Vulnerability of amphibians to global warming

Patrice Pottier[1,2*], Michael R. Kearney[3], Nicholas C. Wu[4], Alex R. Gunderson[5], Julie E. Rej[5], A. Nayelli Rivera-Villanueva[6,7], Pietro Pollo[1], Samantha Burke[1], Szymon M. Drobniak[1,8+], and Shinichi Nakagawa[1,9+]

[1] Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, Australia.

[2] Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, Australian Capital Territory, Australia

[3] School of BioSciences, The University of Melbourne, Melbourne, Victoria, Australia

[4] Hawkesbury Institute for the Environment, Western Sydney University, Richmond, New South Wales, Australia

[5] Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana, USA

[6] Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional Unidad Durango (CIIDIR), Instituto Politécnico Nacional, Durango, México

[7] Laboratorio de Biología de la Conservación y Desarrollo Sostenible de la Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, Monterrey, México

[8] Institute of Environmental Sciences, Jagiellonian University, Kraków, Poland.

[9] Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.

[*]Corresponding author

[+]These authors supervised the work equally

Corresponding author: Patrice Pottier (p.pottier@unsw.edu.au)

ORCID

Patrice Pottier https://orcid.org/0000-0003-2106-6597

Michael R. Kearney https://orcid.org/0000-0002-3349-8744

Nicholas C. Wu https://orcid.org/0000-0002-7130-1279

Alex R. Gunderson https://orcid.org/0000-0002-0120-4246

Julie E. Rej https://orcid.org/0000-0002-3670-067X

A. Nayelli Rivera-Villanueva https://orcid.org/0000-0002-9190-4317

Pietro Pollo https://orcid.org/0000-0001-6555-5400

Samantha Burke https://orcid.org/0000-0001-6902-974X

Szymon M. Drobniak https://orcid.org/0000-0001-8101-6247

Shinichi Nakagawa https://orcid.org/0000-0002-7765-5182

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 phylogenetically-informed 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 (3.8%) 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 non-tropical species are more susceptible in the Northern Hemisphere. Our findings challenge evidence for a general latitudinal gradient in overheating risk and underscore the importance of considering climatic variability in vulnerability assessments. Our conservative estimates assume access to cool shaded microenvironments, thus the impacts of global warming on amphibians may exceed our projections. Our microclimate-explicit analyses demonstrate that vegetation and water bodies are 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, behavioural thermoregulation, microclimate selection, biophysical modelling, global analysis, thermal safety margin, warming tolerance, extreme heat events, climate change.

Main text

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]. Over 40% of amphibian species are currently listed as threatened, and additional pressures due to escalating thermal extremes may further increase their extinction risk[5–8]. Therefore, it is vital to assess the resilience of amphibians to climate change to prioritise where and how conservation actions are taken.

Accurate assessments of resilience to climate change require adequate data on thermal tolerance and environmental exposure[9–11]. However, the most exhaustive dataset on amphibian heat tolerance limits only covers 7.5% of known species and is geographically biased towards temperate regions[12] (Fig. 1). 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[10,11,13–16]. 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[17,18]. Therefore, alternative methods to identify the populations and areas most susceptible to thermal stress are critically needed in a rapidly warming climate.

Climate vulnerability assessments also require environmental data with high spatial and temporal resolution, particularly because extreme heat is more likely to trigger overheating events than increased mean temperatures[19–21]. When heat tolerance limits are known, cutting-edge approaches in biophysical ecology allow fine-scale vulnerability assessments that account for morphology, behaviour, and microhabitat setting in both historical and future climate projections[15,22–24]. While broadly applicable, biophysically informed analyses are particularly relevant for amphibians, whose body temperatures depend on evaporative heat loss and whose microhabitat use span terrestrial, aquatic, and arboreal environments. Because microenvironmental features are essential for behavioural thermoregulation[25–27], modelling microhabitats allow assessments of the effectiveness of different thermal refugia in buffering the impacts of extreme heat events.

Here, we assess the global vulnerability of amphibians to extreme heat events in different climatic scenarios and thermal refugia. By integrating predicted thermal limits for 60% of amphibian species with daily operative body temperatures, our study offers the first comprehensive evaluation of the impact of heat extremes on the physiological viability of amphibians in nature.

Thermal limits and environmental exposure

We first developed an approach to predict standardised thermal limits for 5,203 amphibian species using data imputation based on phylogenetic niche clustering (Pagel's λ[28] = 0.95 [0.91 – 0.98]) and known correlations between critical thermal limits (CT_{max}) and other variables (n = 2,661 estimates measured in 524 species; Fig. S2; Methods). Our phylogenetic model-based imputation approach has expanded our understanding of amphibian thermal tolerance by generating testable predictions for 4,679 unstudied species, particularly in biodiversity hotspots (Fig. 1-2). We confirmed our imputation approach was accurate and unbiased by demonstrating a strong congruence between experimental and imputed data in cross-validations (experimental mean ± standard deviation = 36.19 ± 2.67; imputed mean = 35.93 ± 2.54; n = 375; r = 0.86; Extended Data Fig. 2a,b), though, as expected, the uncertainty in imputed predictions was higher in understudied clades (Extended Data Fig. 2c).

We then integrated predicted thermal limits with daily operative body temperature fluctuations estimated from biophysical models to evaluate the sensitivity of amphibians to extreme heat events in terrestrial, aquatic, and arboreal microhabitats (Extended Data Fig. 1; Methods). Operative body temperatures are the steady-state body temperatures 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[22,23]. For each microhabitat, we modelled daily operative body temperatures during the warmest quarters of 2006-2015 and across the distribution range of each species (Methods). We also used projected future climate data from TerraClimate[29] to generate projections assuming 2°C or 4°C of global warming above pre-industrial levels. These temperatures are within the range projected by the end of the century under low and intermediate/high greenhouse gas emission scenarios, respectively[30]. Notably, recent historical CO_2 emissions most closely align with high warming scenarios[31] (i.e., 4.3°C of predicted warming by 2100). All microenvironmental projections assumed access to 85% of shade and sufficient humidity to maintain wet skin to simulate amphibians in thermal refugia (Methods).

We estimated the vulnerability of amphibians by estimating daily differences between predicted thermal limits and operative body temperatures (Extended Data Fig. 1; Methods). We also adjusted daily thermal limits to assume that species were, on any given day, acclimated to local mean weekly operative body temperatures, effectively accounting for plasticity throughout species' distribution ranges (Methods). In total, we predicted vulnerability metrics for 203,853 local species occurrences (individual species in 1° x 1° grid cells) in terrestrial conditions (5,177 species), 204,808 local species occurrences in water bodies (5,203 species); and 56,210 local species occurrences (1,771 species) in above-ground vegetation, for each warming scenario. The number of species examined in arboreal conditions was lower to reflect morphological adaptations required for climbing in above-ground vegetation. These estimates were then grouped into assemblages (all species occurring in 1° x 1° grid cells), tallying 14,090 and 14,091 assemblages for terrestrial and aquatic species and 6,614 assemblages for arboreal species, respectively.

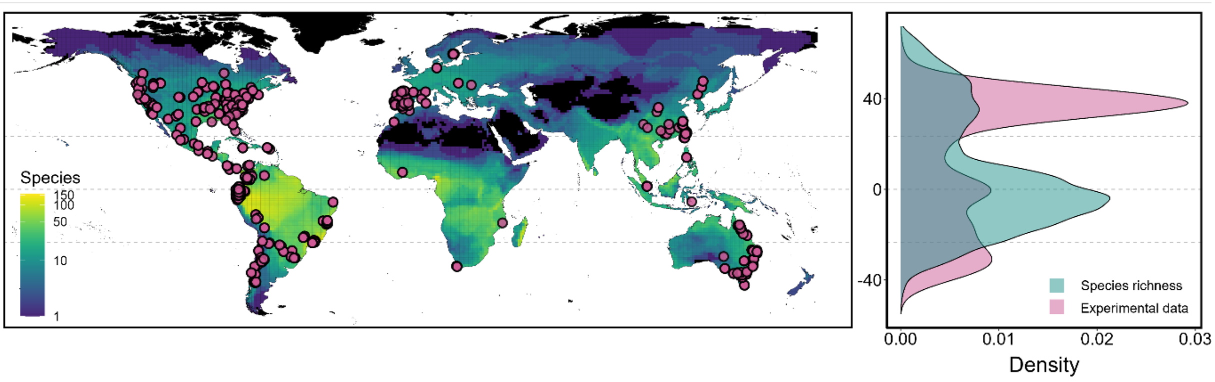

Fig. 1 | Contrast between the geographical locations at which experimental data were collected and patterns in species richness. Pink points denote experimental data, while the colour gradients refer to species richness calculated in 1 x 1 ° grid cells in the imputed data (5,203 species). Density plots on the right panel 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.

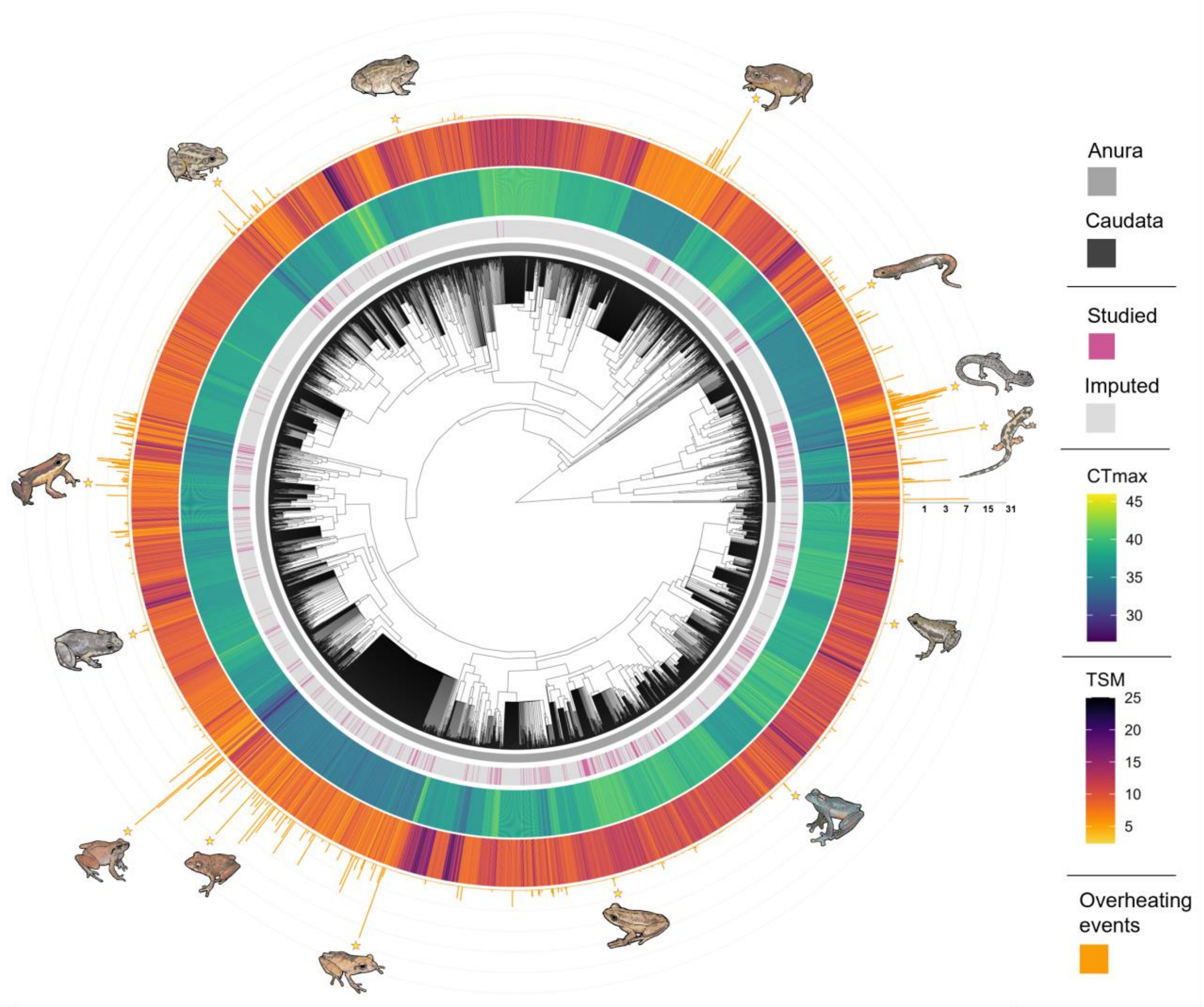

Fig. 2 | Phylogenetic coverage and taxonomic variation in climate vulnerability. Heat maps show heat tolerance limits (CT_{max}) and thermal safety margins (TSM), while histograms show the number of overheating events (days) averaged across each species' distribution range. Pink bars refer to species with prior knowledge, while grey bars refer to entirely imputed species. 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 [32] 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.*

Vulnerability to historical and future heat

We first calculated thermal safety margins (TSM, *sensu* [11]) as the weighted mean difference between heat tolerance limits (CT_{max}) and the maximum daily body temperatures of the warmest quarters of 2006-2015 for each local species occurrence. Thermal safety margins averaged from long-term climatology are routinely used in climate vulnerability analyses[16,33,34]. We found evidence for a decline in TSM towards mid to low latitudes in all microhabitats, a pattern maintained across warming scenarios (Fig. 3, Extended Data Fig. 3). However, warming substantially reduce TSM at all latitudes (Fig. 3), likely reflecting the contrast between weak plastic responses in CT_{max} across latitudes[11,15] (Extended Data Fig. 3; Fig. S3) and large variation in environmental temperatures (Extended Data Fig. 3). Across all conditions simulated, TSM is always positive, even in the highest warming scenario (Fig. 3, Extended Data Fig. 3). The mean TSM is lower for terrestrial (mean [95% confidence intervals]; current = 11.69 [8.86 – 14.43]; +4°C = 9.41 [6.53 – 12.09]) and arboreal conditions (current = 12.23 [9.40 – 14.96]; +4°C = 10.07 [7.23 – 12.80]) than for water bodies (current = 13.60 [10.71 – 16.28]; +4°C = 11.68 [8.80 – 14.36]; Fig. 3; Extended Data Table 1).

