients in overheating risk and underscore the importance of considering climatic variability in vulnerability assessments. Notably, our conservative estimates assume access to shaded microenvironments, implying that global warming's impacts on amphibians may exceed our projections. Our microclimate-explicit analyses also demonstrate how the availability of vegetation and water bodies is critical in buffering amphibians during heat waves. Immediate action is needed to preserve and manage these microhabitat features.

Keywords

Anura, Caudata, critical thermal maximum, behavioral thermoregulation, microclimate selection, biophysical modelling, global analysis, thermal safety margin, warming tolerance, extreme heat events, climate change.

Introduction

Climate change has pervasive impacts on biodiversity, yet the extent and consequences of this environmental crisis vary spatially and taxonomically[1–3]. For ectothermic species, such as amphibians, the link between climate warming and body temperature is clear, with immediate effects on physiological processes[4–6]. Over 40% of amphibian species are currently listed as threatened, and additional pressures due to escalating thermal extremes may further increase their extinction risk[6–9]. Therefore, it is vital to assess the resilience of amphibians to climate change to prioritize where and how conservation actions are taken.

Accurate assessments of resilience to climate change require adequate data on thermal tolerance and environmental exposure[10–12]. Given that extreme heat excursions are more likely to trigger overheating events than increased mean temperatures[13–15], climate vulnerability assessments require environmental data with high spatial and temporal resolution. When heat tolerance limits are known, cutting-edge approaches in biophysical ecology allow fine-scale vulnerability assessments that account for morphology, behavior, and microhabitat setting in both historical and future climate projections[12,16–22]. While broadly applicable, biophysically informed analyses are particularly relevant for amphibians, whose complex life-history transitions and microhabitat preferences span terrestrial, aquatic, and arboreal environments. Because microenvironmental features are essential for behavioral thermoregulation[23–25], modelling microhabitats allow assessments of the effectiveness of different thermal refugia in buffering the impacts of extreme heat events.

However, a comprehensive global analysis of amphibian vulnerability to climate change is lacking[26]. This gap stems primarily from the scarcity of empirical data, confined to a few well-researched species in restricted geographical areas. For instance, the most exhaustive dataset on amphibian heat tolerance limits only covers 7.5% of known species (616 species) and is geographically biased towards temperate regions[27]. This discrepancy is problematic, considering the high species richness in the tropics and the mounting evidence that tropical ectotherms are most susceptible to rising temperatures[11,12,21,28–30]. Such sampling biases call into question the reliability of inferences in under-sampled areas and have implications for conservation strategies. Given the rapid pace of climate change and the finite resources available for research, acquiring sufficient empirical data to fill these knowledge gaps within a realistic timeframe is increasingly untenable[31,32]. Therefore, alternative methods to identify the populations and areas most susceptible to thermal stress are critically needed in a rapidly warming climate.

Here, we assessed the global vulnerability of amphibians to extreme heat events in different climatic scenarios and thermal refugia. We developed a new approach to solve taxonomical and geographical biases in thermal limits using Bayesian phylogenetic data imputation. We then integrated predicted thermal limits with daily body temperature fluctuations estimated from biophysical models to quantify the proximity of heat tolerance limits to temperatures experienced in shaded microhabitats — a best-case scenario assuming effective behavioral thermoregulation. By doing so, our study offers the first comprehensive, global evaluation of the impact of daily temperature extremes on the physiological viability of natural amphibian populations and communities.

Methods

Reporting

We report author contributions using the CRediT (Contributor Roles Taxonomy) statement[33] and MeRIT (Method Reporting with Initials for Transparency) guidelines[34]. We also crafted the study title, abstract and keywords to maximize indexing in search engines and databases[35]. All analyses were performed by PPottier (with conceptual and technical input from MRK, NCW, JER, ARG, SMD and SN) using R statistical software[36] (v. 4.3.0), and most computations used the computational cluster Katana supported by Research Technology Services at UNSW Sydney. All code was reviewed by NCW, ARG, and JER following the recommendations of [37].

Amphibian heat tolerance limits

We leveraged the most comprehensive compilation of amphibian heat tolerance limits[27] for our analyses (Extended Data Fig. 1). Briefly, these data were collated by systematically reviewing the literature in five databases and seven languages, comprising 3,095 heat tolerance limits from 616 amphibian species. To facilitate the comparability and analysis of heat tolerance limits, PPottier only included data matching four specific criteria. First, we only included heat tolerance limits measured using a dynamic methodology (i.e., temperature at which animals lose their motor coordination when exposed to ramping temperatures, critical thermal maximum $CT_{max;}$[38]). Second, we only selected data for which the laboratory acclimation temperature, or the field temperature during the month of capture, was recorded. Third, we only included data from species listed in the phylogeny from [39]. Fourth, we only included species for which their geographical range was reported in the International Union for the Conservation of Nature red list[40] (accessed in January 2023).

These criteria were chosen to perform phylogenetically, climatically, and spatially informed analyses. In total, we selected 2,661 heat tolerance limits estimates with metadata for 524 amphibian species. NCW, PPollo, and ANRV also complemented this dataset with ecotypic data for each species. Amphibians were grouped into six major ecotypes according to [41]:

ground-dwelling, fossorial, aquatic, semi-aquatic, stream-dwelling and arboreal. Cave specialists were excluded because they experience unique microclimatic conditions.

Data-deficient species

Our objective was to assess the thermal tolerance of amphibians globally. However, the data compiled in [27] are geographically and taxonomically biased. Therefore, we employed a data imputation procedure to infer the thermal tolerance of data-deficient species, totaling 5,203 species at a broad geographical coverage (524 species + 4,679 data-deficient species; ~60% of all described amphibian species, amphibiaweb.org; accessed in December 2023). PPottier selected data-deficient species from a species list that matched the phylogeny from [39] (7,238 species), was listed in the IUCN red list along with geographic distribution data, and for which ecotypes were known. We did not consider Caecilians (order Gymnophiona) because, to our knowledge, heat tolerance limits are unknown for all Caecilian species[27]. We also supplemented our dataset with published body mass data retrieved from literature sources or estimated based on length-mass allometries[41–43]. PPottier then estimated the geographical coordinates at which all extant species occurred in their IUCN distribution range at a 1° x 1° resolution to use for biophysical modelling (Extended Data Fig. 1).

Data imputation

PPottier, SMD, and SN developed a phylogenetic imputation procedure here defined as Bayesian Augmentation with Chained Equations (BACE). The BACE procedure combines the powers of Bayesian data augmentation and multiple imputation with chain equations (MICE[44]). Briefly, we ran multiple iterative models using *MCMCglmm*[45] (v. 2.34) and supporting functions from the *hmi* package[46]. In the first cycle, missing data was either taken as the arithmetic mean for continuous predictors, or randomly sampled from existing values for (semi)categorical predictors. Predicted (augmented) values from the models were then extracted from the response variables and used as predictor variables in the next models to predict other response variables. Ultimately, heat tolerance limits were predicted using augmented data from all predictors. PPottier ran 5 cycles where the data from one cycle was iteratively used in the next cycle, and estimations converged after the first cycle (Fig. S1). Our cross-validation approach also demonstrated the ability for our models to back predict known experimental estimates with reasonable error (Extended Data Fig. 2).

Heat tolerance limits were imputed based on the species' acclimation temperatures, the duration of acclimation, the ramping rate and endpoint used in assays, the medium used for measuring heat tolerance limits (i.e., ambient temperatures, water/body temperatures), and the life stage of the animals (adults or larvae). These variables were correlated with amphibian heat tolerance limits (Fig. S2) and were fitted as covariates in Bayesian linear mixed models. We also weighted heat tolerance estimates based on their sampling variance, accounted for phylogenetic non-independence using a correlation matrix of phylogenetic relatedness, and fitted random intercepts for species-specific effects and phylogenetic effects, as well as their correlation with acclimation temperatures (i.e., random slopes). In other words, we accounted for both species-specific slopes (plasticity) and phylogenetic conservatism in these slopes. We imputed data for adult amphibians assuming they were acclimated to the median, 5th, or 95th percentile operative body temperatures experienced across their geographical range (see *Microenvironmental data and biophysical modelling)* for a duration of 10 days, tested using a ramping rate of 1°C/min in water, and for which thermal tolerance endpoint was recorded as the onset of spasms. These methodological parameters were the median values in the experimental dataset, or the most common values (mode). This allowed standardization of heat tolerance limits for the comparative analysis[47–49]. In amphibians, the onset of spasms usually occurs after the loss of righting response[47], meaning that our estimates are conservative. While we did include data from larvae in the training data, we only imputed data for adults to increase the comparability of our estimates.

For both known species and data-deficient species, PPottier generated three ecologically relevant and standardized heat tolerance estimates. In total, we generated data for 5,203 species of amphibians (Extended Data Fig. 1-2). Notably, our imputed estimates are accompanied by standard errors, which provides estimates of uncertainty in the imputation, and errors were propagated throughout our analyses (see *Climate vulnerability analysis*).

Microenvironmental data and biophysical modelling

PPottier (with conceptual insights from MRK, NCW, JER, and ARG) used the package *NicheMapR*[18,19] (v. 3.2.1) to estimate microenvironmental temperatures and operative body temperatures in current (2006-2015) and projected climatic conditions (2°C or 4°C of global warming above pre-industrial levels). Operative body temperatures are the steady-state body temperature that organisms would achieve in a given microenvironment, which can diverge significantly from ambient air temperatures due to, for example, radiative and evaporative heat exchange processes[16,17,25,50–54].

For each geographic location, we generated microclimatic temperatures experienced by amphibians on i) a vegetated ground-level substrate (i.e., terrestrial), ii) in above-ground vegetation (i.e., arboreal), or iii) in a water body (i.e., aquatic) (Extended Data Fig, 1). For terrestrial and aquatic species, we simulated microenvironmental temperatures 1 cm above the surface. For arboreal species, we simulated microenvironmental temperatures 2 meters above ground, applied a reduction of 80% in windspeed to account for reduced wind due to vegetation[55], and assumed that 90% of the solar radiation was diffuse due to canopy cover[56]. All microenvironmental projections were made using 85% shade to simulate animals in thermal refugia, i.e., the microhabitats in which animals would retreat during the hottest times of the day. We did not model temperatures in the sun because ectothermic species most likely behaviorally thermoregulate by retreating to thermal refugia during extreme heat events[24]. Our estimations thus represent conservative estimates of the vulnerability of amphibians to extreme temperature events.

For microclimatic temperature estimates, we used the *micro_ncep* function from *NicheMapR*[18] (v. 3.2.1), which integrates 6-hourly macroclimatic data from the National Center for Environmental Predictions (NCEP). This function also inputs from the *microclima* package[57] (v. 0.1.0) to predict microclimatic temperatures after accounting for variation in radiation, wind speed, altitude, albedo, vegetation, and topography. These data are downscaled to an hourly resolution, producing high-resolution microclimatic data. We used projected future monthly climate data from TerraClimate[58] to generate hourly projections assuming 2°C or 4°C of global warming above pre-industrial levels. These temperatures are within the range projected under low and high greenhouse gas emission scenarios, respectively[59]. TerraClimate projections use monthly data on precipitation, minimum temperature, maximum temperature, wind speed, vapor pressure deficit, soil moisture, and downward surface shortwave radiation. These projections impose monthly climate projections from 23 CMIP5 global circulation models, as described in[60]. The *micro_ncep* function then downscales monthly TerraClimate inputs to hourly by imposing a diurnal cycle to the data. We ran all microclimatic estimations between 2005 and 2015 to match the range of pseudo-years available for TerraClimate future climate projections. We did not use a larger range of historical records to reduce computational demands.

We then used microclimate estimates to generate operative body temperatures using the *ectotherm* function in *NicheMapR*[19]. This modelling system has been extensively validated with field observations[61–63]. We modelled an adult amphibian in the shape of the leopard frog *Lithobates pipiens*, positioned 1 cm above ground (or 2 m for arboreal species), and assumed that 80% of the skin acted as a free water surface (wet skin). To account for the body mass of the organisms, we ran the ectotherm models using the median body mass of the community in each given geographical coordinate. When body mass was unknown, we ran models assuming a body mass of 8.4 grams, the median body mass in our dataset. While it would have been optimal to use species-specific body masses and assign other parameters to the models in each coordinate (e.g., preferred body temperature, *see* [22,64]), it was too computationally intensive given the geographic and taxonomic scale of our study (204,808 species by geographical coordinate combinations).

To model operative body temperatures in water bodies (e.g., pond or wetland), we used the container model from *NicheMapR*. Unlike previous models predicting steady-state temperatures, this approach accounts for transient temperature changes, capturing lags due to thermal inertia (i.e., transient heat budget model[65,66]). For pond simulations, we modelled a container permanently filled with water (12 m width and 1.5 m-depth) and decreased direct solar radiation to zero to simulate full shade. This modelling approach serves as a proxy for estimating the body temperature of ectotherms submerged in water bodies such as ponds or wetlands, which was validated with field measurements (e.g., [61,67]). Ground-level and water temperatures were modelled for all species regardless of their ecotype (apart from paedomorphic salamanders that were only assessed in aquatic environments) because arboreal and terrestrial species may retreat on land or in water occasionally. Temperatures in above-ground vegetation were only estimated for arboreal and semi-arboreal species as reaching 2 meters height in vegetation requires a morphology adapted to climbing. Our biophysical models assume that shaded microhabitats are available to species throughout their range. While this may not hold true, fine-scaled distribution of these microenvironments are not available at global scales. Moreover, assuming that these microenvironments are available serves a functional role, it provides a best-case scenario that is useful for comparative analyses and offers actionable insights for conservation. For instance, reduced exposure to overheating events in aquatic relative to terrestrial environments would suggest that preserving ponds and wetlands may be critical in buffering the impacts of climate change on amphibians.