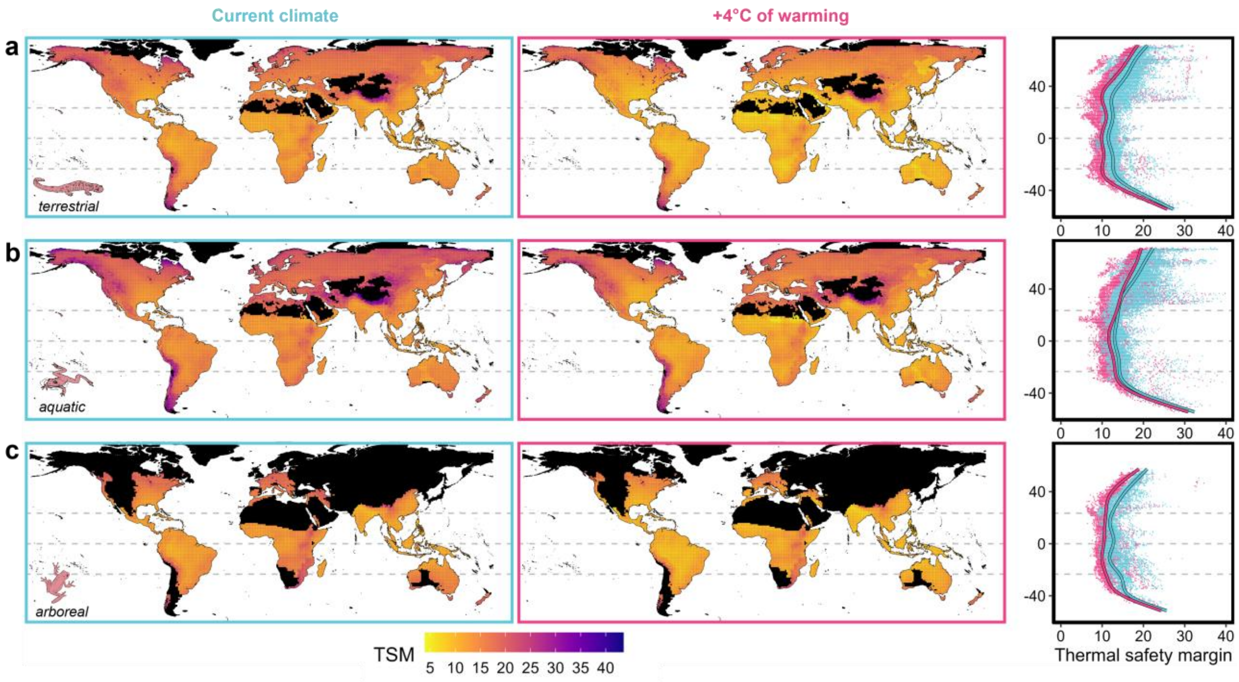

Fig. 3 | Assemblage-level patterns in thermal safety margin for amphibians in terrestrial (a), aquatic (b) or arboreal (c) microhabitats. Thermal safety margins (TSM) were calculated as the weighted mean difference between CT_{max} and the predicted operative body temperature in full shade during the warmest quarters of 2006-2015 in each assemblage (1-degree grid cell). Black colour 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 generalised additive mixed models. Dashed lines represent the equator and tropics.

Because extreme heat events are more likely to trigger overheating events than mean temperatures[9–11], we also calculated the binary probability (0/1) that operative body temperatures exceeded CT_{max} at least once across the warmest quarters of 2006-2015 (i.e., overheating risk). Overall, overheating risk is low, although numerous species are predicted to face overheating events locally (Fig. 4, Extended Data Table 2). In terrestrial conditions, we predict that 198 species (1,497 local species occurrences from 376 assemblages) are likely to experience overheating events in current microclimates (Fig. 4-5). However, under 4°C of warming, 488 species (4,929 local species occurrences from 1,263 assemblages) are expected to overheat, which represents more than a two-fold increase relative to current conditions (Fig. 4-5; Extended Data Table 2-3). The number of species predicted to overheat in each grid cell also increase with warming; each assemblage comprises up to 32 vulnerable species in current climates (mean [95% confidence intervals] = 3.85 [1.03 – 7.76] species) and up to 84 vulnerable species with 4°C of global warming (3.80 [1.11 – 7.46]; Fig. 4; Extended Data Table 3). In addition, the proportion of species predicted to experience overheating events in each assemblage varies geographically and between warming scenarios (Extended Data Fig. 5; Extended Data Table 4). The proportion of species at risk is high in some areas with high species richness (e.g., Northern Australia, Southeastern United States) and not linearly predicted by latitude (Extended Data Fig. 5).

In current conditions for species that can shelter in trees (arboreal), 89 assemblages (comprising 1-11 species; 2.46 [0.31 – 5.72] species) are predicted to overheat, while 301 assemblages (comprising 1-38 species; 3.09 [0.66 – 6.53] species) are predicted to overheat assuming 4°C of global warming (Fig. 4; Extended Data Table 3). While the overheating risk is lower in arboreal conditions, considerably fewer species were examined than in terrestrial conditions (1,771 vs. 5,177 species). In fact, comparing the responses of arboreal species in different microhabitats revealed that occupying above-ground vegetation is only partially beneficial (Extended Data Fig. 4). In current climates, up to 40 arboreal species (469 local species occurrences) are predicted to experience overheating events in terrestrial conditions, whereas 27 arboreal species (286 local species occurrences) are predicted to overheat in above-ground vegetation (Extended Data Fig. 4). Furthermore, under 4°C of warming, 121 arboreal species (1,424 local species occurrences) are predicted to overheat in terrestrial conditions, while retreating to above-ground vegetation only reduces the number of species exposed to overheating events by 21.5% (95 species, 965 local species occurrences) (Extended Data Fig. 4). Contrary to terrestrial and arboreal conditions, no amphibian populations are predicted to overheat in water bodies due to the thermal buffering properties of water.

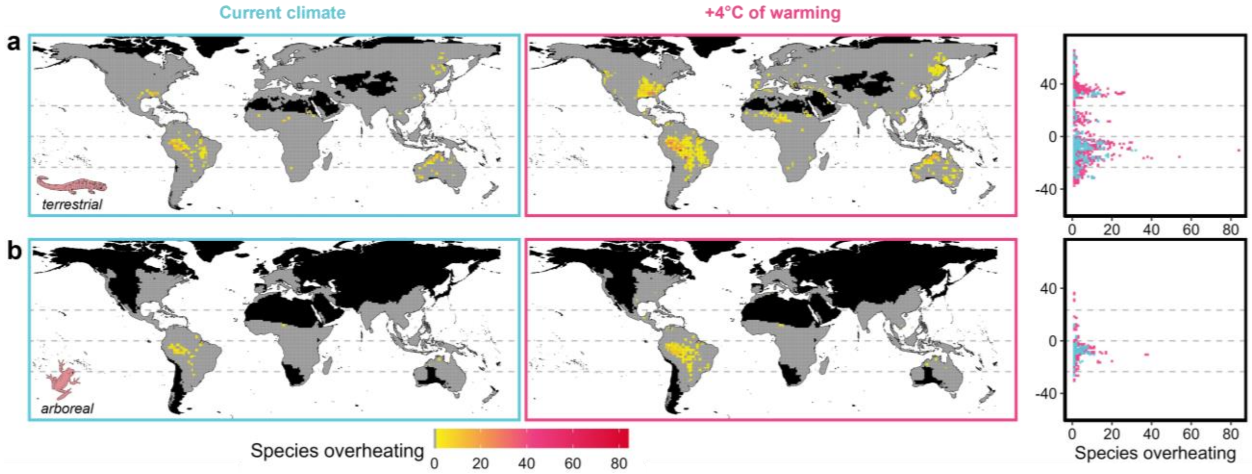

Fig. 4 | Number of species predicted to experience overheating events in terrestrial (a) and arboreal (b) microhabitats. The number of species overheating was assessed as the sum of species overheating at least once in the period surveyed (warmest quarters of 2006-2015) in each assemblage (1-degree grid cell). Black colour depicts areas with no data, and grey colour assemblage without species at risk of overheating. 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.

Finally, we quantified the number of days (out of 910 simulated days across the warmest quarters of 2006-2015) each species was predicted to locally exceed their plasticity-adjusted heat tolerance limits. This metric fully integrates the frequency at which amphibians are predicted to experience temperatures beyond their thermal limits. For current climates, we found that species rarely experience overheating events in shaded terrestrial conditions (overall mean overheating days [95% confidence intervals] = 0.01 [0.01 – 0.07]; mean among overheating species = 1.43 [0.07 – 4.07] days); but these figures increase considerably with global warming (Fig. 5; Extended Data Table 2). Under 4°C of warming, species are predicted to overheat on as many as 131 days, representing up to 14.4% of the warmest days of the year (overall mean = 0.08 [0.01 – 0.30] days; mean among overheating species = 3.30 [0.95 – 6.80] days; Fig. 5; Extended Data Table 2). This is noticeably more than what is predicted under 2°C of warming (overall mean = 0.02 [0.01 – 0.10] days; mean among overheating species = 1.57 [0.11 – 4.28] days; Fig. 5; Extended Data Table 2). In above-ground vegetation, the frequency of overheating events is lower, as expected. Under current climates, arboreal species are predicted to overheat on up to 6 days in total (overall mean = 0.01 [0.01 – 0.04] days; mean among overheating species = 1.23 [0.01 – 3.71] days; Fig. 5; Tab. Extended Data Table 2). Under 4 degrees of warming, arboreal species are predicted to overheat on up to 35 days (overall mean = 0.04 [0.01 – 0.16] days; mean among overheating species = 2.31 [0.28 – 5.47] days; Fig. 5; Extended Data Table 2). Arboreal species retreating to above-ground vegetation are predicted to experience fewer overheating events than those in terrestrial conditions (Extended Data Fig. 4). Interestingly, we found that species predicted to overheat locally have TSMs well above zero, although some are living particularly close to their heat tolerance limits during the warmest months in both terrestrial (mean [95% confidence intervals]; current = 9.13 [7.35 – 11.04], range: 3.02 – 15.36; +4°C = 6.93 [5.17 – 8.84], range: 0.97 – 14.91) and above-ground conditions (current = 9.57 [7.69 – 11.43], range: 3.70 – 11.40; +4°C = 7.36 [5.58 – 9.27], range: 1.75 – 10.00; Fig. 5c,d). 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. 5c,d; Extended Data Table 5). In particular, overheating days increase rapidly as thermal safety margins fall below 5°C (Figure 5c,d).

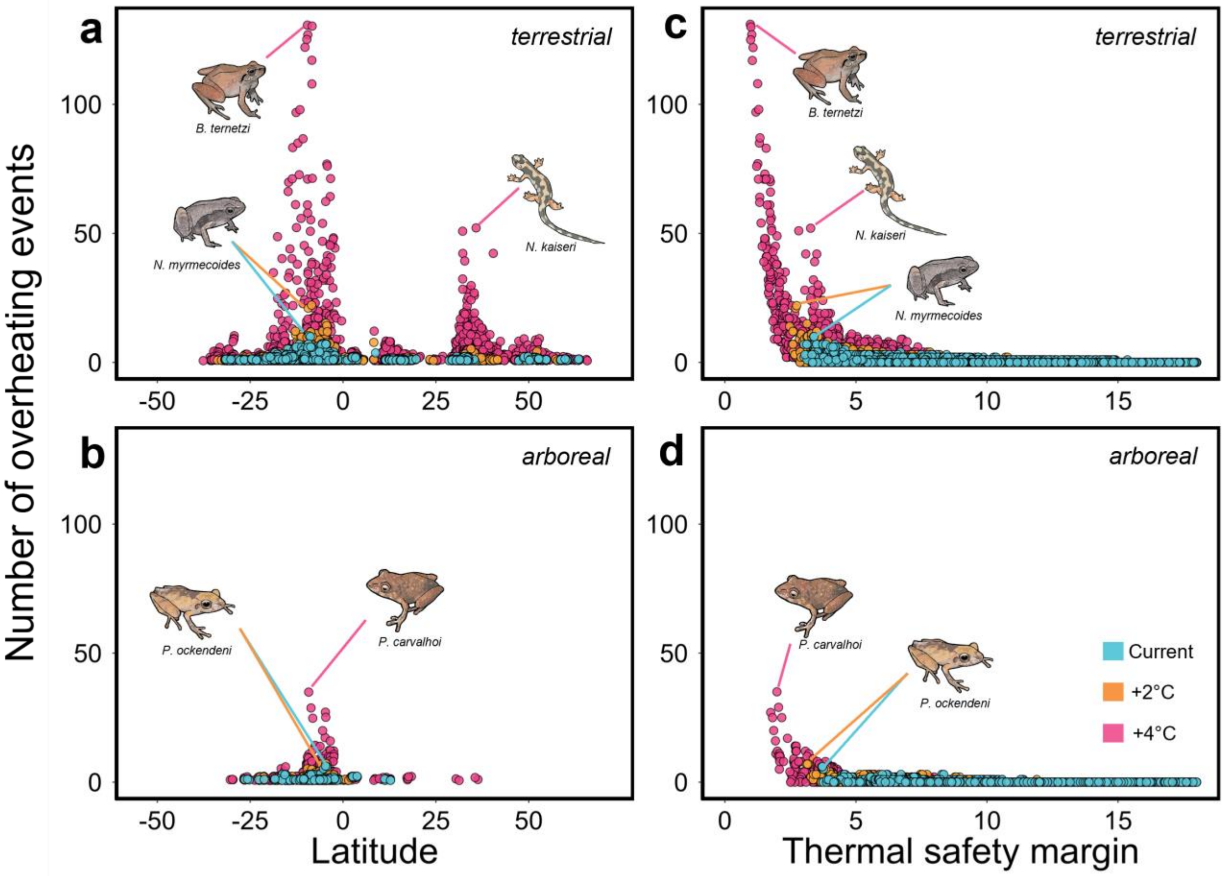

Fig. 5 | Latitudinal variation in the number of overheating events in terrestrial (a,c) and arboreal (b,d) microhabitats as a function of latitude (a,b) and thermal safety margin (c,d). The number of overheating events (days) were calculated as the sum of overheating events (when daily maximum temperatures exceed CT_{max}) during the warmest quarters of 2006-2015 for each species in each grid cell. Blue points depict the number of overheating events in current 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 species predicted to experience overheating events across latitudes are depicted (a,b).

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 show that nearly 200 species may already experience hourly temperatures that would likely result in death over minutes or hours of exposure in thermal refugia. This pattern is only predicted to worsen (Fig. 4-5). Assuming 4°C of global warming, the number of species and assemblages exposed to overheating events would be 2.5- to 3.5-fold higher than currently, totalling 488 out of 5,203 species studied (9.4%; Fig. 4-5).

We also 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[30]. 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[35]. 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; Fig. S3). Our study clearly demonstrates, as others have suggested[19,33,36,37], that physiological plasticity is not a sufficient mechanism to buffer many populations from the impacts of rapidly rising temperatures.

Extreme heat events drive climate vulnerability

We found large spatial heterogeneity in the vulnerability of amphibians. In tropical areas, most vulnerable species are concentrated in South America and Australia, whereas fewer species are impacted in the African and Asian tropics (Fig. 4). Tropical species also experience disproportionately 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 assemblage was not predicted by latitude (Extended Data Fig. 5). Therefore, our findings are inconsistent with the expectation of a general latitudinal gradient in overheating risk based on thermal safety margins[10,11,13,15]. In fact, the overheating risk does not increase linearly with TSM (Fig. 5c,d), and species with seemingly comparable TSMs can have markedly different probabilities of overheating due to varying exposure to daily temperature fluctuations (Fig. 5c,d). 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 when 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[10,11,13,15], revealing a far more nuanced pattern of climate vulnerability across latitudes. While the reliability of TSM-based assessments has been questioned in previous studies[9], our work further emphasises the need to consider natural climatic variability and extreme hourly temperatures[15,19–21] when evaluating the vulnerability of ectotherms to global warming. 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 predicted not 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[38]. Our findings add to the growing evidence that finding access to cooler microhabitats is the main strategy amphibians and other ectotherms can use to maintain sub-lethal body temperatures[11,26,39,40].

However, it is crucial to emphasise that vegetated terrestrial conditions in full shade offer inadequate protection to nearly 10% of species, and many arboreal species 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%. Moreover, although burrows offer cooler microclimates (see Fig. S9), the ability to use underground spaces is not universal among amphibians and can greatly restrict activity, reproduction, and foraging opportunities.

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[41–44], while increased frequencies of droughts will cause water bodies to evaporate[45,46]. These changes compromise not only habitat integrity but also local humidity levels – key for effective thermoregulation[47–49]. Consequently, amphibians will likely experience higher body temperatures and desiccation stress events than our models predict due to inconsistent access to cooler microhabitats[50], particularly in degraded systems.

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[51,52], disruptions to phenology[53,54], reduced reproductive fitness (fertility and fecundity)[34,55–57], and death[58–60]. Although comprehensive data on thermal incapacitation times and fertility impacts are sparse in amphibians, integrating both the duration and intensity of thermal stress[58,60,61] 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.

Alternatively, species that can retreat underground during heat events are likely to experience fewer overheating events than our models predict (see Fig. S9), and prolonged exposure to high temperatures in the permissive range (*sensu* [59]) can enhance performance and fitness, thereby reducing the impacts of extreme heat on natural populations. In addition, some species may adapt to changing temperatures. However, evidence for slow rates of evolution and physiological constraints on thermal tolerance[62–64] challenges the likelihood of local adaptation to occur in rapidly warming climates.

The power of data imputation

Our imputation approach has generated testable predictions of the thermal limits of 5,203 species, expanding the scope of previous research[12] (Fig. 2). We also addressed geographical biases by generating predictions 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), with 69% (338 out of 488) of vulnerable species remaining unstudied. Targeted research efforts in these vulnerability hotspots are instrumental in validating our model predictions and advancing 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 scientists could expedite data collection and result in timely conservation measures. Exemplary initiatives to sample numerous species in South America (e.g., [25,65,66]) are promising steps in this direction, and we hope our findings will catalyse 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. Most species will not experience overheating events throughout their entire range, and these overheating events may not occur simultaneously. Hence, most species are likely to only experience local extirpation due to overheating, according to our models. Nevertheless, local extirpations carry their own sets of ecological repercussions, such as reshuffling community compositions and eroding genetic and ecological diversity[67–69].

Some amphibian populations may also undergo range shifts, permanently or transiently relocating to habitats with more hospitable weather patterns[70]. However, this is only possible if suitable habitats are available for establishment. Given the low dispersal rates of some amphibians and their common reliance on water bodies for reproduction and thermoregulation, opportunities for range shifts are likely to be rare for many species. Identifying which species at high risk of overheating are simultaneously predicted to have limited ability to extend their range is an interesting avenue for research. In addition, we stress that amphibians living close to their physiological limits for extended times at the warm edge of their distribution 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[59,60,71,72].

Overall, our study contributes to the evidence that climate change is a mounting threat to amphibians[8,73] and emphasises the importance of limiting global temperature rises below 2°C to minimise 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 conditions with cooler and more stable temperatures 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[6,8,74]. These actions are critical for the amphibians at risk and the ecosystems they support[75] in a planet undergoing perilous climatic changes.

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Methods

Reporting

We report author contributions using the CRediT (Contributor Roles Taxonomy) statement[76] and MeRIT (Method Reporting with Initials for Transparency) guidelines[77]. We also crafted the study title, abstract and keywords to maximise indexing in search engines and databases[78]. All analyses were performed using R statistical software[79] (v. 4.3.0), and most computations used the computational cluster Katana supported by Research Technology Services at UNSW Sydney.

Amphibian heat tolerance limits

We leveraged the most comprehensive compilation of amphibian heat tolerance limits[12] 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, we 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}[80]) because it was the most used and comparable metric. 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 [32]. Fourth, we only included species for which their geographical range was reported in the International Union for the Conservation of Nature red list[81] (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 (mean = 5.08; range = 1 - 146 estimates per species; 287 species with more than one estimate). We also complemented this dataset with ecotypic data for each species. Amphibians were grouped into six major ecotypes according to [50]: 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 [12] are geographically and taxonomically biased. Therefore, we employed a data imputation procedure to infer the thermal tolerance of data-deficient species, totalling 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). We selected data-deficient species from a species list that matched the phylogeny from [32] (7,238 species), was listed in the IUCN red list[81] along with geographic distribution data (5,792 species), and for which ecotypes were known (6,245 species). We did not consider Caecilians (order Gymnophiona) because, to our knowledge, heat tolerance limits are unknown for all Caecilian species[12]. Of the 5,792 species for which we had distribution and phylogenetic data, 5,268 were data-deficient for CT_{max}, of which 4,822 had a known ecotype. After removing Caecilians, we were left with 4,679 species to impute. We also supplemented our dataset with published body mass data retrieved from literature sources or estimated based on length-mass allometries[50,82,83]. We 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

We developed a phylogenetic imputation procedure, here named Bayesian Augmentation with Chained Equations (BACE). The BACE procedure combines the powers of Bayesian data augmentation and multiple imputation with chain equations (MICE[84]). Briefly, we ran multiple iterative models using *MCMCglmm*[85] (v. 2.34) and supporting functions from the *hmi* package[86]. 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. We 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). Although the proportion of missing data was large (89.9%), imputations based on large amounts of missing data are common[13,87], and although estimate uncertainty increases with the proportion of missing data, as expected, simulation studies have shown estimations remain unbiased[88,89]. Our cross-validation approach also demonstrated the ability of our models to predict back known experimental estimates with reasonable error (experimental mean ± standard deviation = 36.19 ± 2.67; imputed mean = 35.93 ± 2.54; $r = 0.86$; 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), and their ecotype. 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 modelled species-specific slopes (plasticity; see Fig. S2) and partitioned the variance among phylogenetic and non-phylogenetic effects. 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 a container filled with 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[90–92]. In amphibians, the onset of spasms usually occurs after the loss of righting response[90], 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, we generated three ecologically relevant and standardised heat tolerance estimates, and all analyses were built upon these standardised imputed 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 provide estimates of uncertainty in the imputation, and errors were propagated throughout our analyses (see *Climate vulnerability analysis*).

Microenvironmental data and biophysical modelling

We used the package *NicheMapR*[93,94] (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 temperatures 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[22,23,27,95–99].

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[100], and assumed that 90% of the solar radiation was diffused due to canopy cover[101]. 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 behaviourally thermoregulate by retreating to thermal refugia during extreme heat events[26]. Our calculations 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*[93] (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[102] (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[29] to generate hourly projections assuming 2°C or 4°C of global warming above pre-industrial levels. These temperatures are within the range projected by the end of the century under low (Shared Socioeconomic Pathway SSP 1-2.6 to SSP 2-4.5) and high (SSP 3-7.0 to SSP 5-8.5) greenhouse gas emission scenarios, respectively[30]. 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[103]. 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 and only used climate projections available in TerraClimate (i.e., 2°C and 4°C) to reduce computational demands.

We then used microclimate estimates to generate operative body temperatures using the *ectotherm* function in *NicheMapR*[94]. This modelling system has been extensively validated with field observations[104–106] (*see also* Fig. S12). 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). Estimating body mass-specific operative body temperatures for each grid cell, species, and microhabitat was too computationally extensive, given the geographic and taxonomic scale of our study (464,871 local species occurrences). Therefore, we ran the ectotherm models using the median body mass of the species assemblage in each geographical coordinate. When body mass was unknown, we ran models assuming a body mass of 8.4 grams, the median assemblage-level body mass. Given that most amphibians in our dataset are small (median = 1.4 g, mean = 27.5 g), body temperatures equilibrate quickly with the environment, and operative body temperatures are likely representative of core body temperatures.