PPottier then estimated, for each geographical coordinate, the maximum daily body temperature and the mean and maximum weekly maximum body temperature experienced in the 7 days prior to each given day to account for acclimation responses and to assess climate vulnerability metrics[13] (see *Climate vulnerability analyses*). Of relevance, we only used data for the 91 warmest days (i.e., warmest quarter) of each year, as we were interested in the responses of amphibians to extreme heat events[13]. Note that data from the year 2005 was excluded *a posteriori* as a burn-in to remove the effects of initial conditions on soil temperature, soil moisture, and pond calculations. Therefore, our analyses are based on 910 days (91 days per year in the range 2006-2015) for each climatic scenario (current climate, 2°C above pre-industrial levels, 4°C above pre-industrial levels).

PPottier also used maximum daily body temperatures on terrestrial conditions to calculate the median, 5th percentile and 95th percentile maximum body temperature experienced by each species across their range of distribution. These values were used as acclimation temperatures in the training data to calibrate the data imputation with ecologically-relevant environmental temperatures (see *Data imputation*); while maximizing the range of temperatures used to infer the plasticity of heat tolerance limits (see *Climate vulnerability analysis*).

Climate vulnerability analysis

Using the imputed data, PPottier (with assistance from SN) fitted a meta-analytic model for each species to estimate the plasticity of heat tolerance limits (CT_{max}) to changes in operative body temperatures using the *metafor* package[68] (v. 4.2-0). Weights were used to account for differences in the precision of imputed estimates. From these models, we used out-of-sample model predictions to estimate the CT_{max} of each species in each 1° x 1° grid cell across their distribution range in different warming scenarios. Specifically, we assumed that species were, on any given day, acclimated to the mean daily body temperature experienced in the 7 days prior[13]. Therefore, CT_{max} was simulated as a plastic trait, which varied daily, as animals acclimate to new environmental conditions (Extended Data Fig. 1). We propagated errors from the imputation when estimating the predicted CT_{max} across geographical coordinates. Predicted CT_{max} values and their associated standard errors thus reflect variation in both the imputation procedure and the estimation of plastic responses.

PPottier then estimated the vulnerability of amphibians to global warming using three metrics (Extended Data Fig. 1). First, we calculated the difference between CT_{max} and the maximum daily body temperature, i.e., the thermal safety margin (i.e., TSM, *sensu* [12]). We averaged thermal safety margins across years to estimate the mean difference between CT_{max} and the maximum temperature during the warmest quarters. Using TSM averaged from the maximum temperature of the warmest quarter is common in the literature (e.g., [69–71]). Second, we calculated the binary probability (1-0) that operative body temperatures exceeded CT_{max} at least once across the 910 days surveyed (warmest quarters of 2006-2015), i.e., the overheating risk. Third, we calculated the number of days the operative body temperature exceeded CT_{max} across the warmest quarters of 2006-2015, i.e., the number of overheating events. The latter two metrics provide a finer resolution than TSMs, as they capture daily temperature fluctuations and potential overheating events[13].

Macroecological patterns

The objective of this study was to characterize the vulnerability of amphibian populations and whole communities to global warming. We define a population as individuals of the same species in a 1° x 1° grid cell, allowing to identify specific populations and species that may be more susceptible to heat stress and direct targeted research efforts. We define a community as the species assemblage within a grid cell. Community-level analyses allow to identify areas containing a higher number of vulnerable species, offering actionable insights for broader-scale conservation initiatives.

PPottier (with assistance from SN) used the *gamm4* package[72] to fit generalized additive mixed models (GAMM) against latitude. For population-level patterns, we fitted latitude as a fixed factor, and nested genus and species identity as random terms to account for phylogenetic non-independence. Note that we did not include family as a random term because models failed at estimating higher taxonomic variation. While better methods exist to model phylogenetic patterns, generalized additive linear models do not allow for phylogenetic correlation matrices, and other functions such as *brms*[73] exceeded our computational capacities. Nevertheless, imputed estimates already reflect variation due to phylogeny (see *Data imputation*), and phylogeny was further modelled when deriving mean estimates in each microhabitat and climatic scenario (see below). PPottier fitted models using the three metrics as response variables independently: the thermal safety margin, overheating risk, and number of overheating events. The former was modelled using a gaussian distribution of residuals, overheating risk was modelled using binomial error structure, and the latter using a Poisson error structure. Thermal safety margin estimates were weighted by their sampling variance to account for the uncertainty in the imputation and predictions across geographical coordinates. PPottier fitted separate models for each climatic scenario (current climate, 2°C above preindustrial levels, 4°C above preindustrial levels) and microhabitat (terrestrial, aquatic, arboreal).

To investigate the mean TSM in each microhabitat and climatic scenarios, PPottier fitted models with the interaction between microhabitat and climatic scenario as a fixed effect using

MCMCglmm[45] (v. 2.34) and flat, parameter-expanded priors. In these models, we weighted estimates based on their standard error, species identity was fitted as a random effect, and we accounted for phylogenetic non-independence using a variance-covariance matrix of phylogenetic relatedness (calculated from the consensus tree of [39]). To investigate the overall overheating risk and number of overheating events in each condition, we attempted to fit models in *MCMCglmm* but these models failed to converge. Therefore, PPottier fitted Poisson and binomial models using *lme4*[74] (v. 1.1-33) and nested genus, species, and observation as random terms. We used similar Poisson models to investigate the relationship between the number of overheating events and thermal safety margin.

We also investigated patterns of climate vulnerability at the community level. We calculated the weighted average of TSM and overheating risk in each 1-degree grid cell (14,091; 14,090; or 6,614 grid cells for terrestrial, aquatic, and arboreal species, respectively), and mapped patterns geographically. Averaging overheating risk effectively returned the proportion of species overheating in each coordinate; and we also calculated the number of species overheating in each grid cell. For community-level models, we fitted Gaussian, binomial or Poisson models as described above, but without taxon-level random effects because these cannot be modelled at the community level. All models were fitted without an intercept, and with two-sided contrasts with current terrestrial conditions.

Sensitivity analyses

PPottier assessed the accuracy of the data imputation procedure using a cross-validation approach. Specifically, PPottier removed heat tolerance estimates for 5% of the species in the experimental data and 5% of the data-deficient species (maintaining the same proportion of missing data) and assessed how well experimental values could be predicted from the models. Of relevance, we only removed data that were comparable to the data that were imputed. That is, data from adult animals tested using a ramping rate of 1°C/min, and for which thermal limits were recorded as the onset of spasms. While we could have trimmed any data entry in the experimental data, validation of the imputation performance can only be achieved by comparing comparable entries, and imputing data from species tested in unusual settings would naturally result in large errors. In total, we cross-validated experimental estimates for 77 species.

We also investigated alternative ways to i) calculate thermal safety margins, ii) account for acclimation responses, and iii) control for prediction uncertainty (see *Supplementary methods;* Fig. S5-7). Results from all statistical models and additional data visualizations are available at https://p-pottier.github.io/Vulnerability_amphibians_global_warming/.

Results

Description of the dataset

We predicted heat tolerance limits and daily operative body temperatures for 5,203 species of amphibians in different microclimates and under different warming scenarios. This covers most of the distribution of amphibians (Fig. 1), and ~60% of described species (Fig. 2). In total, we predicted heat tolerance limits for 203,853 populations (individual species in 1° x 1° grid cells) in terrestrial conditions (5,177 species), 204,808 populations in water bodies (5,203 species); and 56,210 populations (1,771 species) in above-ground vegetation, for each warming scenario. These estimates were then grouped into communities (1° x 1° grid cells), tallying 14,090 and 14,091 communities for terrestrial and aquatic analyses and 6,614 communities for arboreal species, respectively. Our phylogenetic model-based imputation approach has significantly increased the depth of knowledge, effectively solving major taxonomic and geographic biases in experimental data, particularly in areas harboring the greatest diversity of species (Fig. 1-2). The accuracy of our imputation procedure was confirmed by the strong congruence between known experimental values and imputed data (experimental mean ± standard deviation = 36.186 ± 2.670; imputed mean = 35.934 ± 2.544; n = 375; Extended Data Fig. 2).

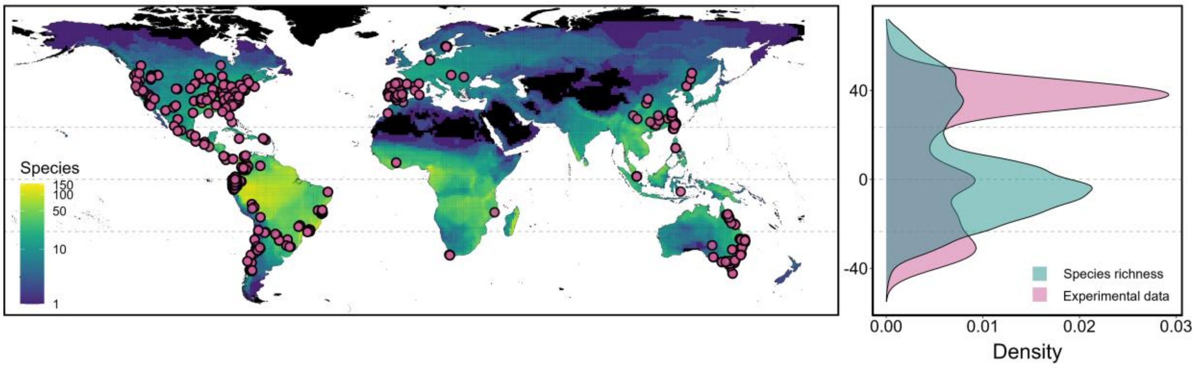


Fig. 1 | Contrast between the geographical locations at which experimental data were collected, and patterns in species richness. Pink points denote experimental data, while the color gradients refer to species richness calculated in 1 x 1 ° grid cells in the imputed data (5,203 species). Density plots represent the distribution of experimental data (pink) and the number of species inhabiting these areas (blue) across latitudes. Dashed lines represent the equator and tropics.

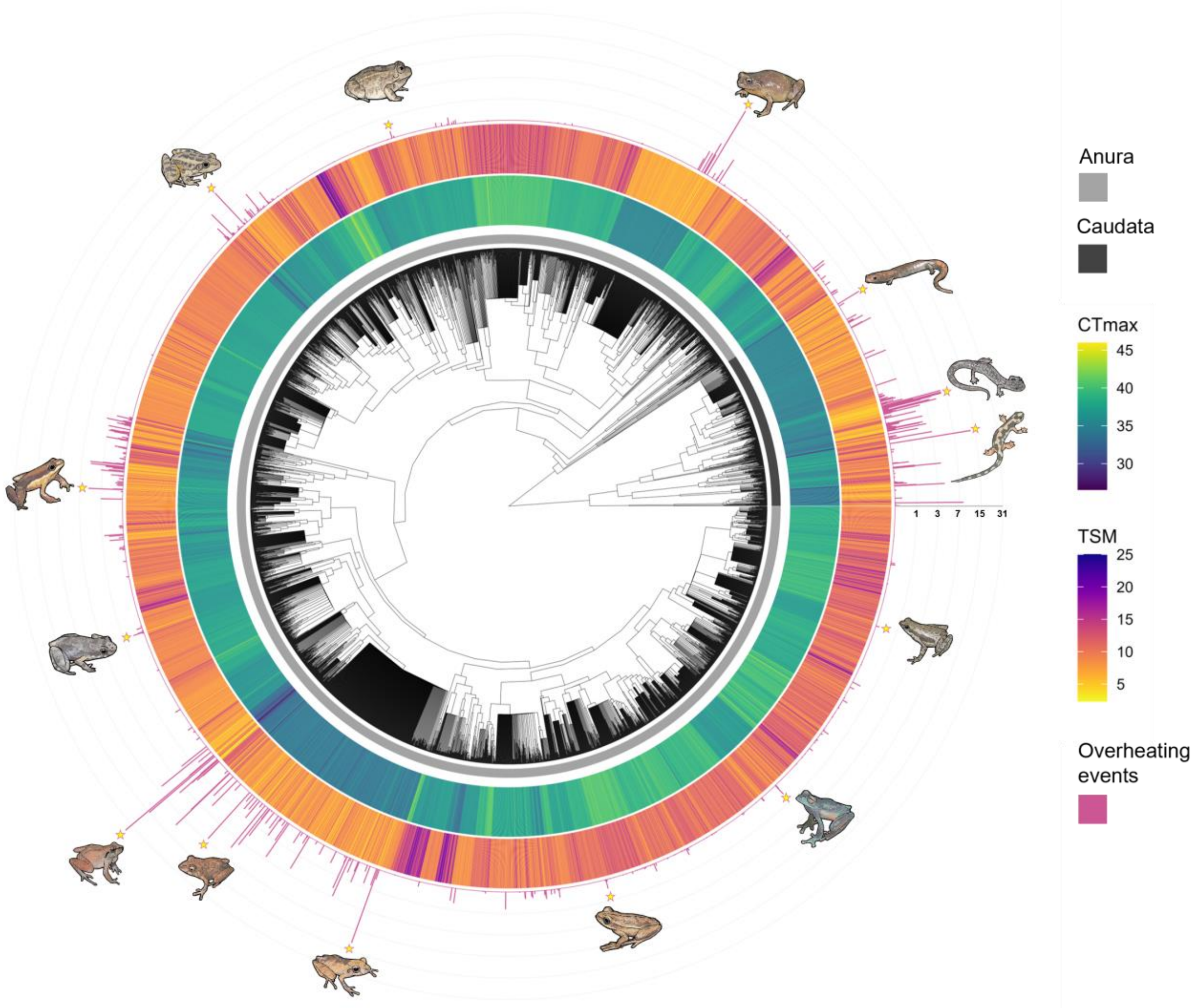


Fig. 2 | Phylogenetic coverage and taxonomic variation in climate vulnerability. Chronograms show heat tolerance limits (CT_{max}), thermal safety margins (TSM), and histograms the number of overheating events (days) averaged across each species' distribution range. This figure was constructed assuming ground-level microclimates occurring under 4°C of global warming above pre-industrial levels. Phylogeny is based on the consensus of 10,000 trees sampled from a posterior distribution (see [39] for details). Highlighted species starting from the right side, anti-clockwise: *Neurergus kaiseri, Plethodon kiamichi, Bolitoglossa altamazonica, Cophixalus aenigma, Tomaptera cryptotis, Lithobates palustris, Allobates subfolionidificans, Phyzelaphryne miriamae, Barycholos ternetzi, Pristimantis carvalhoi, Pristimantis ockendeni, Boana curupi, Teratohyla adenocheira, Atelopus spumarius.*