To model operative body temperatures in water bodies (e.g., ponds or wetlands), we used the container model from *NicheMapR*. Unlike previously mentioned calculations predicting steady-state temperatures, this approach accounts for transient temperature changes, capturing lags due to thermal inertia (i.e., transient heat budget model[107,108]). 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., [49,104]). 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.

We 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[19] (see *Climate vulnerability analyses*). 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[19]. 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).

We 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, we fitted an individual meta-analytic model for each species to estimate the plasticity of imputed heat tolerance limits (CT_{max}) to changes in operative body temperatures using the *metafor* package[109] (v. 4.2-0). CT_{max} was used as the response variable, acclimation temperature (i.e., median, 5th percentile, or 95th percentile daily maximum body temperature experienced by a species across its distribution range) was used as the predictor variable, and imputed estimates were weighted based on their standard error. From these models, we used out-of-sample model predictions (using the *predict* function) to estimate the CT_{max} of each species in each 1° x 1° grid cell across their distribution range in different warming scenarios, based on predicted mean weekly body temperatures. Specifically, we assumed that species were, on any given day, acclimated to the mean daily body temperature experienced in the 7 days prior[19]. Therefore, CT_{max} was simulated as a plastic trait, which varied daily, as animals acclimate to new environmental conditions (Extended Data Fig. 1). While evidence in small amphibians suggests the full acclimation potential is reached within 3-4 days[110–112], other evidence points to some variation after longer periods[113]. Therefore, we chose 7 days to reflect that some amphibians may require longer to acclimate. Because we used out-of-sample model predictions, 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. Our approach to accounting for plasticity assumes that plasticity is homogeneous within species and ignores the possible influence of local adaptation. However, given the low variability in plasticity among species (Fig. S2-3), lack of evidence for latitudinal variation in plasticity ([33,36,114]), high phylogenetic signal in thermal tolerance (Pagel's λ[28] = 0.95 [0.91 – 0.98]; see *Sensitivity Analyses*), and evidence for slow rates of evolution and physiological constraints on CT_{max}[62,64], geographic variation in thermal tolerance and plasticity is unlikely to have a major influence on our results.

We 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* [11]). We calculated weighted means and standard errors (*sensu* [115]) of 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[16,33,34]. Second, we calculated the binary probability (0/1) 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[19].

Macroecological patterns

The objective of this study was to characterise the vulnerability of amphibians to global warming. We investigated patterns at the level of local species occurrences (presence of a given species in a 1° x 1° grid cell based on IUCN data), allowing one to identify specific populations and species that may be more susceptible to heat stress and direct targeted research efforts. We also analysed data at the assemblage level, the species composition within a grid cell. In such case, we calculated the weighted mean and standard error of TSM (*sensu* [115]) across species in each grid cell. Assemblage-level analyses allow one to identify areas containing a higher number of vulnerable species, offering actionable insights for broader-scale conservation initiatives.

We used the *gamm4* package[116] to fit generalised additive mixed models (GAMM) against latitude. For local species occurrences, 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, generalised additive linear models do not allow for phylogenetic correlation matrices, and other functions such as *brms*[117] surpassed our computational time and memory limits. 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). We 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 a binomial error structure, and the latter using a Poisson error structure. Thermal safety margin estimates were weighted by the inverse of their sampling variance to account for the uncertainty in the imputation and predictions across geographical coordinates. 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 species 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 (see *Sensitivity analyses*; Fig. S8). We 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 scenario, we fitted models with the interaction between microhabitat and climatic scenario as a fixed effect using *MCMCglmm*[85] (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 [32]). 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, we fitted Poisson and binomial models using *lme4*[118] (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 margins. While the mean estimates from these simpler models should be unbiased, estimate uncertainty is likely underestimated[119].

We also investigated patterns of climate vulnerability at the assemblage 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 assemblage-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 assemblage level. All models were fitted without a contrast structure to estimate mean effects in each microhabitat and climatic scenario, and with two-sided contrasts to draw comparisons with current terrestrial conditions.

Cross-validation and sensitivity analyses

We assessed the accuracy of the data imputation procedure using a cross-validation approach. Specifically, we 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 where 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 investigated alternative ways to i) calculate thermal safety margins, ii) account for acclimation responses, and iii) control for prediction uncertainty (see *Supplementary methods;* Fig. S6-8) and investigated the influence of different parameters of our biophysical models (i.e., shade and burrow availability, plant height, solar radiation, wind speed, pond depth) on predicted vulnerability risks (see *Supplementary methods;* Fig. S9-11). Our results were generally robust to changes in model parameters, although amphibians are likely to experience more overheating events in open habitats[11,52] (Fig. S9) and shallow ponds (Fig. S10), and lower risks in underground conditions[120] (Fig. S9). We also confirmed that predicted operative body temperatures were comparable to field body temperatures measured in wild frogs (see *Supplementary methods;* Fig. S12).

Finally, we confirmed the presence of a phylogenetic signal in the experimental dataset by fitting a Bayesian linear mixed model using all complete (no missing data) predictors (i.e., acclimation temperature, endpoint, acclimation status, life stage, and ecotype) in *MCMCglmm*. We accounted for phylogenetic non-independence using a correlation matrix of phylogenetic relatedness and fitted random intercepts for non-phylogenetic species effects. The phylogenetic signal (Pagel's λ[28], which is equivalent to phylogenetic heritability[121,122]) was calculated as the proportion of variance explained by phylogenetic effects relative to the total non-residual variance.

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

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. TerraClimate data is available from https://www.climatologylab.org/terraclimate.html and NCEP data is available from https://psl.noaa.gov/thredds/catalog/Datasets/ncep.reanalysis2/gaussian_grid/catalog.html.

Code availability

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

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Authors' contributions

This study was conceptualized by PPottier, MRK, SB, SMD, and SN. All data manipulation and analyses were performed by PPottier (with conceptual and technical input from SMD and SN for the imputation methods and statistical analyses, MRK, ARG, JER, and NCW for the biophysical modelling and climate vulnerability analyses). All code was reviewed by NCW, ARG, and JER following the recommendations of [123]. Ecotype information was collected by NCW, PPollo, and ANRV. PPottier, NCW, and SMD contributed to data visualization. PPottier wrote the initial draft, and all authors were involved in the review and editing. PPottier oversaw the project administration, while SMD and SN were in charge of the supervision.

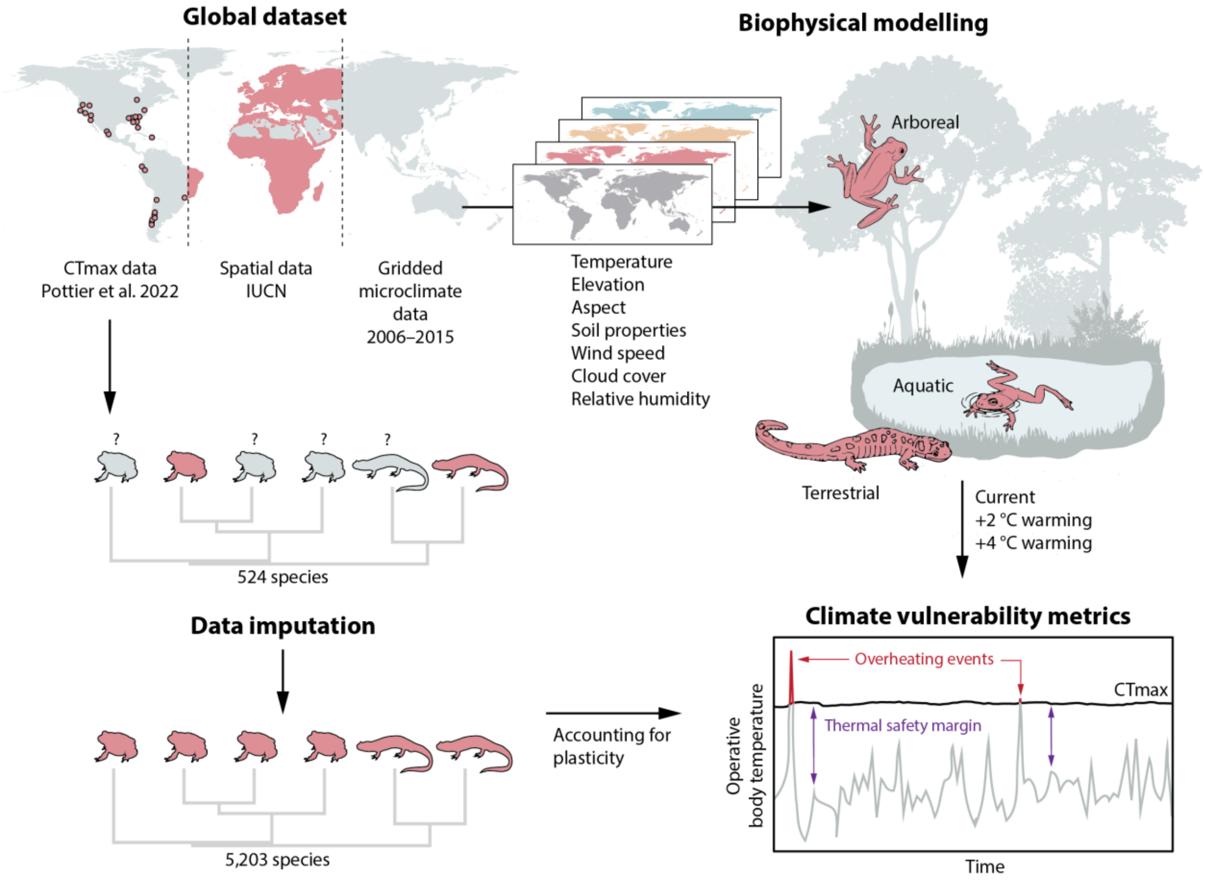
Inclusion & ethics statement

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).*

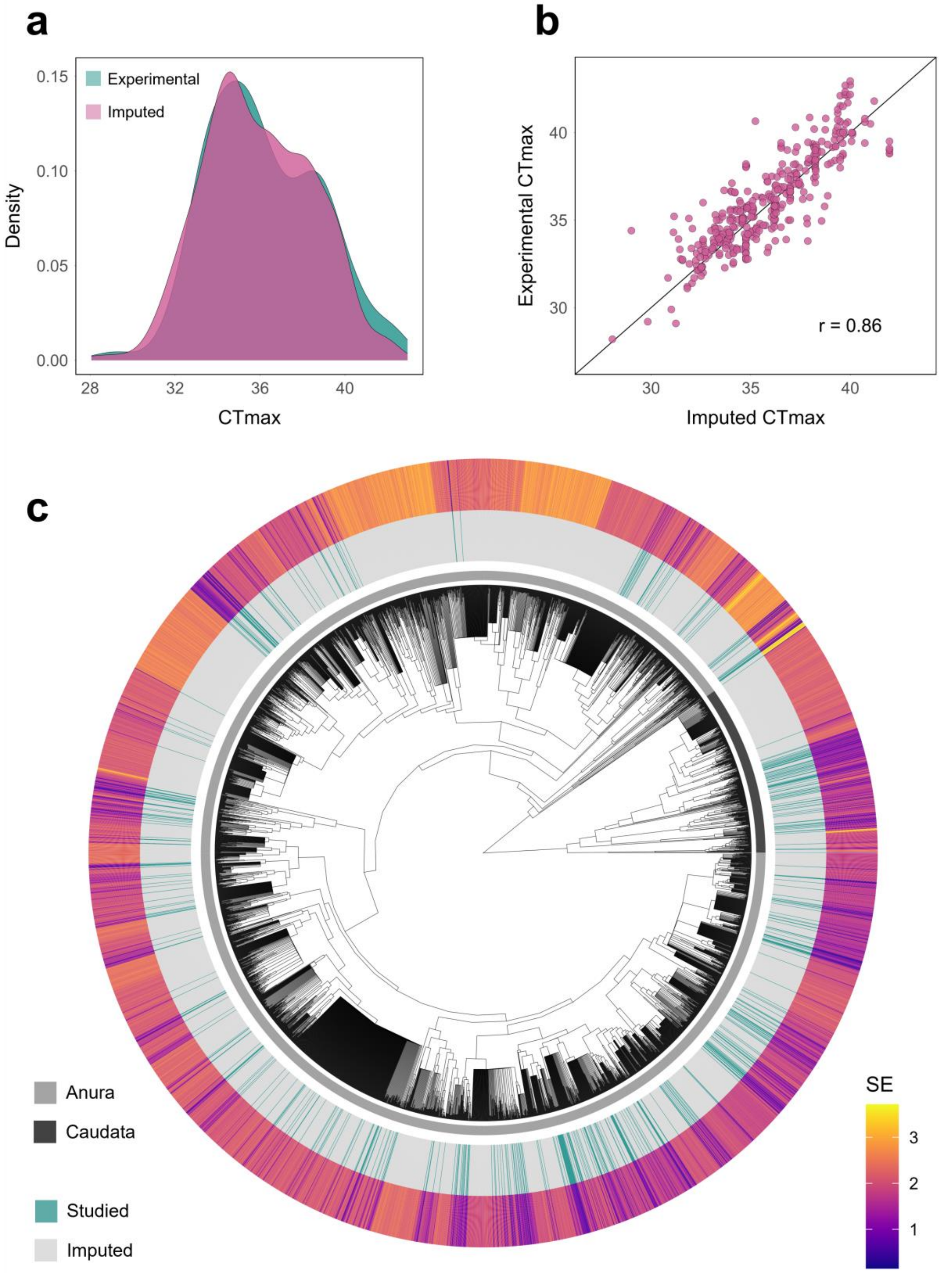
Competing interest declaration

The authors declare no conflict or competing interests.