Thermal safety margins

We quantified thermal safety margins (TSM) as the average difference between heat tolerance limits and operative body temperatures experienced during the warmest quarters. We found evidence for a decline in TSM towards mid to low latitudes, at both population and community levels, and in all microhabitats (Fig. 3, Extended Data Fig. 3). This latitudinal pattern was consistent across warming scenarios, although warming did substantially reduce TSM at all latitudes (Fig. 3). Across all conditions simulated, TSM was always positive, even in the highest warming scenario (Fig. 3, Extended Data Fig. 3). The mean TSM was lower for terrestrial (mean [95% confidence intervals]; current = 12.055 [9.115 – 14.950]; +4°C = 9.818 [6.884 – 12.717]) and arboreal conditions (current = 12.576 [9.641 – 15.474]; +4°C = 10.455 [7.514 – 13.346]) than for water bodies (current = 13.946 [11.013 – 16.840]; +4°C = 11.605 [8.673 – 14.496]; Fig. 3; Extended Data Table 1).

Populations predicted to overheat had TSMs well above zero, although some populations were living particularly close to their heat tolerance limits during the warmest months in both terrestrial conditions (mean [95% confidence intervals]; current = 9.159 [7.255 – 11.020], range: 3.020 – 15.359; +4°C = 6.796 [4.929 – 8.692], range: 0.971 – 14.911) and above-ground vegetation (current = 9.588 [7.709 – 11.490], range: 3.699 – 11.395; +4°C = 7.307 [5.422 – 9.208], range: 1.747 – 9.995).

Patterns at the community-level were consistent with population-level patterns, although TSMs were lower when calculated at the population level, on average (Extended Data Table 1).

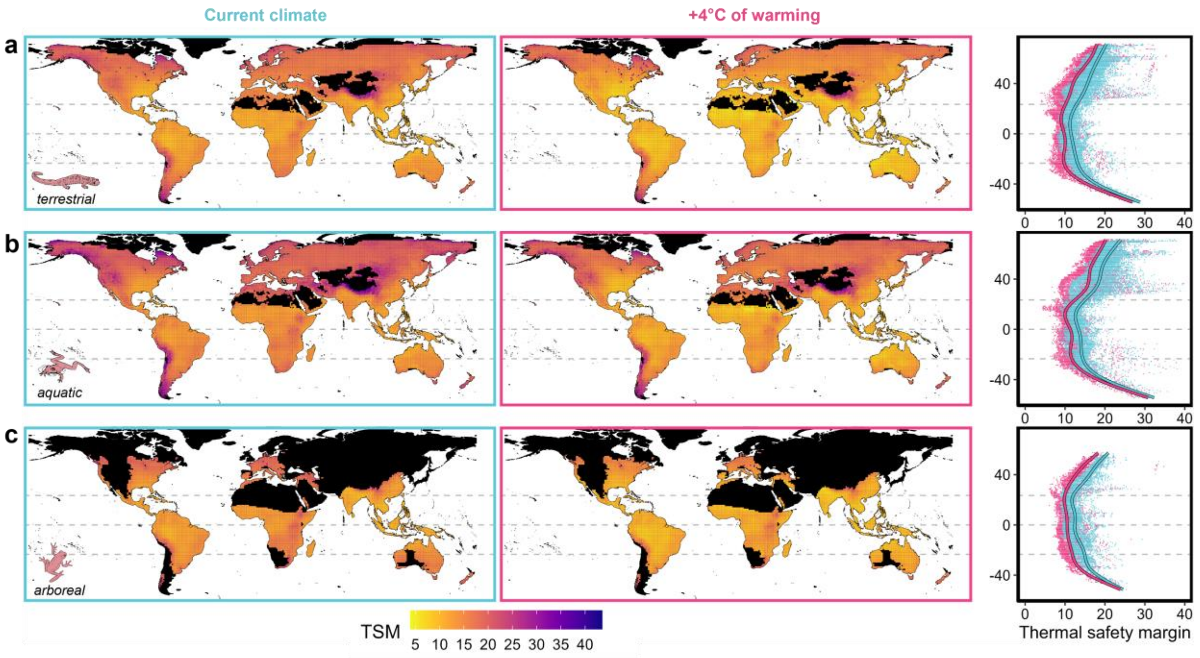


Fig. 3 | Community-level patterns in thermal safety margin for amphibians in terrestrial (a), aquatic (b) or arboreal (c) microhabitats. Thermal safety margins (TSM) were calculated as the mean difference between CT_{max} and the predicted operative body temperature in full shade during the warmest quarters of 2006-2015 in each community (1-degree grid cell). Black color depicts areas with no data. The right panel depicts latitudinal patterns in TSM in current climates (blue) or assuming 4°C of global warming above pre-industrial levels (pink), as predicted from generalized additive mixed models. Dashed lines represent the equator and tropics.

Overheating risk

We quantified overheating risk as the binary probability (1-0) that operative body temperatures exceeded heat tolerance limits at least once in the 910 days that serve as our representative current conditions. Overall, overheating risk was low, although numerous populations are predicted to face overheating events (Fig. 4, Extended Data Table 2). In terrestrial conditions, we found 1,487 populations (198 species) likely to experience overheating events in current microclimates (Fig. 4-5). However, under 4°C of warming, 4,929 populations (488 species) are expected to overheat; which represents more than a three-fold increase (Fig. 4-5; Extended Data Table 2). We also found that occupying above-ground vegetation was only partially beneficial to arboreal species (Extended Data Fig. 4). In current climates, up to 469 arboreal populations (40 species) are predicted to experience an overheating event in terrestrial conditions, whereas 286 populations (27 species) are predicted to overheat in above-ground vegetation (Extended Data Fig. 4). Furthermore, under 4°C of warming, 1,424 arboreal populations (121 species) are predicted to overheat in terrestrial conditions, while retreating to above-ground vegetation only reduced the number of species exposed to overheating events by 21.5% (95 species, 965 populations) (Extended Data Fig. 4). No amphibian populations were predicted to overheat in water bodies.

At the community level, we quantified the number of species with overheating risk in each grid cell. In current climates, we found 376 communities with at least one species at risk of overheating in terrestrial conditions, and we predicted 1,263 communities will experience overheating events under 4°C of global warming (Fig. 4; Extended Data Table 3). Notably, the number of species predicted to overheat in each grid cell increased with warming; each community comprised up to 32 vulnerable species in current climates (mean [95% confidence intervals] = 3.852 [1.032 – 7.757] species), and up to 84 vulnerable species with 4°C of global warming (3.796 [1.111 – 7.456]; Fig. 4; Extended Data Table 3). In arboreal conditions, 89 communities (comprising 1-11 species; 2.461 [0.306 – 5.722] species) were predicted to overheat in current climates, while 301 communities (comprising 1-38 species; 3.094 [0.664 – 6.529] species) were predicted to overheat assuming 4°C of global warming (Fig. 4; Extended Data Table 3). We also found that the species predicted to experience overheating events comprise a significant proportion of the community diversity in each grid cell, in both tropical and non-tropical regions (Extended Data Fig. 5; Extended Data Table 4).

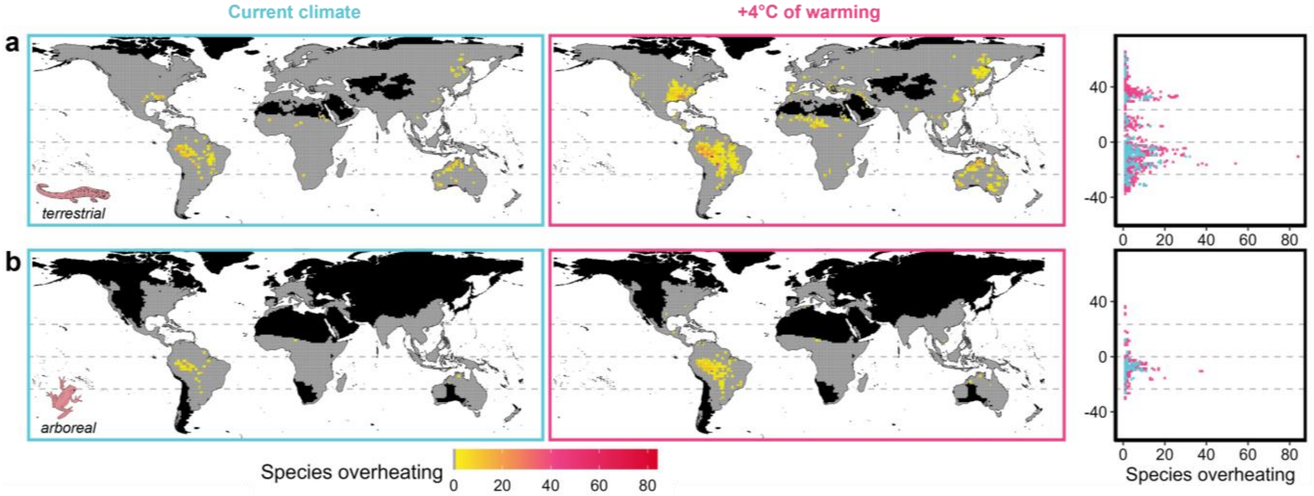


Fig. 4 | Number of species predicted to experience overheating events in terrestrial (a) and arboreal (b) microhabitats. The number of species overheating was assessed as the sum of species overheating at least once in the period surveyed (warmest quarters of 2006-2015) in each community (1-degree grid cell). Black color depicts areas with no data, and gray color communities without species at risk. The right panel depicts latitudinal patterns in the number of species predicted to overheat in current climates (blue) or assuming 4°C of global warming above pre-industrial levels (pink). Dashed lines represent the equator and tropics. No species were predicted to experience overheating events in water bodies, and hence were not displayed.

Number of overheating events

We quantified the number of days (out of 910 simulated days) each amphibian population was predicted to exceed their plasticity-adjusted heat tolerance limits for each climatic scenario. For current climates, we found that populations rarely experience overheating events in shaded terrestrial conditions (overall mean overheating days [95% confidence intervals] = 0.011 [0.001 – 0.070]; mean among overheating populations = 1.430 [0.067 – 4.067] days); but these figures increase considerably with global warming (Fig. 5; Extended Data Table 2). Under 4°C of warming, populations were predicted to overheat on as many as 131 days, representing up to 14.4% of the warmest days of the year (overall mean = 0.080 [0.013 – 0.304] days; mean among overheating populations = 3.301 [0.947 – 6.799] days; Fig. 5; Extended Data Table 2). This is noticeably more than what was predicted under 2°C of warming (overall mean = 0.018 [0.001 – 0104] days; mean among overheating populations = 1.571 [0.110 – 4.275] days; Fig. 5; Extended Data Table 2). In above-ground vegetation, the frequency of overheating was lower, as expected. Under current climates, arboreal populations were predicted to overheat on up to 6 days in total (overall mean = 0.006 [0.001 – 0.039] days; mean among overheating populations = 1.230 [0.010 – 3.714] days; Fig. 5; Tab. Extended Data Table 2). Under 4 degrees of warming, arboreal populations were predicted to overheat on up to 35 days (overall mean = 0.040 [0.001 – 0.162] days; mean among overheating populations = 2.311 [0.283 – 5.474] days; Fig. 5; Extended Data Table 2). Notably, arboreal species retreating to above-ground vegetation were predicted to experience fewer overheating events than those experiencing terrestrial conditions (Extended Data Fig. 4). Finally, we found a strong non-linear negative association between the number of overheating events and the thermal safety margin, with stark contrasts between warming scenarios (Fig. 5; Extended Data Table 5). In particular, overheating days increased rapidly as thermal safety margins fell below 5°C (Figure 5c,d).