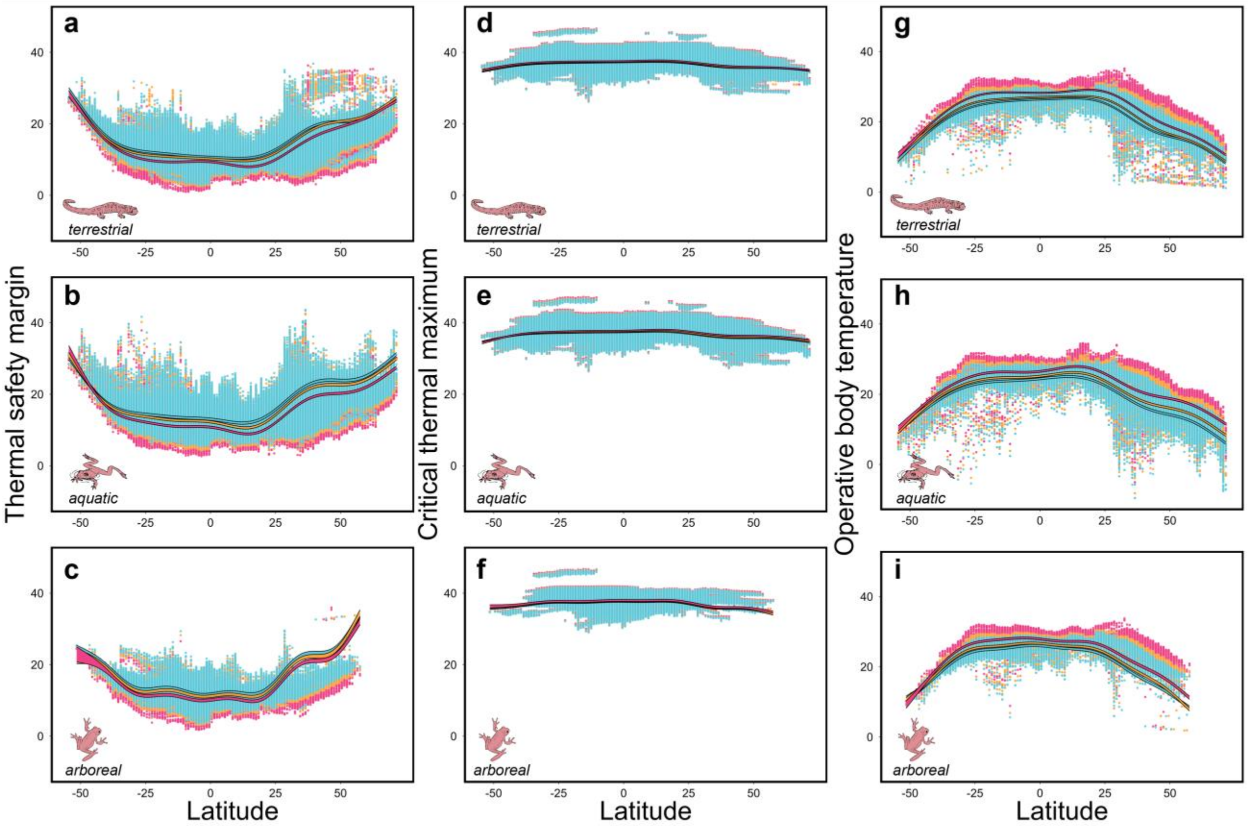
Extended data



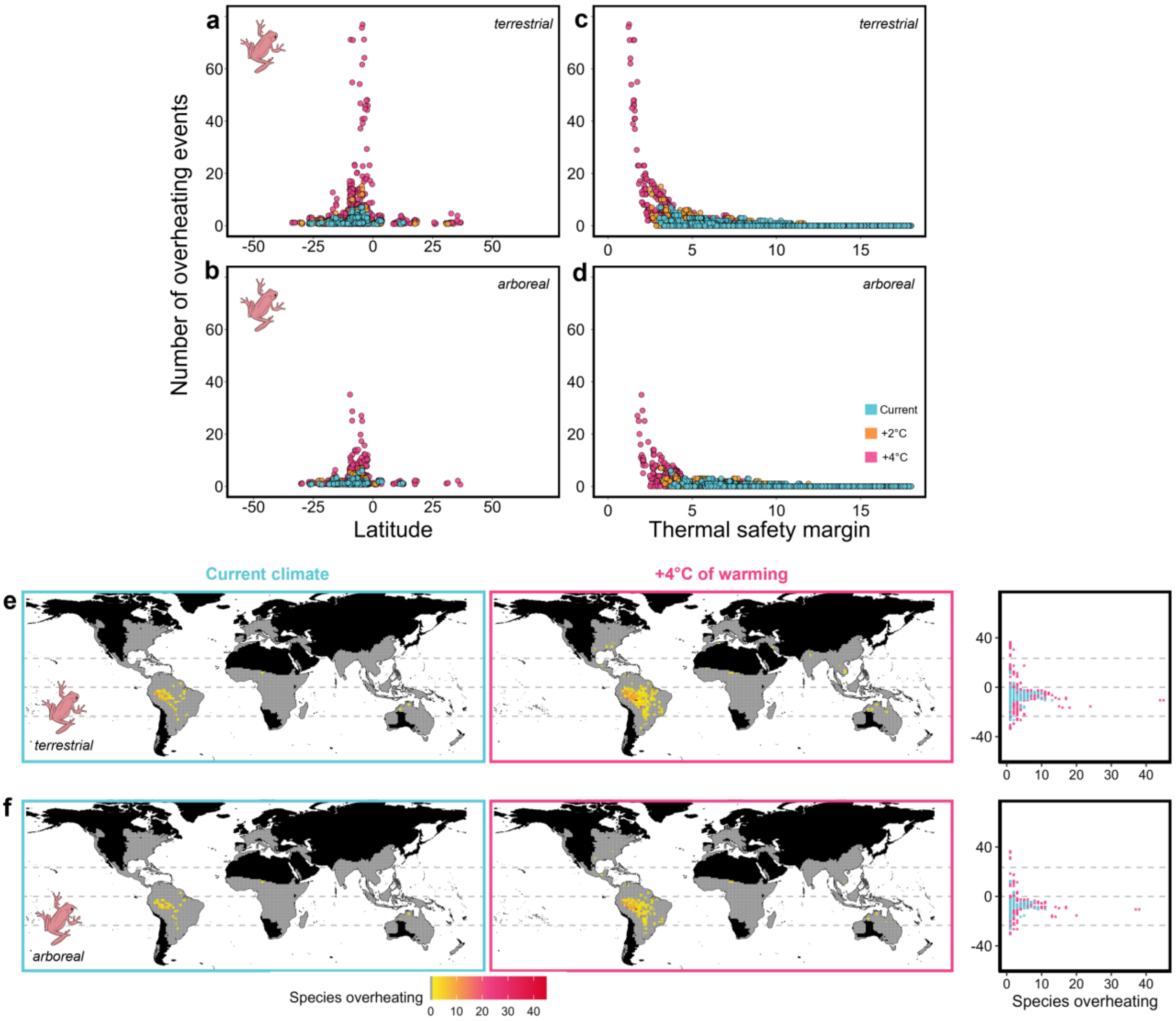
Extended Data Fig. 1 | Conceptual overview of the methods employed to assess the vulnerability of amphibians to global warming.



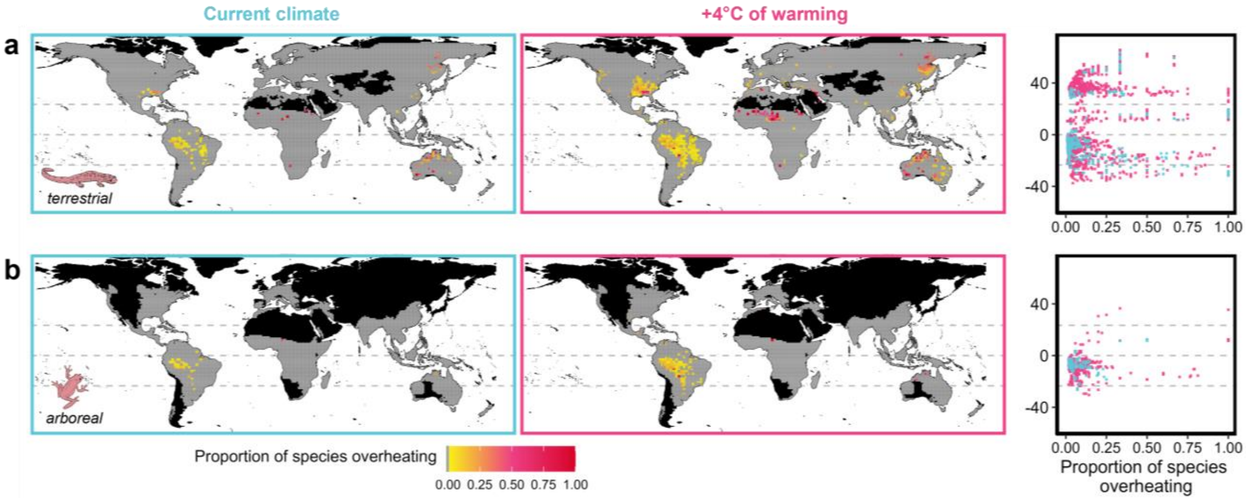
Extended Data Fig. 2 | Accuracy of the data imputation procedure. a) Probability density distributions (n = 375 observations, 77 species) of experimental CT_{max} (blue) and CT_{max} cross-validated using our data imputation procedure (pink). b) Correlation between experimental and imputed CT_{max} values. c) Variation in the uncertainty (standard error, SE) of imputed CT_{max} predictions (outer heat map) across studied (blue) and imputed (grey) species.



Extended Data Fig. 3 | Thermal safety margin, critical thermal maximum, and operative body temperatures in different microhabitats and climatic scenarios. Weighted 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 generalised additive mixed models. Each point represents a species in a given grid cell.



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 species in each grid cell. 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 species predicted to overheat are displayed. The number of arboreal species predicted to experience overheating events terrestrial (e) and arboreal (f) microhabitats in each assemblage 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 assemblage (1-degree grid cell). Black colour depicts areas with no data, and grey colour assemblages 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 assemblage (1-degree grid cell). Black colour depicts areas with no data, and grey colour assemblages 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 for local species occurrences and assemblages 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.

Local species patterns in thermal safety margin

	mean	**CI.lb**	**CI.ub**	**k_{sp}**	**k_{obs}**	**Var_{sp}**	**Var_{phy}**	**Var_{obs}**
Terrestrial (current)	11.694	8.856	14.428	5177	203853			
Terrestrial (+2°C)	10.914	8.025	13.594	5177	203853			
Terrestrial (+4°C)	9.409	6.530	12.090	5177	203853			
Arboreal (current)	12.235	9.402	14.960	1771	56210			
Arboreal (+2°C)	11.517	8.660	14.236	1771	56210	1.295	11.960	1.828
Arboreal (+4°C)	10.073	7.229	12.797	1771	56210			
Aquatic (current)	13.598	10.708	16.276	5203	204808			
Aquatic (+2°C)	12.827	8.796	14.361	5203	204808			
Aquatic (+4°C)	11.682	8.796	14.361	5203	204808			

Assemblage-level patterns in thermal safety margin

	mean	**CI.lb**	**CI.ub**	**k_{obs}**	**Var_{obs}**
Terrestrial (current)	15.279	15.208	15.330	14090	
Terrestrial (+2°C)	14.328	14.279	14.396	14090	
Terrestrial (+4°C)	12.602	12.542	12.657	14090	
Arboreal (current)	14.279	14.191	14.381	6614	11.06
Arboreal (+2°C)	13.393	13.298	13.478	6614	
Arboreal (+4°C)	11.746	11.666	11.830	6614	
Aquatic (current)	17.408	17.352	17.471	14091	
Aquatic (+2°C)	16.528	16.468	16.581	14091	
Aquatic (+4°C)	15.287	15.225	15.346	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 species predicted to experience at least one overheating event (i.e., overheating species) are also depicted. Model estimates for aquatic microhabitats are not displayed because no species 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 species)

	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 species)

	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 assemblages containing at least one species predicted to experience at least one overheating event (i.e., overheating assemblages) are also depicted. Model estimates for aquatic microhabitats are not displayed because no species 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 assemblages)

	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 assemblages)

	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 assemblages containing at least one species predicted to experience at least one overheating event (i.e., overheating assemblages) are also depicted. Model estimates for aquatic microhabitats are not displayed because no species 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 assemblages)

	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 assemblages)

	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 species 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						

Supplementary materials

Supplementary methods

Sensitivity analyses

In this study, we projected CT_{max} 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 (Fig. S7).