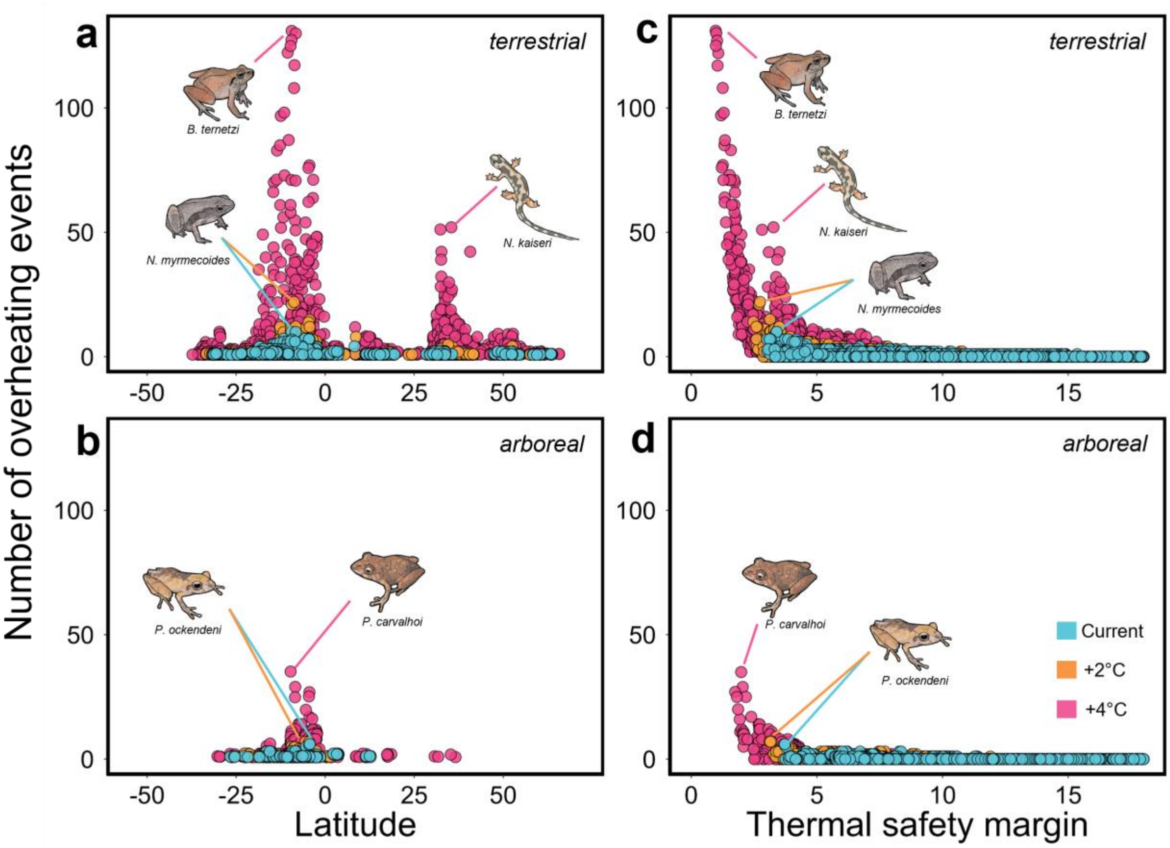


Fig. 5 | Latitudinal variation in the number of overheating events in terrestrial (a,c) and arboreal (b,d) microhabitats as a function of latitude (a,b) and thermal safety margin (c,d). The number of overheating events (days) were calculated as the sum of overheating events (when daily maximum temperatures exceed CT_{max}) during the warmest quarters of 2006-2015 for each population. Blue points depict the number of overheating events in historical microclimates, while orange and pink points depict the number of overheating events assuming 2°C and 4°C of global warming above pre-industrial levels, respectively. For clarity, only the populations predicted to experience overheating events across latitudes are depicted (a,b).

Discussion

The mounting impacts of global warming

Quantifying the resilience of biodiversity to a changing climate is one of the most pressing challenges for contemporary science[1,2]. Here, we have shown that nearly 1,500 amphibian populations may already experience temperatures beyond their physiological limits in thermal refugia, and this pattern is only predicted to worsen (Fig. 4-5). Assuming 4°C of global warming, the number of populations and communities exposed to overheating events would be 2.5- to 3.5-fold higher than currently, totaling 488 out of 5,203 species studied (9.4%; Fig. 4-5).

We found striking disparities in overheating risk between the 2°C and 4°C warming projections (Fig. 5; Extended Data Table 1), which are anticipated by the end of the century under low and high greenhouse gas emission scenarios, respectively[59]. The more extreme warming scenario considerably increased the number overheating events experienced by amphibian populations (Fig. 5), highlighting the escalating and abrupt impacts of global warming[75]. Such an increase is attributable to the contrast between the rapid pace at which temperatures are increasing and the low ability of amphibians to acclimate to new thermal environments via plasticity (Extended Data Fig. 3). Our study clearly demonstrates, as others have suggested[13,70,76,77], that physiological plasticity is not a sufficient mechanism to buffer populations from the impacts of rapidly rising temperatures.

Extreme heat events drive climate vulnerability

We found large spatial heterogeneity in the vulnerability amphibians. In tropical areas, most vulnerable species are concentrated in South America and Australia, while fewer species are impacted in the African and Asian tropics (Fig. 4). Tropical species also experience disproportionally more overheating events in the Southern Hemisphere, while non-tropical species are more susceptible in the Northern Hemisphere (Fig. 5). Furthermore, the proportion of species experiencing overheating events in each community was not predicted by latitude (Extended Data Fig. 5). Therefore, our findings are inconsistent with the expectation of a latitudinal gradient in overheating risk based on thermal safety margins (e.g., [11,12,21,29]). In fact, overheating risk does not increase linearly with TSM (Fig. 5), and populations with seemingly comparable TSMs can have markedly different probabilities of overheating (Fig. 5). None of the populations were also predicted to overheat in water bodies, despite having TSMs only ~1.89°C higher than those of amphibians on terrestrial conditions (Fig. 3; Extended Data Table 1). Therefore, TSMs alone hide critical tipping points for thermal stress (Fig. 5c,d).

Our study questions the reliability of thermal safety margins and other climate vulnerability metrics averaged across large time scales (e.g., using the maximum temperature of the warmest quarter) for detecting species most vulnerable to thermal extremes. It also challenges the general notion that low-latitude species are uniformly most vulnerable to warming[11,12,21,29], revealing a far more nuanced pattern of climate vulnerability across latitudes. While the reliability of TSM-based assessments has been questioned in previous studies[10], our work further emphasizes the need to consider natural climatic variability in evaluating the vulnerability of ectothermic animals to global warming[13-15,78]. Considering alternative metrics, such as the number of predicted overheating events, may prove particularly useful in identifying the most vulnerable species and populations.

The vital yet limited role of thermal retreats

Our study highlights the critical yet sometimes insufficient role that thermal retreats play in buffering the impacts of warming on amphibians. Most amphibian species are not predicted to experience overheating events in full shade (Fig. 4), and the availability of water bodies allows all amphibians to maintain their body temperatures below critical levels, even in the most extreme warming scenario investigated. This is attributable to the higher specific heat capacity of water relative to air, delaying rapid temperature rises and affording a more stable environment during heat waves[79]. Our findings add to the growing evidence that behavioral thermoregulation is the main mechanism by which amphibians and other ectotherms can maintain sub-lethal body temperatures[12,24,80,81].

However, it is crucial to emphasize that vegetated terrestrial conditions in full shade offer inadequate protection to nearly 10% of species; and many arboreal populations predicted to overheat at ground level face similar risks in above-ground vegetation (Fig. 4-5, Extended Data Fig. 4). In fact, although reducing the frequency of overheating events (Extended Data Fig. 4), access to shaded above-ground vegetation only reduces the number of vulnerable species by 21.5%.

Warming impacts may exceed projections

Our predictions are largely conservative, and likely overestimate the resilience of amphibians to global warming in two main ways. First, we assume that microhabitats such as shaded ground-level substrates, above-ground vegetation, and water bodies are available throughout a species' range, and that amphibians can maintain wet skin. These assumptions will often be violated as habitats are degraded. Deforestation and urbanization are diminishing vital shaded areas[82–85], while increased frequencies of droughts will cause water bodies to evaporate[86,87]. These changes not only compromise habitat integrity but also local humidity levels – key for effective thermoregulation[67,88,89]. Consequently, amphibians will likely experience higher body temperatures and desiccation stress events than our models predict due to inconsistent access to cooler microhabitats.

Second, ectotherms can experience deleterious effects from heat stress before reaching their heat tolerance limits. Prolonged exposure to sub-lethal temperatures can lead to altered activity windows[90,91], disruptions to phenology[92,93], reduced reproductive fitness (fertility and fecundity)[71,94–96], and death[5,97,98]. Although comprehensive data on thermal incapacitation times and fertility impacts are sparse in amphibians, integrating both the duration and intensity of thermal stress[97–99] will likely point to more extreme vulnerability estimates. This represents a vital avenue for future research, albeit one requiring a large collection of empirical data.

The power of data imputation

Our imputation approach has significantly expanded the scope of previous research[27], magnifying taxonomic coverage from 616 to 5,203 species (Fig. 2). We also effectively addressed geographical biases, especially in under-sampled but ecologically critical regions of Africa, Asia, and South America (Fig. 2). We found that these understudied regions frequently harbor species exhibiting the highest susceptibility to extreme heat events (Fig. 1,4-5). Targeted research efforts in these vulnerability hotspots will prove instrumental in validating our model predictions and advance our understanding of amphibian thermal physiology to inform their conservation. Though undeniable logistical and financial challenges exist in accessing some of these remote locations, collaboration with local experts could expedite data collections and result in timely conservation measures. Exemplary initiatives to sample numerous species in South America (e.g., [23,100,101]) are promising steps in this direction, and we hope our findings will catalyze research activity in these regions.

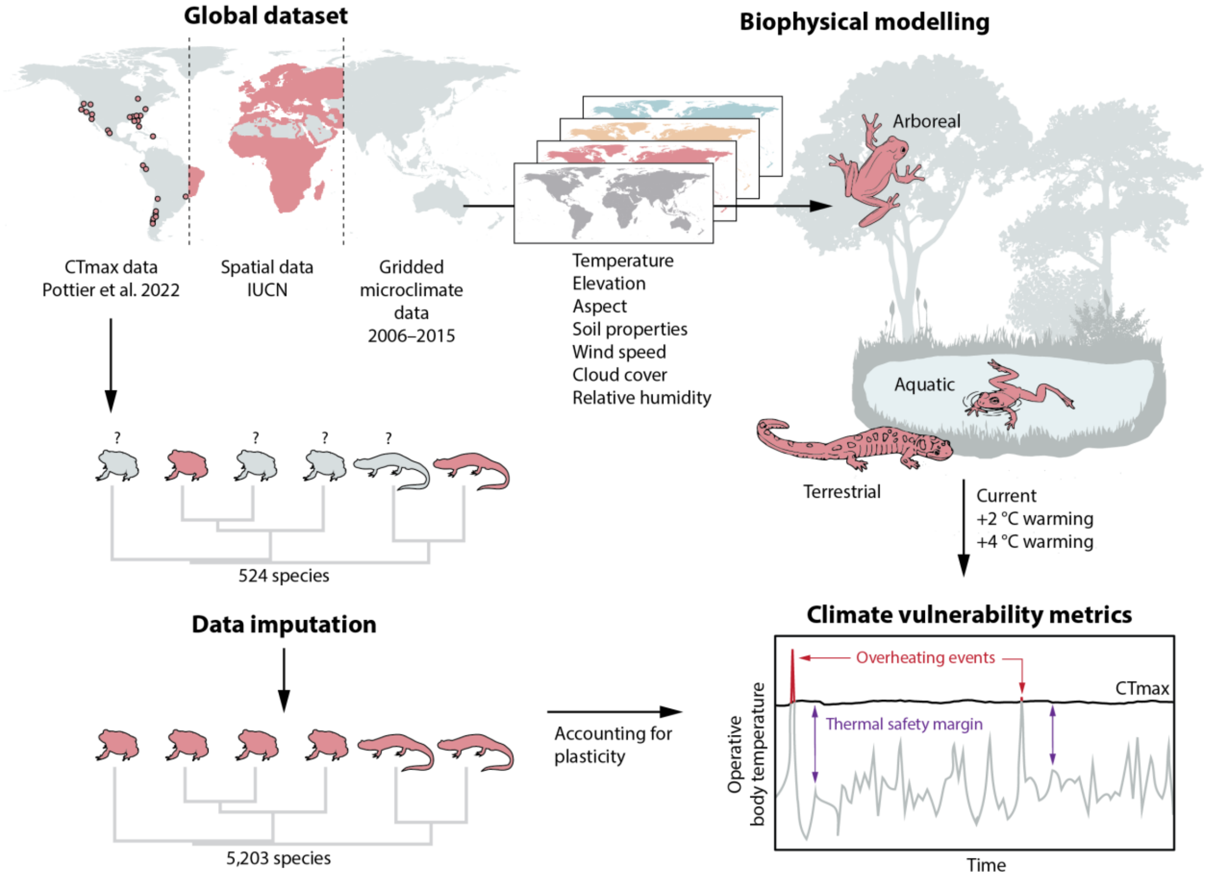
Amphibian biodiversity in a warming world

Our study highlights the dire consequences of global warming on amphibians. Yet it is crucial to differentiate between global extinction and local extirpations – the latter being confined extinctions within specific geographic areas. Only 27 species are projected to experience overheating events across their entire range, and these overheating events may not occur simultaneously. Hence, most species are likely to only experience local extirpation. Nevertheless, local extirpations carry their own sets of ecological repercussions, such as reshuffling community compositions and eroding genetic and ecological diversity[102–104].

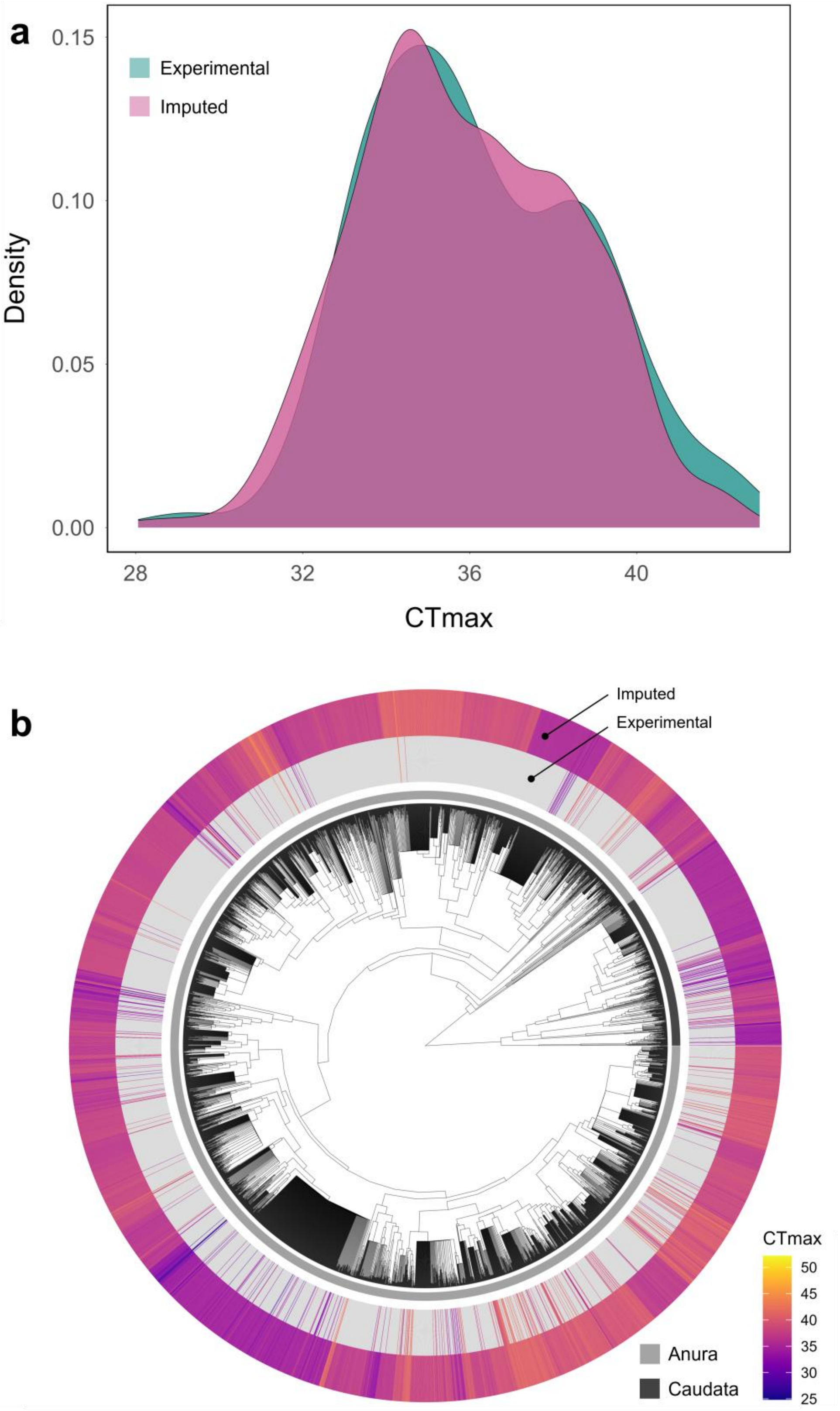
Some amphibian populations may also undergo range shifts, permanently or transiently relocating to habitats with more hospitable weather patterns[105]. However, this is only possible if suitable habitats are available for colonization. Given the low dispersal rates of amphibians and their reliance on water bodies for reproduction and thermoregulation, opportunities for range shifts are likely to be rare. In addition, we stress that amphibians living close to their physiological limits for extended times are likely to experience heat stress that could hamper activity, foraging opportunities, and reproductive success, adding layers of complexity to their survival challenges and potentially leading to population declines[5,91,98,106].

Overall, our study contributes to the evidence that climate change is a mounting threat to amphibians[8,107] and emphasizes the importance of limiting global temperature rises below 2°C to minimize the risk of overheating to amphibian populations. A 4°C temperature rise would not just increase these risks but create a step-change in impact severity (e.g., Fig. 5c). The mechanistic basis of our species- and habitat-specific predictions also leads to clear management priorities. Particularly, our analyses revealed the critical importance of preserving dense vegetation cover and water bodies. These microhabitats provide thermal refugia during extreme events and increase the potential for amphibians and other ectothermic species to disperse to more suitable microhabitats. Establishing protected areas and undertaking habitat restoration initiatives may support amphibians in a changing climate and buffer additional anthropogenic threats, in turn mitigating amphibian population declines[8,108,109]. These actions are critical not only for the amphibians at risk, but also for the broader ecosystems they support in a planet undergoing a rapid and perilous climatic metamorphosis.

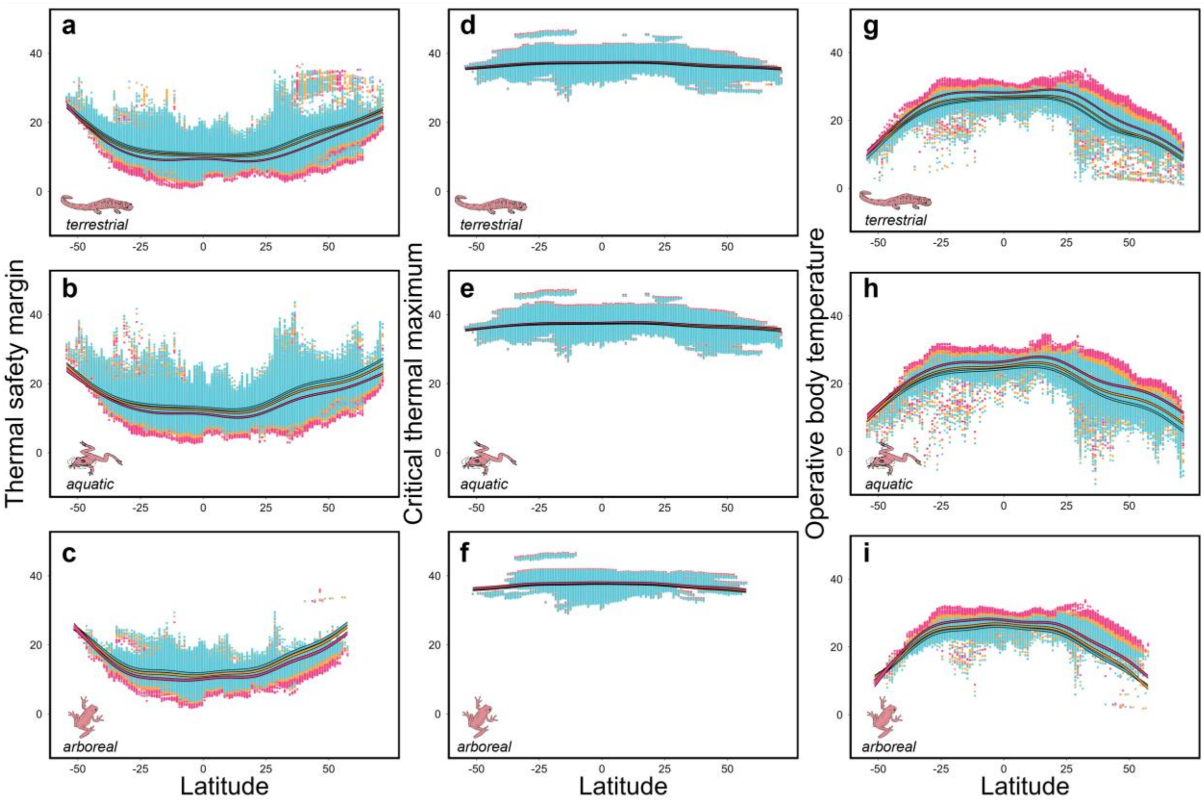
Extended data



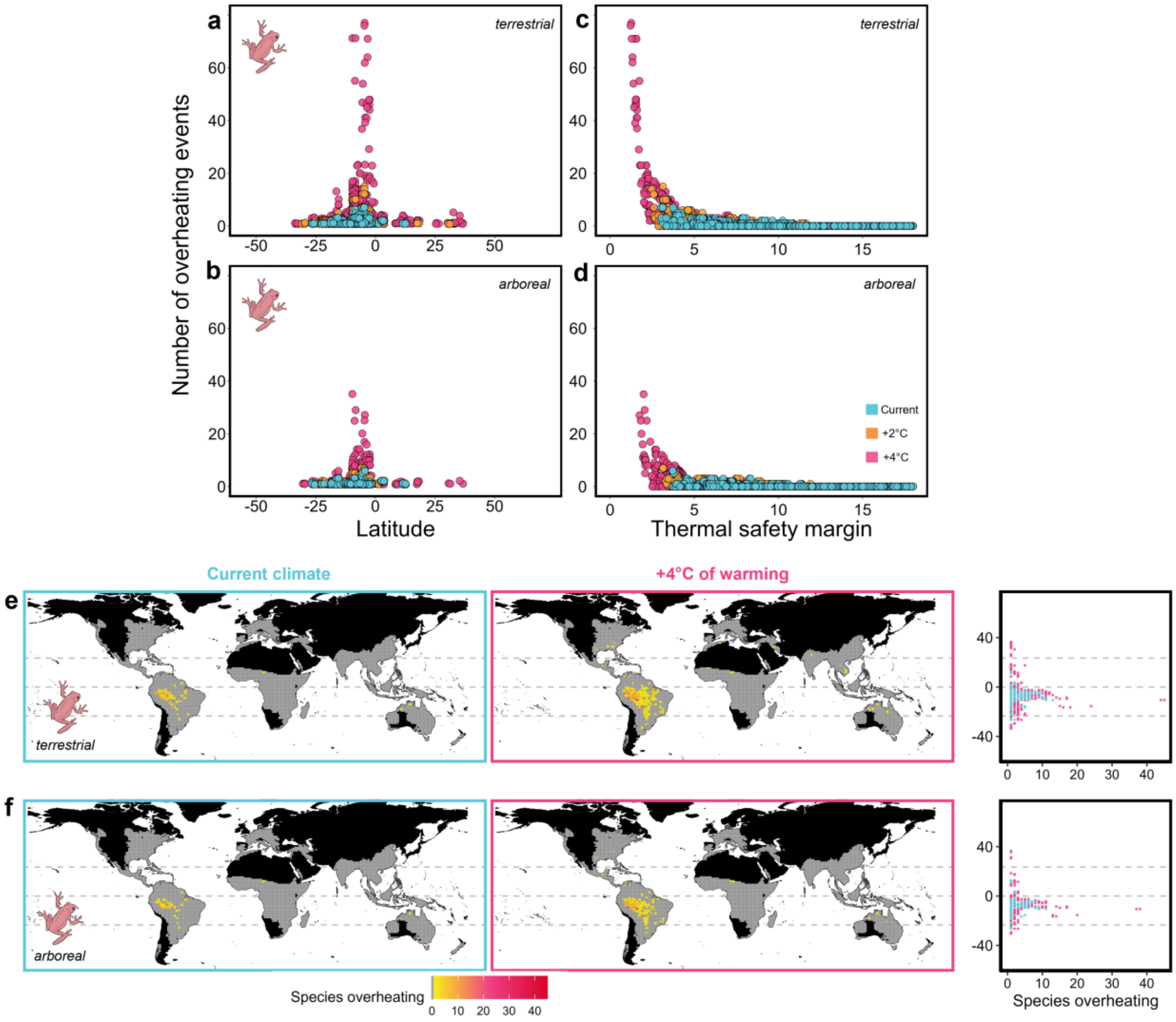
Extended Data Fig. 1 | Conceptual overview of the methods employed to assess the vulnerability of amphibians to global warming.



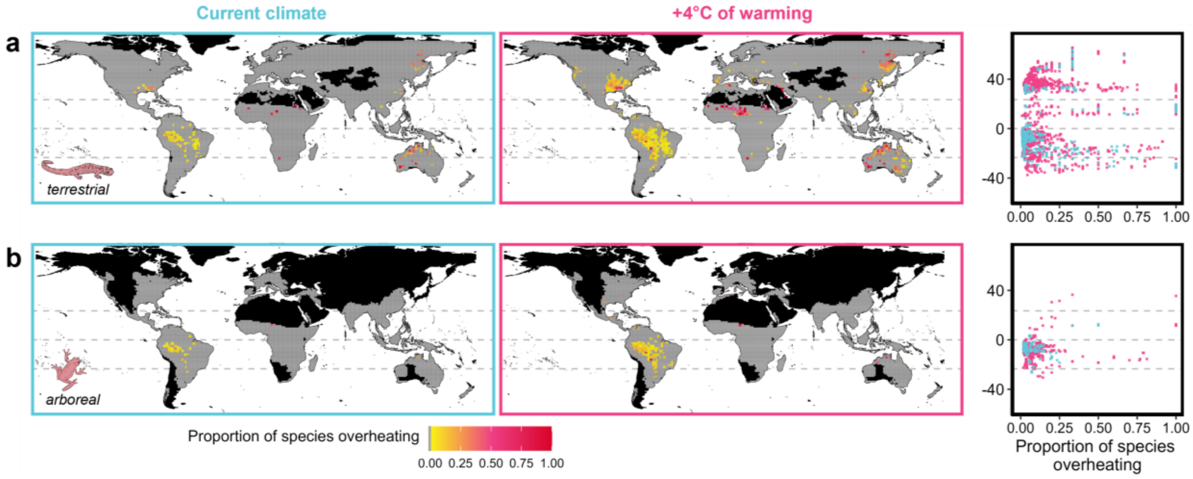
Extended Data Fig. 2 | Accuracy of the data imputation procedure. a) Probability density distributions of experimental CT_{max} (blue) and CT_{max} cross-validated using our data imputation procedure (pink). b) Mean experimental (inner chronogram) and imputed (outer chronogram) critical thermal maximum (CT_{max}) across the phylogeny of studied species. Missing values are indicated in light grey in the inner chronogram.