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 CT_{max} to investigate the consequences of averaging temperatures when calculating TSMs (Fig. S6). 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 (Fig. S6). 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 the inverse of their sampling variance 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 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 (Fig. S8).

We also investigated the influence of different parameters of our biophysical models (i.e., shade and burrow availability, height in above-ground vegetation, solar radiation, wind speed, pond depth) on predicted vulnerability risks (Fig. S9-11). Specifically, we modelled the responses of the species at highest risk in terrestrial and aquatic conditions, *Noblella myrmecoides,* in its most vulnerable location (latitude, longitude = -9.5, -69.5). For terrestrial conditions, we modelled the response of amphibians with different body sizes (0.5, 4.28, or 50 grams), and with different levels of exposure to open habitat conditions. Specifically, we modelled an amphibian exposed to 50% of shade to simulate an open habitat lightly covered by vegetation, and inferred temperatures at different soil depths (2.5, 5, 10, 15, or 20 cm underground). For aquatic conditions, we adjusted pond depths to simulate a very shallow pond (50 cm) and compared it to deeper ponds (1.5- or 3-meters depth). For arboreal conditions, we modelled the responses of *Pristimantis ockendeni*, in its most vulnerable location (-4.5, -71.5), and adjusted the height in above-ground vegetation (0.5, 2, or 5 meters), the percentage of radiation diffused by vegetation (50%, 75%, or 90% of radiation diffused), and the percentage of wind speed reduced by vegetation (0%. 50%, or 80% of wind speed reduced by vegetation). We did not estimate the influence of these parameters on all species and at all locations because of the scale of our study, but these results should provide insight into how varying microenvironmental features and biological characteristics may impact our general conclusions.

Finally, we compared our predictions of operative body temperatures with field body temperature measurements. We extracted field body temperatures measured for 11 species of frogs in Mexico (21.48° N, -104.85° W; and 21.45° N, -105.03° W) between June and October of 2013 and 2015 from Table 1 of [5]. We chose this study because it provided the data and location of body temperature measurements, covered multiple species from different sites, and matched our study timeframe (2006-2015). We then compare these estimates with hourly operative body temperatures predicted in shaded terrestrial conditions (Fig. S12).

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*[6–218].

Supplementary figures

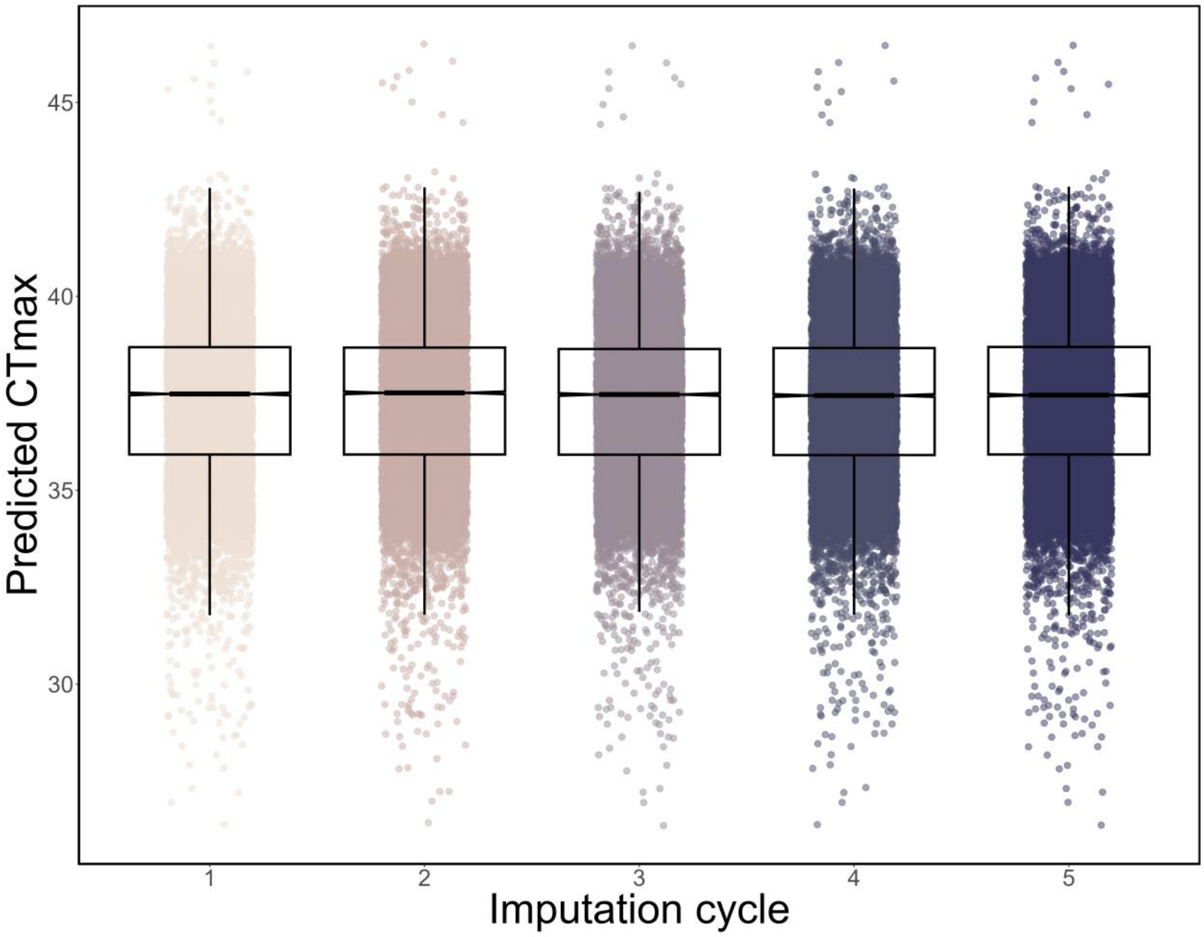


Fig. S1 | Predicted critical thermal maximum (CT_{max}) across imputation cycles. Boxplots depict median (horizontal line), interquartile ranges (boxes), and whiskers extend to 1.5 times the interquartile range.

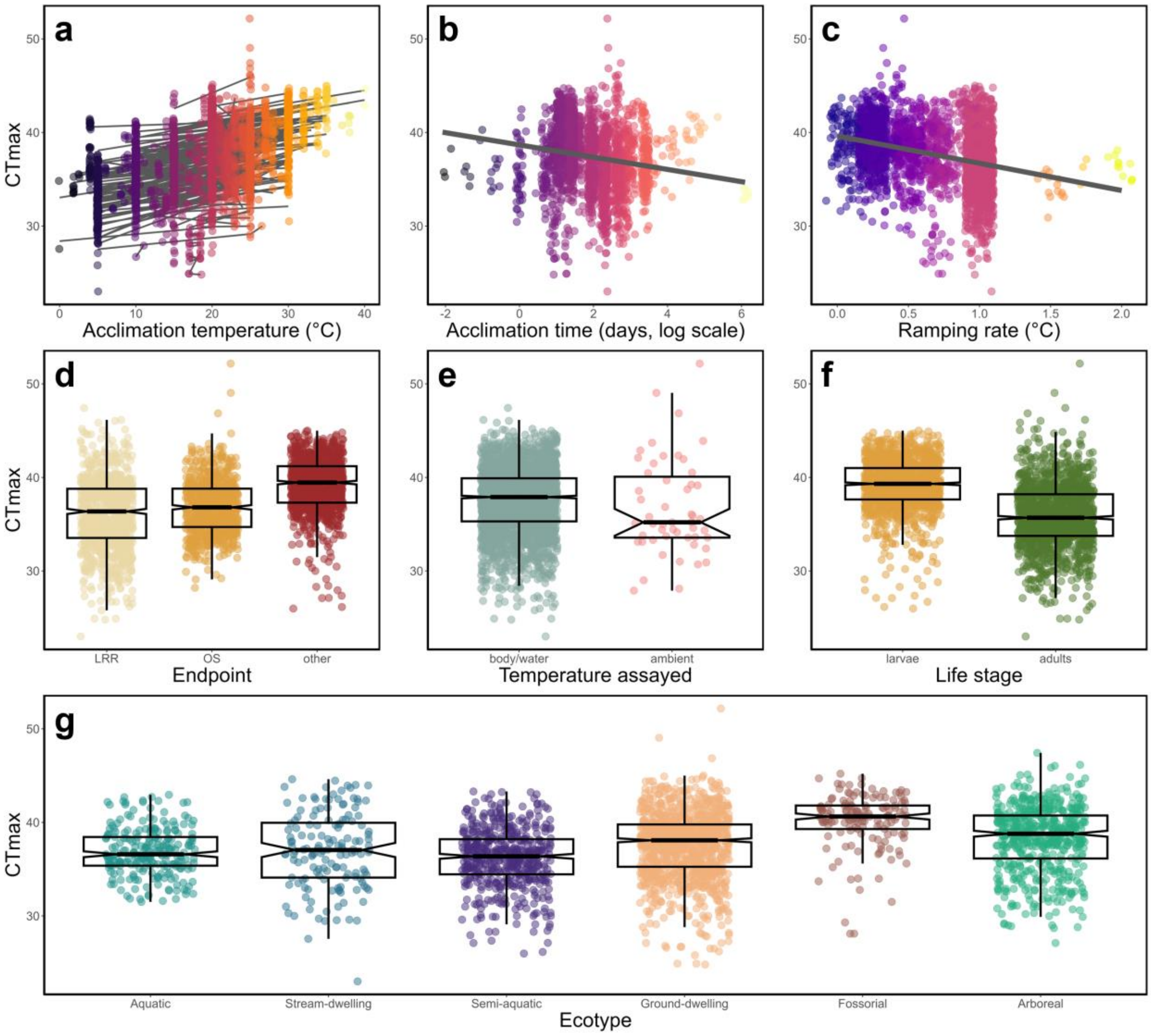


Fig. S2 | Correlations between critical thermal maximum (CT$_{max}$) and predictors used for the imputation. CT$_{max}$ from the experimental dataset was plotted against acclimation temperature (a), acclimation time (b, log scale), ramping rate (c). Colours are proportional to the values of the continuous predictors and the line refers to predictions from a simple linear regression between CT$_{max}$ and the predictors. Individual slopes for each species are depicted for species when CT$_{max}$ was estimated at different acclimation temperatures (a). Depicted is also the variation in CT$_{max}$ with different endpoints (d), media used to infer body temperature (e), life stages (f), and ecotypes (g). Boxplots depict median (horizontal line), interquartile ranges (boxes), and whiskers extend to 1.5 times the interquartile range. LRR: loss of righting response. OS: onset of spasms.