Extended Data Fig. 3 | Thermal safety margin, critical thermal maximum, and operative body temperatures in different microhabitats and climatic scenarios. Population-level mean thermal safety margins (TSM; a-c), critical thermal maximum (CT_{max}; d-f) and operative body temperatures (g-i) in terrestrial (a,d,g), aquatic (b,e,h) and arboreal (c,f,i) microhabitats are depicted in current microclimates (blue data points), or assuming 2°C and 4°C of global warming above pre-industrial levels (orange, and pink data points, respectively) across latitudes. Lines represent 95% confidence intervals of model predictions from generalized additive mixed models.



Extended Data Fig. 4 | Vulnerability of arboreal amphibians in terrestrial and arboreal microhabitats. Depicted are the number of overheating events experienced by arboreal species across latitudes (a-b) and in relation to thermal safety margins (c-d) in terrestrial (a-c) and arboreal microhabitats (b-d). The number of overheating events were calculated as the sum of overheating events (when daily maximum temperatures exceed CT_{max}) during the warmest quarters of 2006-2015 for each population. Blue points depict the number of overheating events in historical microclimates, while orange and pink points depict the number of overheating events assuming 2°C and 4°C of global warming above pre-industrial levels, respectively. In panel a) and b), only the populations predicted to overheat are displayed. The number of arboreal species predicted to experience overheating events terrestrial (e) and arboreal (f) microhabitats in each community is also depicted. The number of species overheating was assessed as the sum of species overheating at least once in the period surveyed (warmest quarters of 2006-2015) in each community (1-degree grid cell). Black color depicts areas with no data, and gray color communities without species at risk. The right panel depicts latitudinal patterns in the number of species predicted to overheat in current climates (blue) or assuming 4°C of global warming above pre-industrial levels (pink). Dashed lines represent the equator and tropics. No species were predicted to experience overheating events in water bodies, and hence are not displayed.



Extended Data Fig. 5 | Proportion of species predicted to experience overheating events in terrestrial (a) and arboreal (b) microhabitats. The proportion of species overheating was assessed as the sum of species overheating at least once in the period surveyed (warmest quarters of 2006-2015) divided by the number of species in each community (1-degree grid cell). Black color depicts areas with no data, and gray color communities without species at risk. The right panel depicts latitudinal patterns in the proportion of species predicted to overheat in current climates (blue) or assuming 4°C of global warming above pre-industrial levels (pink). Dashed lines represent the equator and tropics. No species were predicted to experience overheating events in water bodies, and hence are not displayed.

Extended Data Table 1 | Statistical model estimates for thermal safety margins calculated at population- and community levels. Model estimates for each microhabitat (terrestrial, arboreal, aquatic) and each climatic scenario (current, +2°C, or +4°C of global warming above pre-industrial levels) are depicted. mean: mean model estimate; CI.lb: lower bound of the 95% confidence interval; CI.ub: upper bound of the 95% confidence interval; k_{sp}: number of species; k_{obs}: number of observations; Var_{sp}: variance explained by differences between species; Var_{phy}: variance explained by shared evolutionary history; Var_{obs}: residual variance.

Population-level patterns in thermal safety margin

	mean	**CI.lb**	**CI.ub**	**k_{sp}**	**k_{obs}**	**Var_{sp}**	**Var_{phy}**	**Var_{obs}**
Terrestrial (current)	12.055	9.115	14.950	5177	203853	1.586	13.700	2.291
Terrestrial (+2°C)	11.333	8.402	14.231	5177	203853			
Terrestrial (+4°C)	9.818	6.884	12.717	5177	203853			
Arboreal (current)	12.576	9.641	15.474	1771	56210			
Arboreal (+2°C)	11.893	8.947	14.784	1771	56210			
Arboreal (+4°C)	10.455	7.514	13.346	1771	56210			
Aquatic (current)	13.946	11.013	16.840	5203	204808			
Aquatic (+2°C)	13.046	10.115	15.941	5203	204808			
Aquatic (+4°C)	11.605	8.673	14.496	5203	204808			

Community-level patterns in thermal safety margin

	mean	**CI.lb**	**CI.ub**	**k_{obs}**	**Var_{obs}**
Terrestrial (current)	15.074	15.005	15.137	14090	12.96
Terrestrial (+2°C)	14.151	14.092	14.216	14090	
Terrestrial (+4°C)	12.378	12.315	12.443	14090	
Arboreal (current)	13.960	13.862	14.047	6614	
Arboreal (+2°C)	13.148	13.046	13.232	6614	
Arboreal (+4°C)	11.540	11.454	11.634	6614	
Aquatic (current)	17.487	17.423	17.551	14091	
Aquatic (+2°C)	16.500	16.440	16.562	14091	
Aquatic (+4°C)	14.954	14.881	15.015	14091	

Extended Data Table 2 | Statistical model estimates for overheating risk and the number of overheating events. Model estimates for each microhabitat (terrestrial, arboreal) and each climatic scenario (current, +2°C, or +4°C of global warming above pre-industrial levels) are depicted. The estimated number of overheating events in populations predicted to experience at least one overheating event (i.e., overheating populations) are also depicted. Model estimates for aquatic microhabitats are not displayed because no population was predicted to experience overheating events in this microhabitat. mean: mean model estimate; CI.lb: lower bound of the 95% confidence interval; CI.ub: upper bound of the 95% confidence interval; k_{sp}: number of genera; k_{sp}: number of species; k_{obs}: number of observations; Var_{genus}: variance explained by differences between genera; Var_{sp}: variance explained by differences between species; Var_{obs}: residual variance.

Overheating risk

	mean	**CI.lb**	**CI.ub**	k_{genus}	k_{sp}	k_{obs}	Var_{genus}	Var_{sp}
Terrestrial (current)	4.89×10^{-6}	2.75×10^{-6}	8.70×10^{-6}	464	5177	203853	0.143	51.565
Terrestrial (+2°C)	8.31×10^{-6}	4.68×10^{-6}	1.47×10^{-5}	464	5177	203853		
Terrestrial (+4°C)	2.29×10^{-5}	1.29×10^{-5}	4.04×10^{-5}	464	5177	203853		
Arboreal (current)	2.64×10^{-6}	1.47×10^{-6}	4.77×10^{-6}	174	1771	56210		
Arboreal (+2°C)	4.56×10^{-6}	2.55×10^{-6}	8.16×10^{-6}	174	1771	56210		
Arboreal (+4°C)	1.23×10^{-5}	6.87×10^{-6}	2.19×10^{-5}	174	1771	56210		

Number of overheating events (all populations)

	mean	**CI.lb**	**CI.ub**	k_{genus}	k_{sp}	k_{obs}	Var_{genus}	Var_{sp}
Terrestrial (current)	0.011	0.001	0.070	464	5177	203853	0.145	53.851
Terrestrial (+2°C)	0.018	0.001	0.104	464	5177	203853		
Terrestrial (+4°C)	0.080	0.013	0.304	464	5177	203853		
Arboreal (current)	0.006	0.001	0.039	174	1771	56210		
Arboreal (+2°C)	0.011	0.001	0.076	174	1771	56210		
Arboreal (+4°C)	0.040	0.001	0.162	174	1771	56210		

Number of overheating events (among overheating populations)

	mean	**CI.lb**	**CI.ub**	k_{genus}	k_{sp}	k_{obs}	Var_{genus}	Var_{sp}	Var_{obs}
Terrestrial (current)	1.430	0.067	4.067	73	198	1487	0.129	0.105	0.218
Terrestrial (+2°C)	1.571	0.110	4.275	100	287	2299			
Terrestrial (+4°C)	3.301	0.947	6.799	140	488	4929			
Arboreal (current)	1.230	0.010	3.714	10	27	286			
Arboreal (+2°C)	1.385	0.015	3.981	14	44	455			
Arboreal (+4°C)	2.311	0.283	5.474	28	95	965			

Extended Data Table 3 | Statistical model estimates for the number of species predicted to experience overheating events. Model estimates for each microhabitat (terrestrial, arboreal) and each climatic scenario (current, +2°C, or +4°C of global warming above pre-industrial levels) are depicted. The estimated number of species overheating in communities containing at least one species predicted to experience at least one overheating event (i.e., overheating communities) are also depicted. Model estimates for aquatic microhabitats are not displayed because no population was predicted to experience overheating events in this microhabitat. mean: mean model estimate; CI.lb: lower bound of the 95% confidence interval; CI.ub: upper bound of the 95% confidence interval; k_{obs}: number of observations; Var_{obs}: residual variance.

Number of species overheating (all communities)

	mean	**CI.lb**	**CI.ub**	**k_{obs}**	**Var_{obs}**
Terrestrial (current)	0.101	0.034	0.199	14090	58.64
Terrestrial (+2°C)	0.157	0.059	0.299	14090	
Terrestrial (+4°C)	0.337	0.123	0.655	14090	
Arboreal (current)	0.041	0.008	0.094	6614	
Arboreal (+2°C)	0.065	0.015	0.141	6614	
Arboreal (+4°C)	0.139	0.038	0.292	6614	

Number of species overheating (among overheating communities)

	mean	**CI.lb**	**CI.ub**	**k_{obs}**	**Var_{obs}**
Terrestrial (current)	3.852	1.032	7.757	376	0.802
Terrestrial (+2°C)	4.160	1.289	8.146	539	
Terrestrial (+4°C)	3.796	1.111	7.456	1263	
Arboreal (current)	2.461	0.306	5.722	111	
Arboreal (+2°C)	2.947	0.510	6.378	149	
Arboreal (+4°C)	3.094	0.664	6.529	301	

Extended Data Table 4 | Statistical model estimates for the proportion of species predicted to experience overheating events. Model estimates for each microhabitat (terrestrial, arboreal) and each climatic scenario (current, +2°C, or +4°C of global warming above pre-industrial levels) are depicted. The estimated proportion of species overheating in communities containing at least one species predicted to experience at least one overheating event (i.e., overheating communities) are also depicted. Model estimates for aquatic microhabitats are not displayed because no population was predicted to experience overheating events in this microhabitat. mean: mean model estimate; CI.lb: lower bound of the 95% confidence interval; CI.ub: upper bound of the 95% confidence interval; k_{obs}: number of observations; Var_{obs}: residual variance.

Proportion of species overheating (all communities)

	mean	**CI.lb**	**CI.ub**	**k_{obs}**	**Var_{obs}**
Terrestrial (current)	1.345×10^{-5}	1.018×10^{-5}	1.778×10^{-5}	14090	51.85
Terrestrial (+2°C)	1.976×10^{-5}	1.539×10^{-5}	2.537×10^{-5}	14090	
Terrestrial (+4°C)	5.339×10^{-5}	4.346×10^{-5}	6.560×10^{-5}	14090	
Arboreal (current)	1.289×10^{-5}	8.064×10^{-6}	2.060×10^{-5}	6614	
Arboreal (+2°C)	1.769×10^{-5}	1.162×10^{-5}	2.694×10^{-5}	6614	
Arboreal (+4°C)	3.819×10^{-5}	2.764×10^{-5}	5.277×10^{-5}	6614	

Proportion of species overheating (among overheating communities)

	mean	**CI.lb**	**CI.ub**	**k_{obs}**	**Var_{obs}**
Terrestrial (current)	0.085	0.074	0.097	376	1.534
Terrestrial (+2°C)	0.091	0.081	0.102	539	
Terrestrial (+4°C)	0.105	0.098	0.113	1263	
Arboreal (current)	0.053	0.041	0.068	111	
Arboreal (+2°C)	0.063	0.051	0.079	149	
Arboreal (+4°C)	0.076	0.065	0.088	301	

Extended Data Table 5 | Statistical model estimates for the association between the number of overheating events and thermal safety margins. Model estimates for each microhabitat (terrestrial, arboreal) and each climatic scenario (current, +2°C, or +4°C of global warming above pre-industrial levels) are depicted. Model estimates for aquatic microhabitats are not displayed because no population was predicted to experience overheating events in this microhabitat. All model estimates are on the log scale. mean: mean model estimate; se: standard error; k_{sp}: number of genera; k_{sp}: number of species; k_{obs}: number of observations; Var_{genus}: variance explained by differences between genera; Var_{sp}: variance explained by differences between species; Var_{obs}: residual variance.

	mean	**se**	**p**	**k_{genus}**	**k_{sp}**	**k_{obs}**	**Var_{genus}**	**Var_{sp}**	**Var_{obs}**
Terrestrial (current)									
Intercept	2.236	0.409	<0.001	464	5177	203853	4.688	4.334	0.325
Slope (TSM)	-1.072	0.033	<0.001						
Terrestrial (+2°C)									
Intercept	4.791	0.325	<0.001	464	5177	203853	4.995	2.419	0.248
Slope (TSM)	-1.302	0.029	<0.001						
Terrestrial (+4°C)									
Intercept	6.143	0.204	<0.001	464	5177	203853	3.213	1.344	0.624
Slope (TSM)	-1.528	0.019	<0.001						
Arboreal (current)									
Intercept	4.295	1.145	<0.001	174	1771	56210	0.001	13.384	0.190
Slope (TSM)	-1.423	0.100	<0.001						
Arboreal (+2°C)									
Intercept	6.515	0.806	<0.001	174	1771	56210	2.955	2.216	0.013
Slope (TSM)	-1.556	0.080	<0.001						
Arboreal (+4°C)									
Intercept	8.834	0.636	<0.001	174	1771	56210	8.258	1.115	0.079
Slope (TSM)	-1.947	0.056	<0.001						

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Authors' contributions

Conceptualization: PPottier, MRK, SB, SMD, SN

Methodology: PPottier, MRK, NCW, ARG, JER, SMD, SN

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Resources: None.