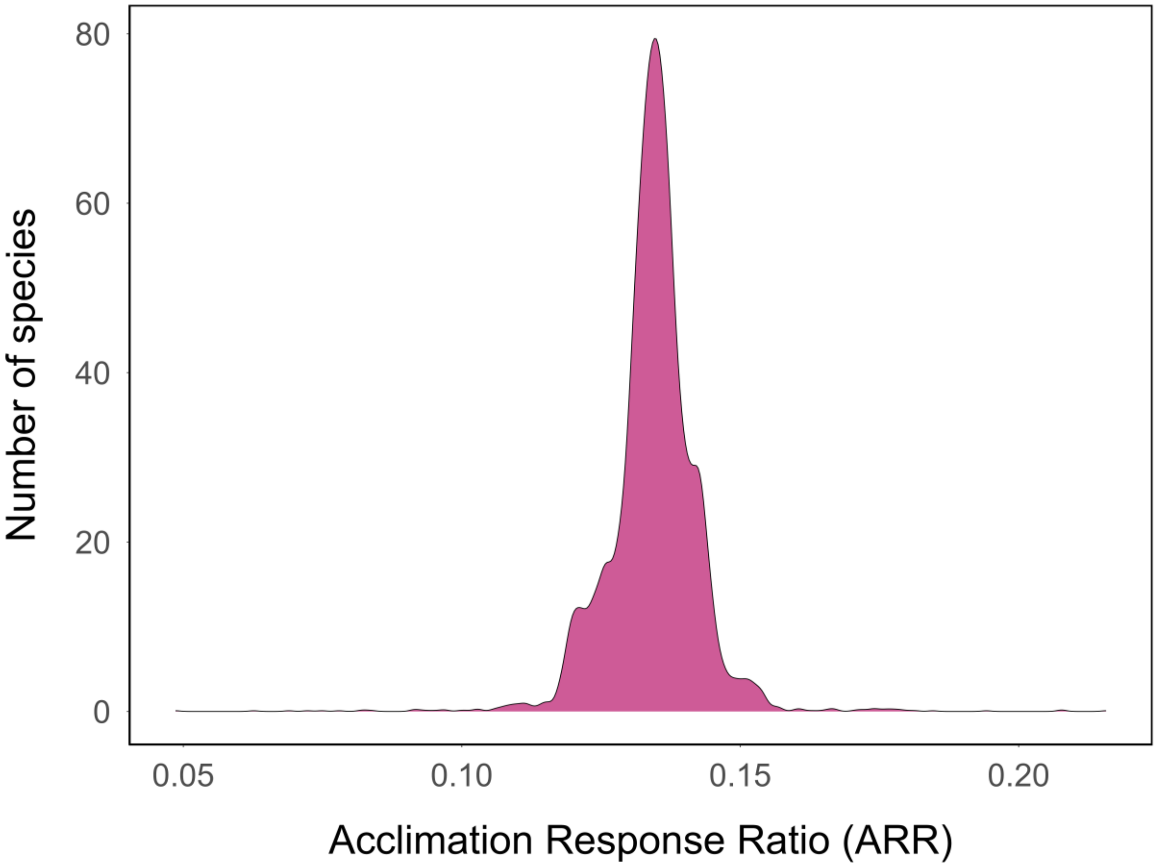


Fig. S3 | Variation in plastic responses across species. The acclimation response ratio (ARR) represents the magnitude change in heat tolerance limits for each degree change in environmental temperature. We found limited variation in ARR (mean ± standard deviation = 0.134 ± 0.008; range = 0.049 – 0.216; n = 5203).

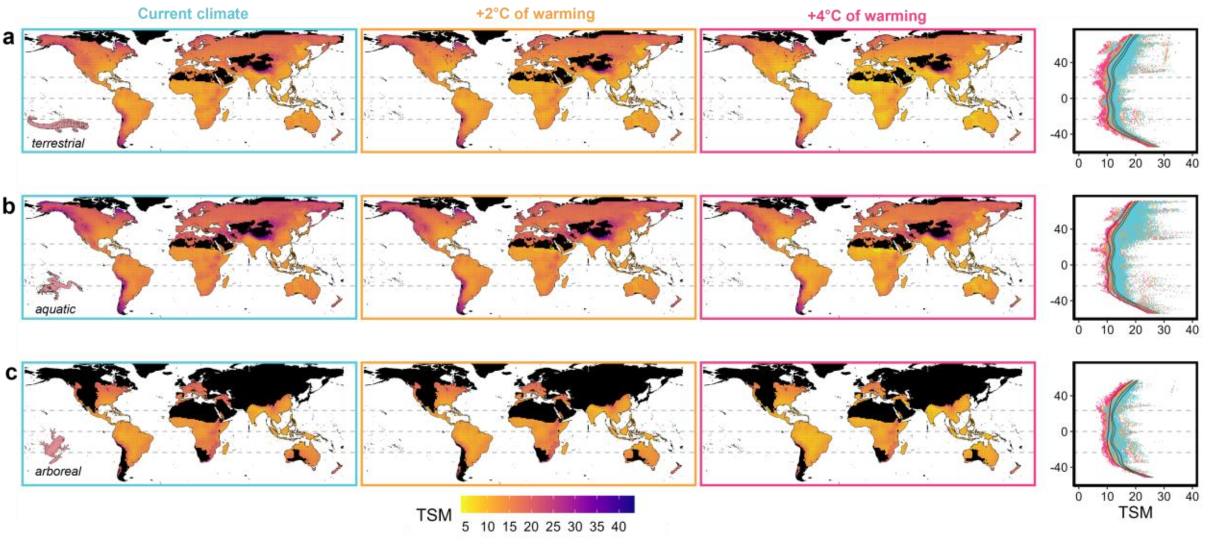


Fig. S4 | Assemblage-level patterns in thermal safety margin for amphibians on terrestrial (a), aquatic (b), or arboreal (c) microhabitats. Thermal safety margins (TSM) were calculated as the mean difference between CT_{max} and the predicted operative body temperature in full shade during the warmest quarters of 2006-2015 in each assemblage (1-degree grid cell). Black colour 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.

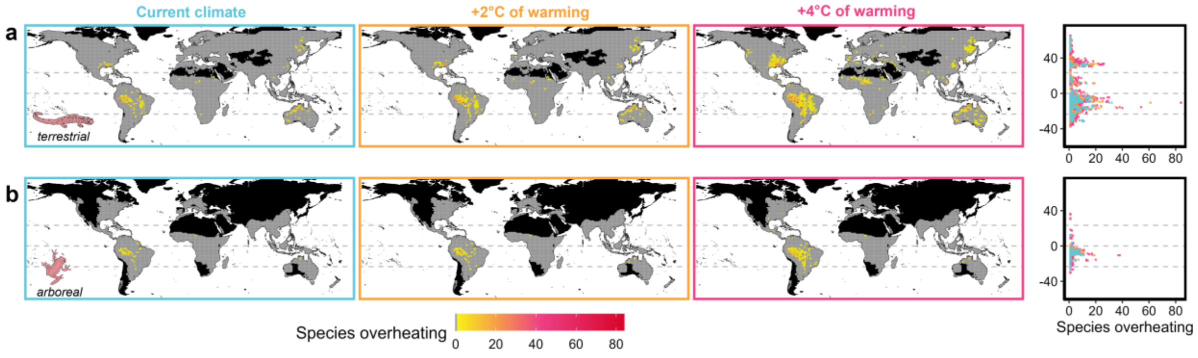


Fig. S5 | Number of species predicted to experience overheating events in terrestrial (a) and arboreal (b) microhabitats. The number of species overheating was assessed as the sum of species overheating at least once in the period surveyed (warmest quarters of 2006-2015) in each assemblage (1-degree grid cell). Black colour depicts areas with no data and grey colour assemblages 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.

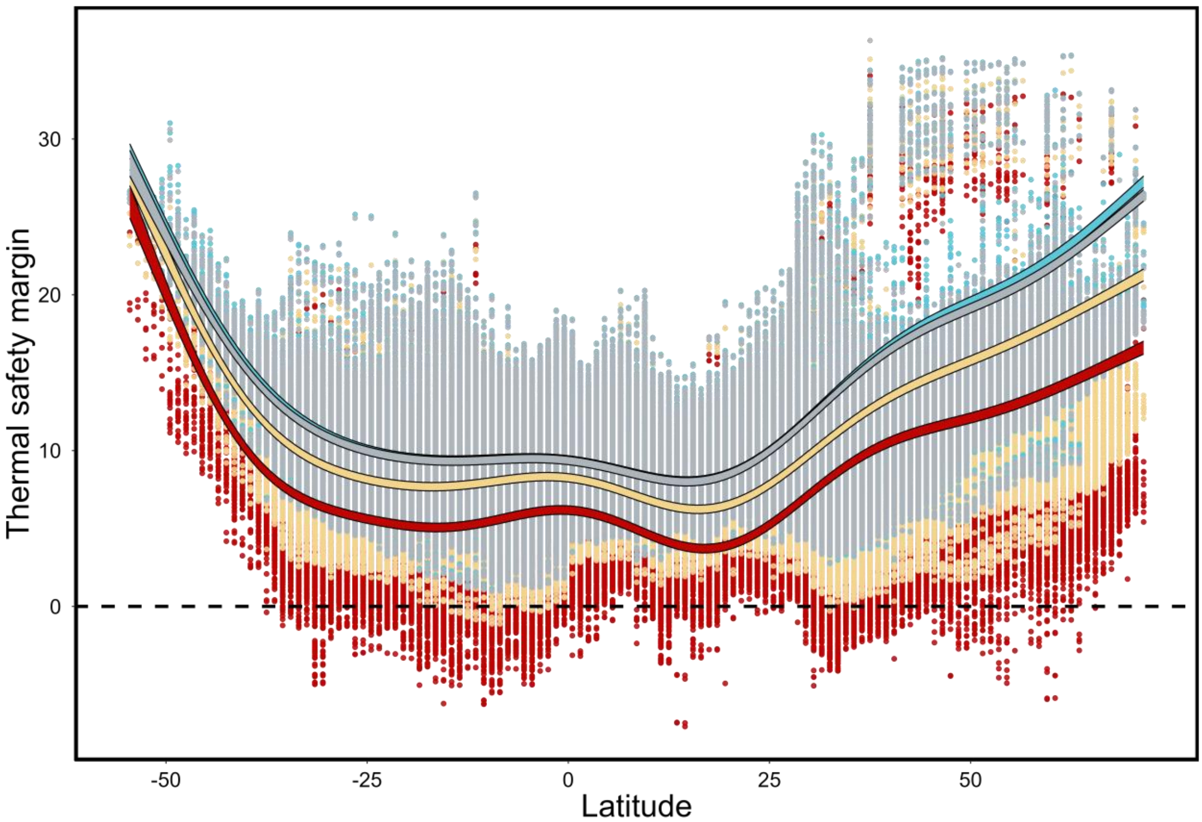


Fig. S6 | Variation in thermal safety margins calculated using different assumptions. Thermal safety margins (TSM) were calculated as the mean difference between CT_{max} and the predicted operative body temperature in full shade during the warmest quarters of 2006-2015 (grey), as the mean difference between CT_{max} 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 CT_{max} (yellow), or as the difference between the maximum operative body temperature and the corresponding CT_{max} (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.

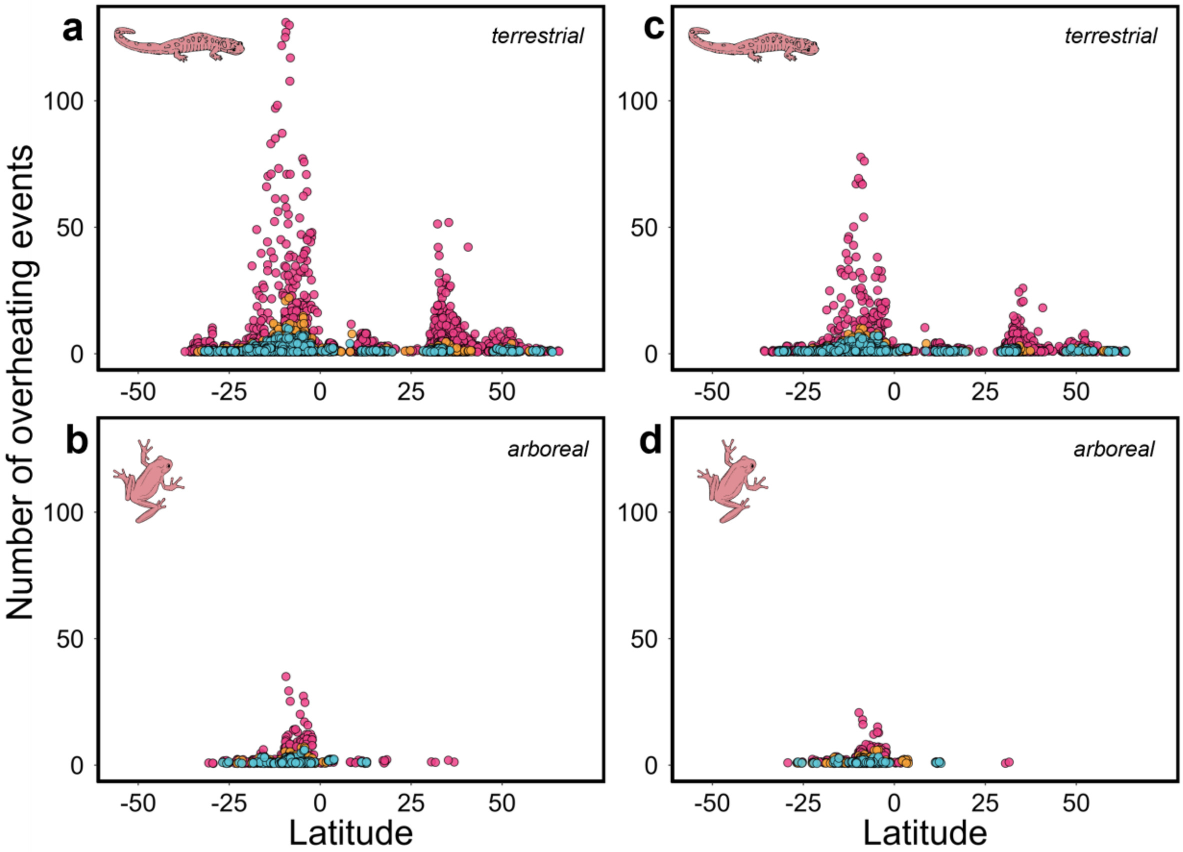


Fig. S7 | Latitudinal variation in the number of overheating events when animals are acclimated to the mean (a,b) or maximum (c,d) weekly body temperature experienced in the seven days prior in terrestrial (a,c) and arboreal (b,d) microhabitats. The number of overheating events (days) were calculated as the sum of overheating events (when daily maximum temperatures exceeded CT_{max}) during the warmest quarters of 2006-2015 for each species in each grid cell. 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 species predicted to experience overheating events across latitudes are depicted.