Data curation: PPottier

Writing – Original Draft: PPottier

Writing – Review & Editing: All authors

Visualization: PPottier, NCW, SMD

Supervision: SMD, SN

Project administration: PPottier

Funding acquisition: None.

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Inclusion & ethics statement

This study did not involve researchers who collected the original data. All data used for the analyses were taken from a previous data compilation, and original references are listed in Supplementary materials (*Data sources).*

Competing interest declaration

The authors declare no conflict or competing interests.

Data availability

Raw and processed data are available at https://github.com/p-pottier/Vulnerability_amphibians_global_warming. Note, however, that some intermediate data files were too large to be shared online. These files are available upon request and will be uploaded to a permanent repository upon acceptance.

Code availability

All code needed to reproduce the analyses is available at https://github.com/p-pottier/Vulnerability_amphibians_global_warming.

Supplementary materials

Supplementary methods

Sensitivity analyses

In this study, we projected CTmax estimates assuming animals were acclimated to the mean weekly temperature experienced prior to each day. We also assessed the climate vulnerability of amphibians assuming they were acclimated to weekly maximum body temperatures (*cf.* [1]), which reflects more conservative estimates.

We also calculated thermal safety margins as the difference between the maximum (or 95th percentile, *cf.* [2]) hourly body temperature experienced by each population and their predicted CTmax to investigate the consequences of averaging temperatures when calculating TSMs.

To increase the comparability of our estimations with similar studies (e.g., [2]), we also calculated climate vulnerability metrics more conservatively. Specifically, we excluded temperature data falling below the 5th percentile and above the 95th percentile body temperature for each population to mitigate the impact of outliers. However, extreme weather events, which are typically captured by these outlier values, are the very phenomena most likely to precipitate mortality events[3,4]. Omitting these outliers could therefore obscure the ecological significance of extreme temperatures, thereby underestimating true overheating risks.

We controlled for the uncertainty in predicted heat tolerance limits by weighing TSM estimates by their standard error in our analyses. However, addressing prediction uncertainty for overheating risk and the number of overheating events was complex due to the dichotomous nature of these metrics (i.e., the population overheats or not). As a remedy, we provide conservative analyses where overheating events were counted only when operative body temperatures exceeded 50% or 95% of the predicted distribution of heat tolerance limits.

Results from all statistical models and additional data visualizations are available at https://p-pottier.github.io/Vulnerability_amphibians_global_warming/.

Original studies on which our analyses are built upon are listed in *Data sources*[5–217].

Supplementary figures

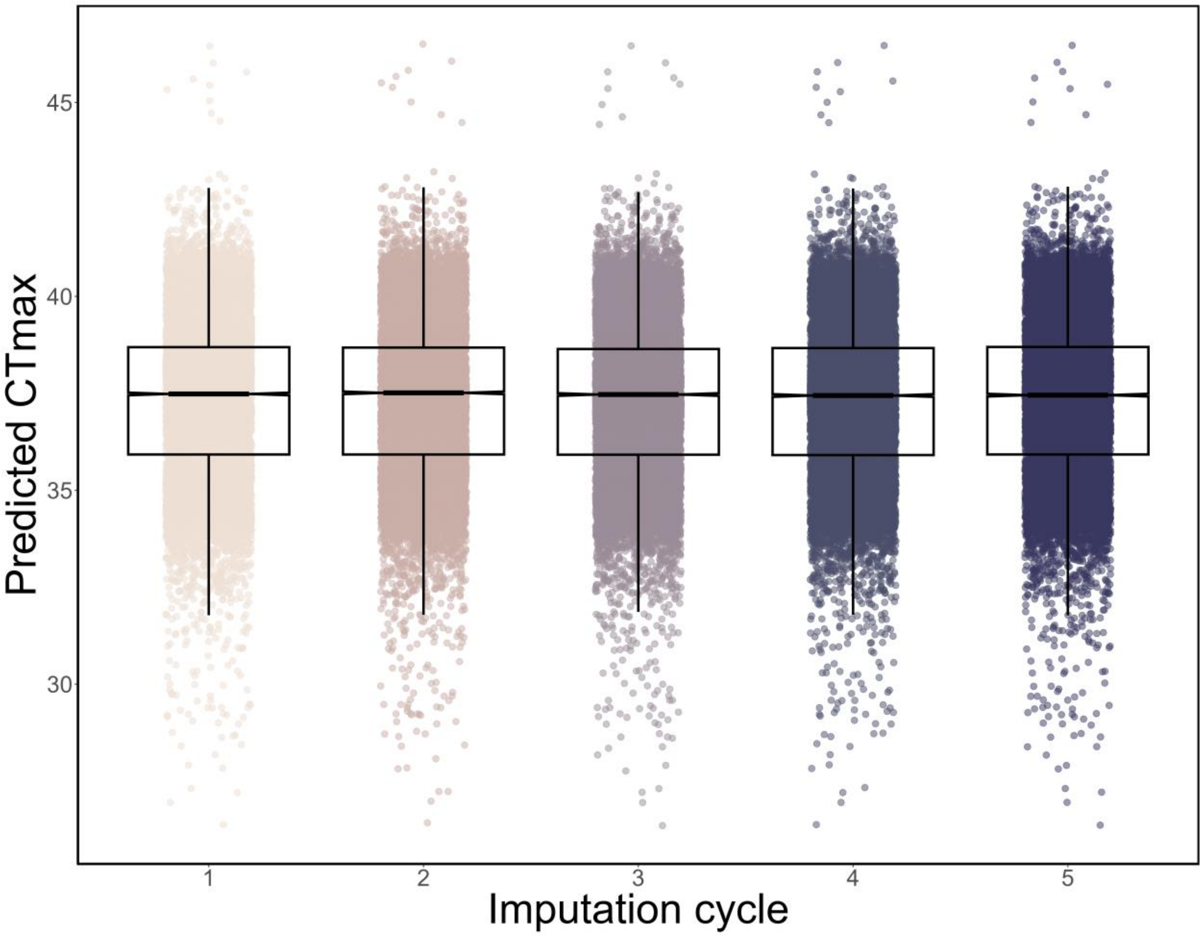

Fig. S1 | Predicted critical thermal maximum (CTmax) across imputation cycles. Boxplots depict median (horizontal line), interquartile ranges (boxes), and whiskers extend to 1.5 times the interquartile range.

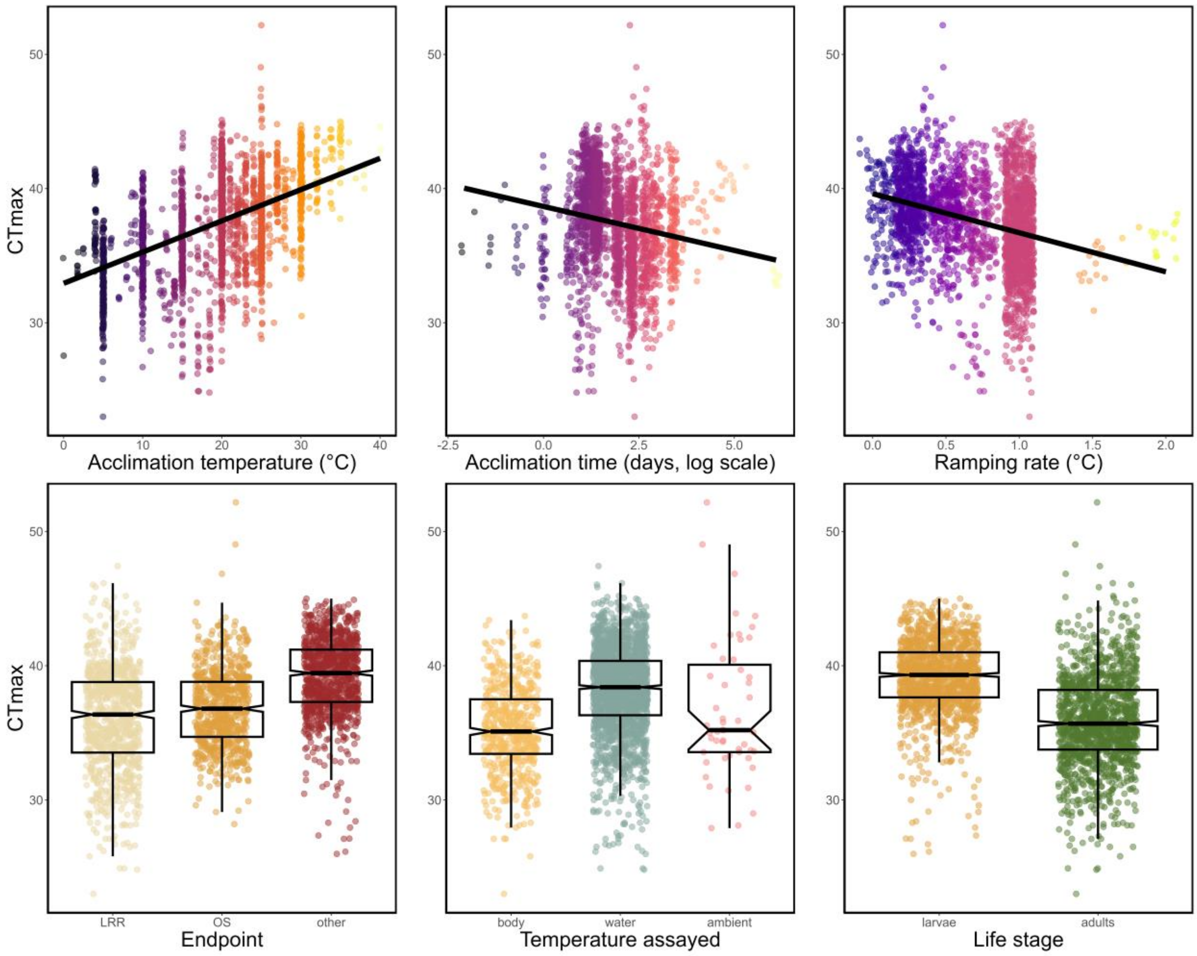

Fig. S2 | Correlations between critical thermal maximum (CTmax) and predictors used for the imputation. LRR: loss of righting response. OS: onset of spasms.

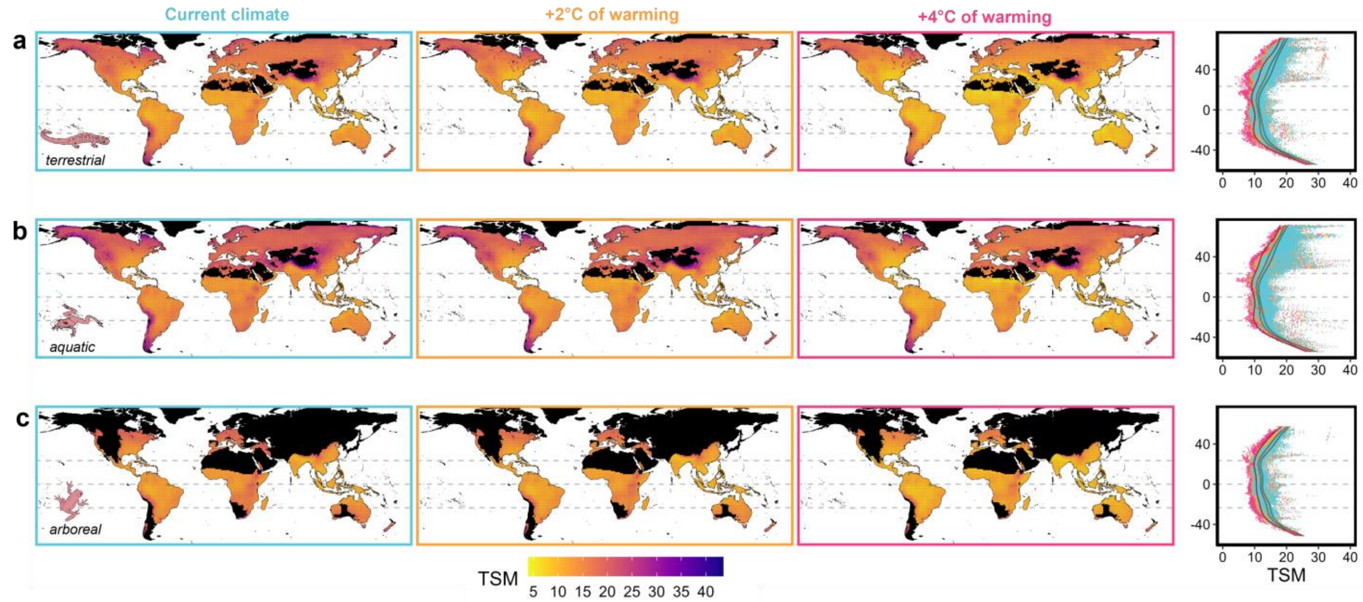

Fig. S3 | Community-level patterns in thermal safety margin for amphibians on terrestrial (a), aquatic (b), or arboreal (c) microhabitats. Thermal safety margins (TSM) were calculated as the mean difference between CTmax and the predicted operative body temperature in full shade during the warmest quarters of 2006-2015 in each community (1-degree grid cell). Black color depicts areas with no data. The right panel depicts latitudinal patterns in TSM in current climates (blue) or assuming 2°C (orange) or 4°C of global warming above pre-industrial levels (pink), as predicted from generalized additive mixed models. Dashed lines represent the equator and tropics.

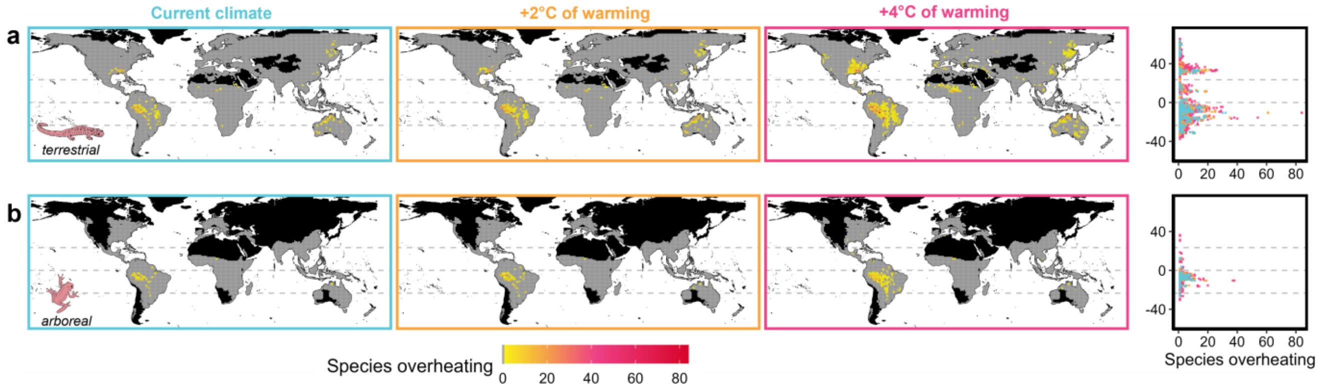

Fig. S4 | Number of species predicted to experience overheating events in terrestrial (a) and arboreal (b) microhabitats. The number of species overheating was assessed as the sum of species overheating at least once in the period surveyed (warmest quarters of 2006-2015) in each community (1-degree grid cell). Black color depicts areas with no data and gray color communities without species at risk. The right panel depicts latitudinal patterns in the number of species predicted to overheat in current climates (blue) or assuming 2°C (orange) or 4°C of global warming above pre-industrial levels (pink). Dashed lines represent the equator and tropics. No species were predicted to experience overheating events in water bodies, and hence are not displayed.

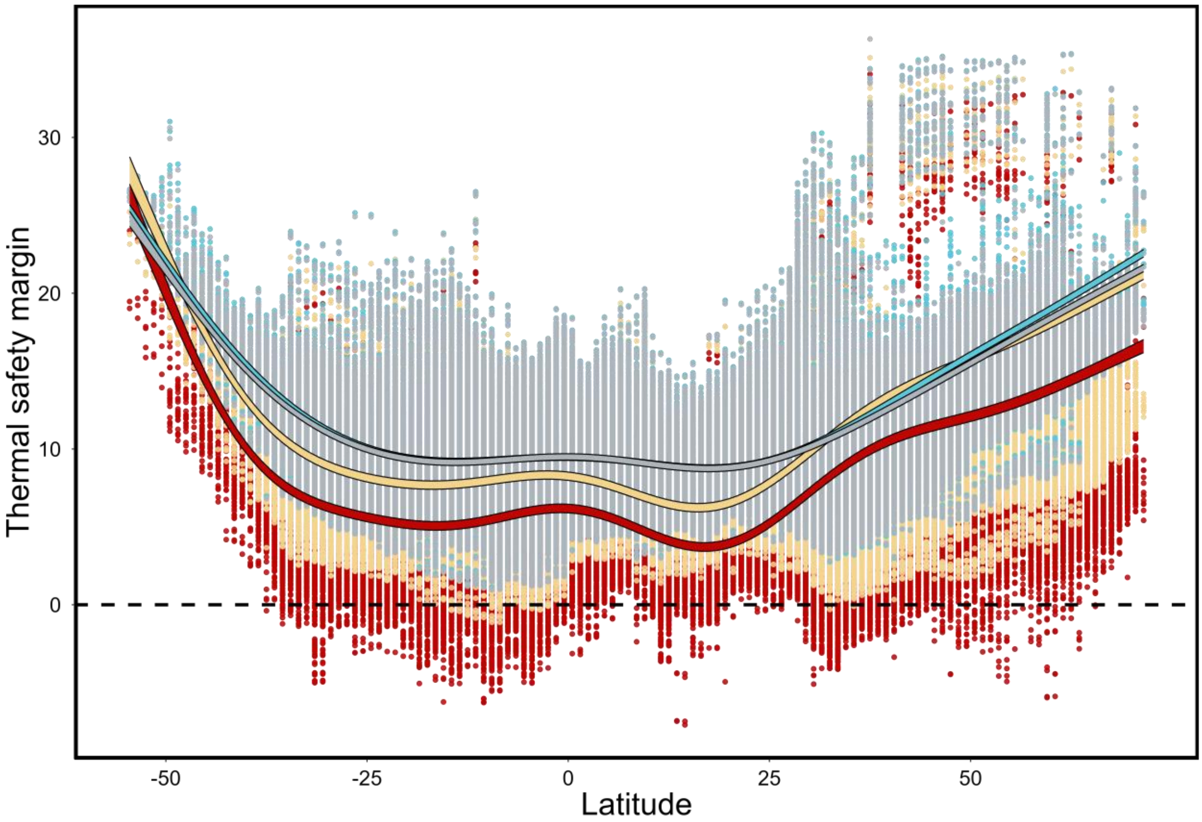

Fig. S5 | Variation in thermal safety margins calculated using different assumptions. Thermal safety margins (TSM) were calculated as the mean difference between CTmax and the predicted operative body temperature in full shade during the warmest quarters of 2006-2015 (grey), as the mean difference between CTmax and the predicted operative body temperature in full shade during the warmest quarters of 2006-2015 excluding body temperatures falling outside the 5% and 95% percentile temperatures (blue), as the difference between the 95% percentile operative body temperature and the corresponding CTmax (yellow), or as the difference between the maximum operative body temperature and the corresponding CTmax (red). Lines represented 95% confidence interval ranges predicted from generalized additive mixed models. This figure was constructed assuming ground-level microclimates occurring under 4°C of global warming above pre-industrial levels.

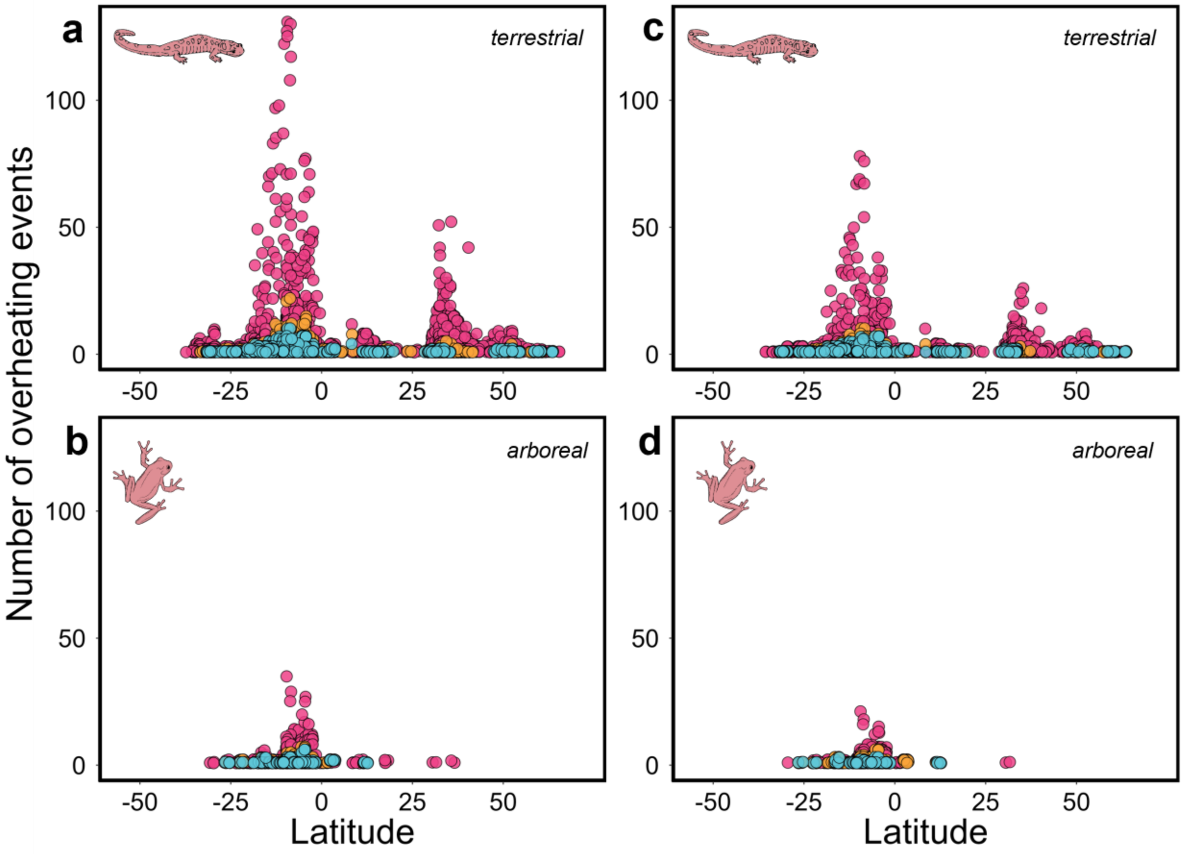

Fig. S6 | Latitudinal variation in the number of overheating events when animals are acclimated to the mean (a,b) or maximum (c,d) weekly body temperature experienced in the seven days prior in terrestrial (a,c) and arboreal (b,d) microhabitats. The number of overheating events (days) were calculated as the sum of overheating events (when daily maximum temperatures exceeded CTmax) during the warmest quarters of 2006-2015 for each population. Blue points depict the number of overheating events in historical microclimates, while orange and pink points depict the number of overheating events assuming 2°C and 4°C of global warming above pre-industrial levels, respectively. For clarity, only the populations predicted to experience overheating events across latitudes are depicted.

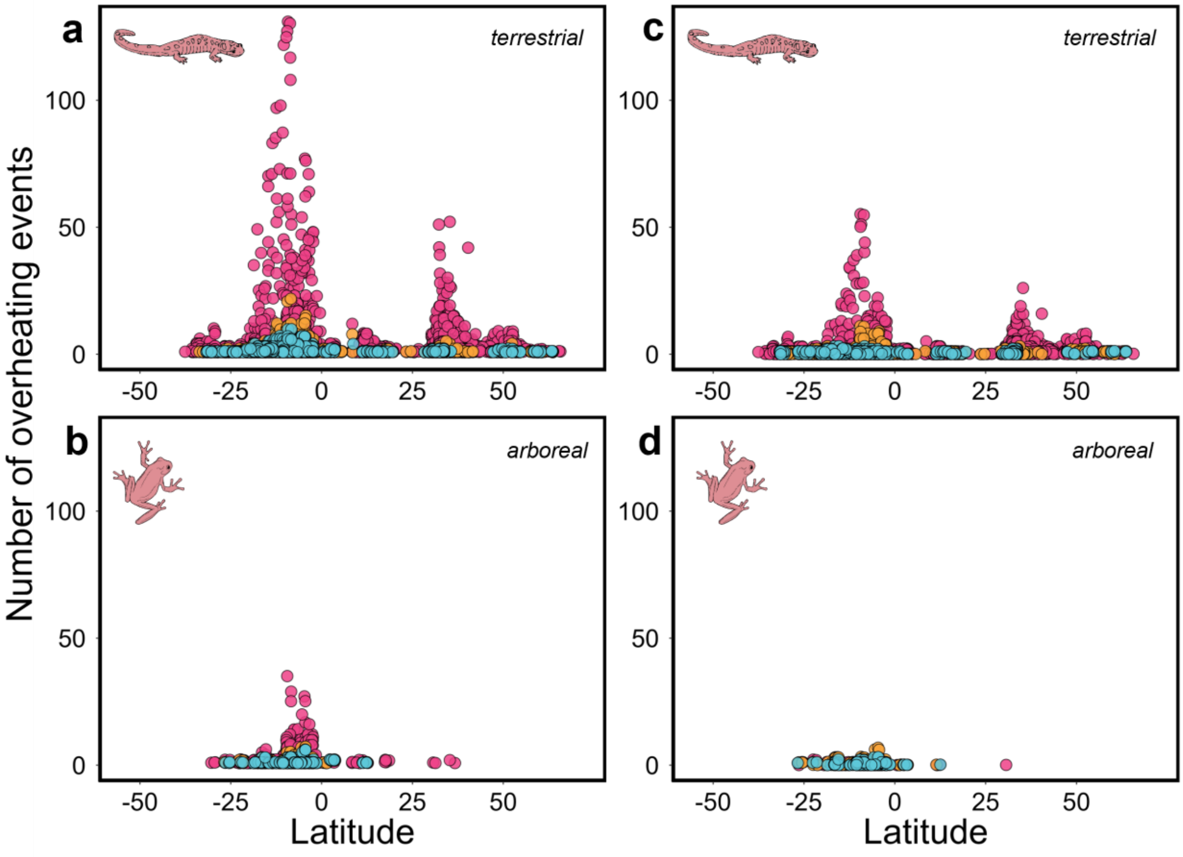

Fig. S7 | Latitudinal variation in the number of overheating events using regular (a,b) or conservative estimates (c,d) in terrestrial (a,c) and arboreal (b,d) microhabitats. The number of overheating events (days) were calculated as the sum of overheating events (when daily maximum temperatures exceeded CTmax) during the warmest quarters of 2006-2015 for each population. Conservative estimates are those where overheating events were counted only when operative body temperatures exceeded 50% of the predicted distribution of CTmax. Blue points depict the number of overheating events in historical microclimates, while orange and pink points depict the number of overheating events assuming 2°C and 4°C of global warming above pre-industrial levels, respectively. For clarity, only the populations predicted to experience overheating events across latitudes are depicted.

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