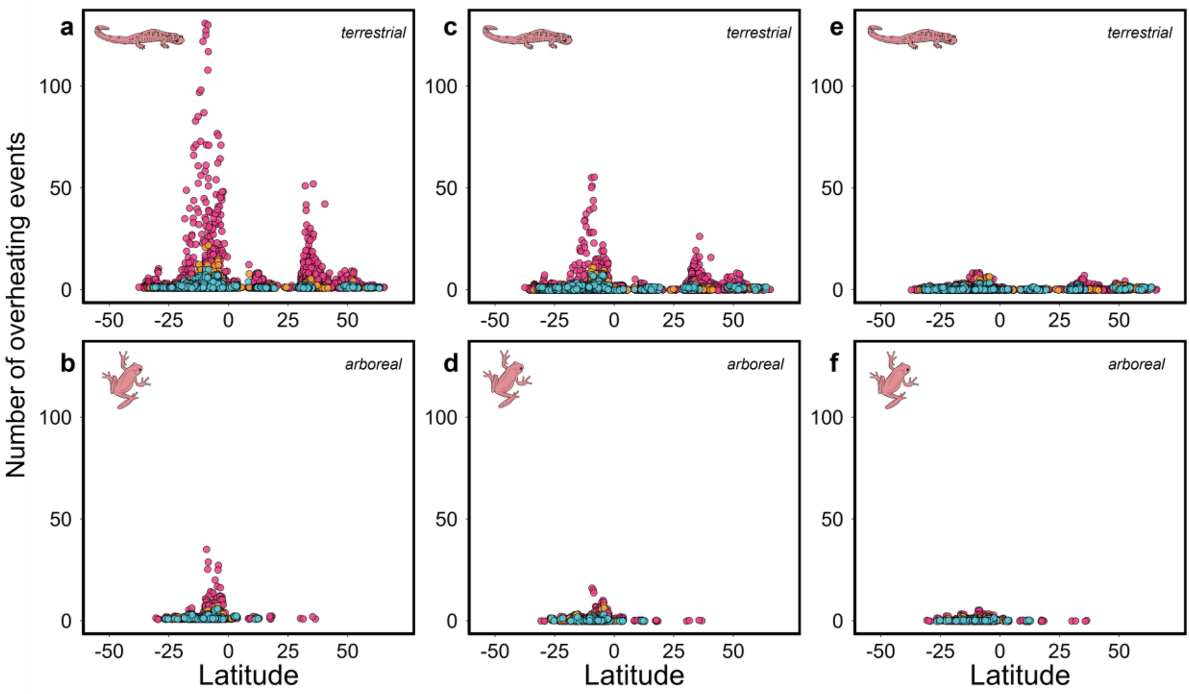


Fig. S8 | Latitudinal variation in the number of overheating events using regular (a,b) or conservative estimates (c,d,e,f) in terrestrial (a,c,e) and arboreal (b,d,f) microhabitats. The number of overheating events (days) were calculated as the sum of overheating events (when daily maximum temperatures exceeded CT_{max}) during the warmest quarters of 2006-2015 for each species in each grid cell. Conservative estimates are those where overheating events were counted only when operative body temperatures exceeded 50% (c,d) or 95% (e,f) of the predicted distribution of CT_{max}. 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 species predicted to experience overheating events across latitudes are depicted.

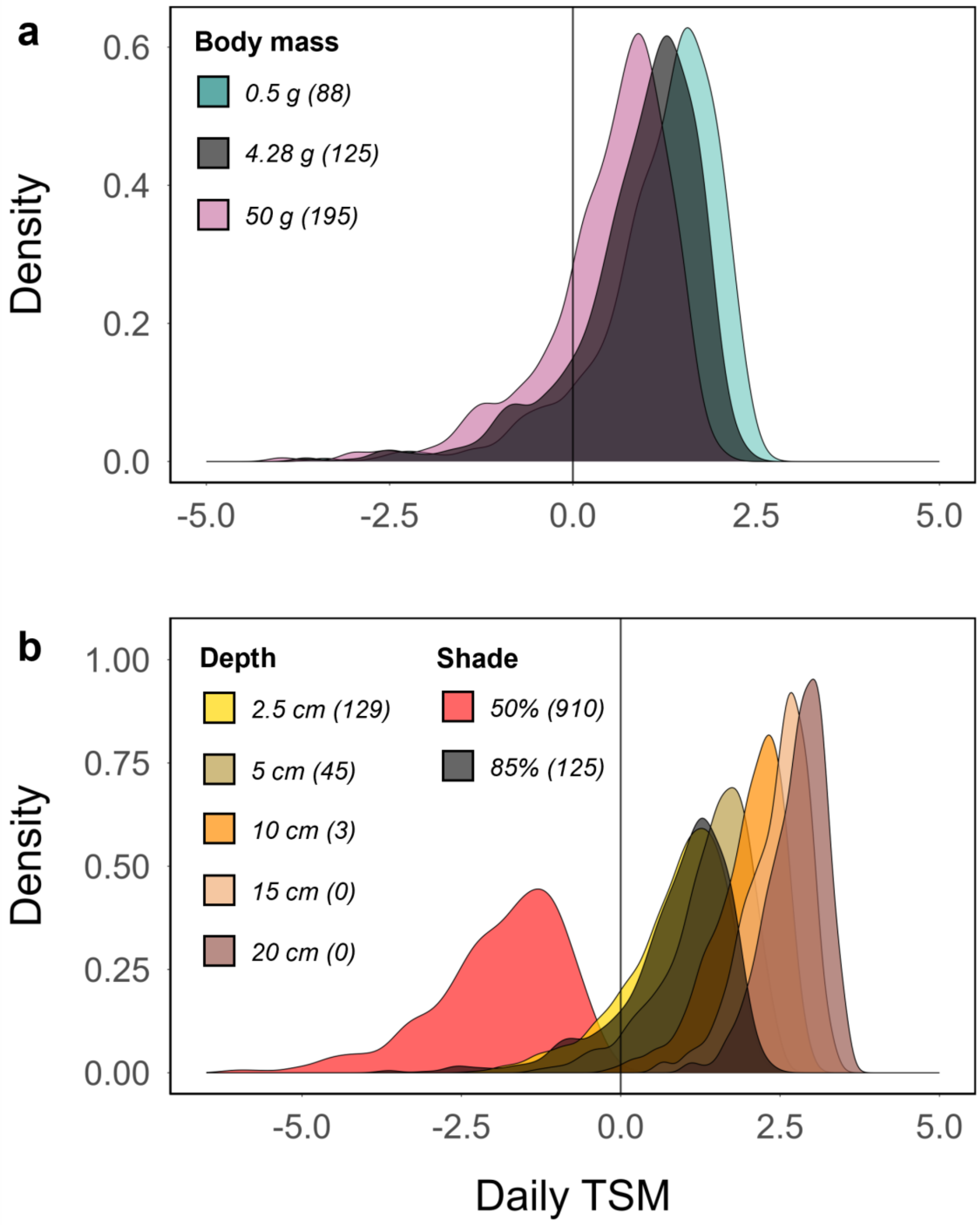


Fig. S9 | Influence of biophysical model parameters on the estimation of terrestrial thermal safety margins. Depicted is the variation in daily thermal safety margins (TSM) as density distributions according to body mass (a), shade availability and soil depth (b). All simulations were performed assuming 4°C of global warming above pre-industrial levels in a specific grid cell (latitude, longitude = -9.5, -69.5; where the highest number of overheating events was predicted), for the most vulnerable species (*Noblella myrmecoides*). Negative daily TSMs were recorded as overheating events, and conditions depicted in dark grey reflect the results presented in the manuscript. The number of predicted overheating events is indicated in brackets for each condition.

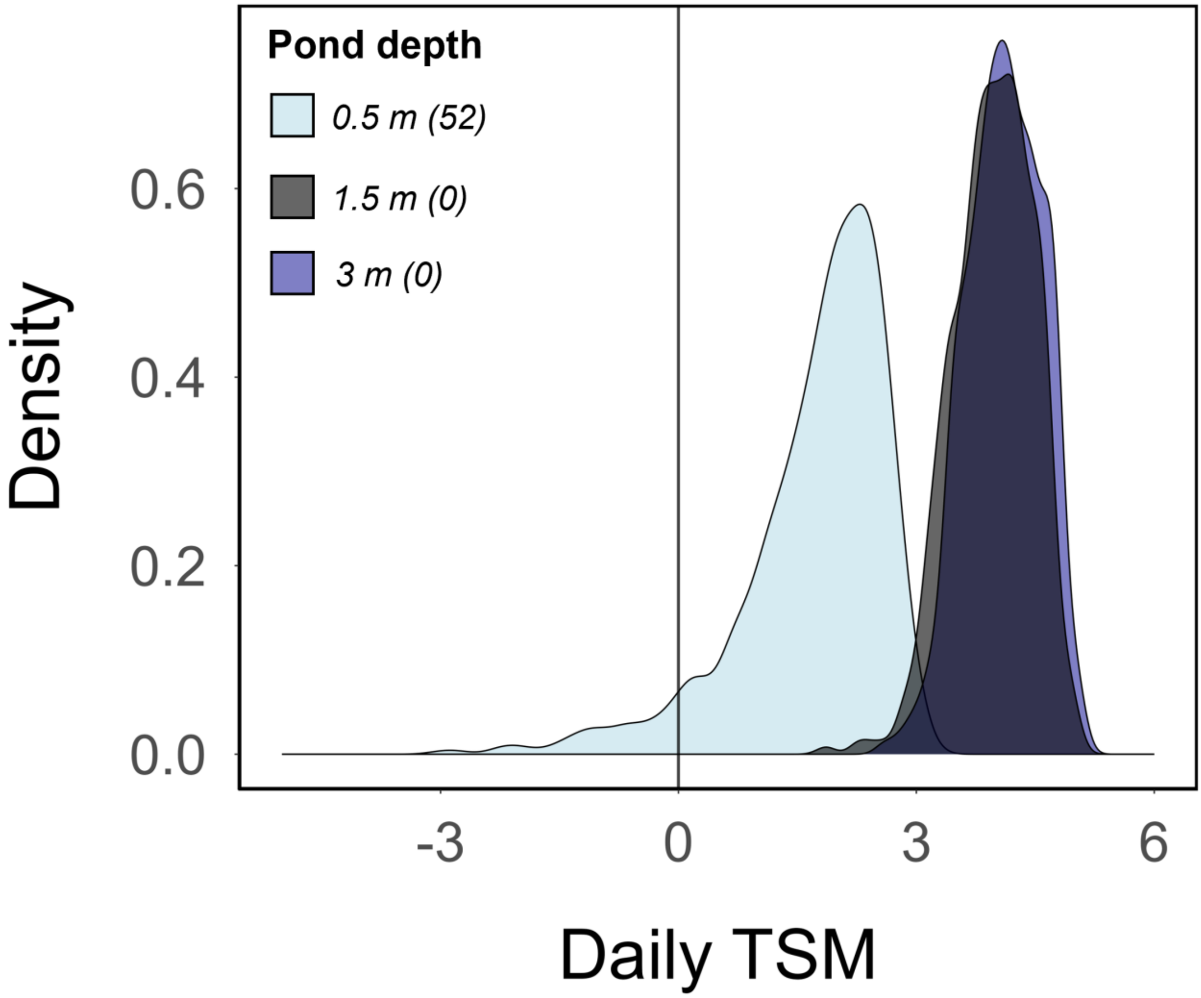


Fig. S10 | Influence of pond depth on the estimation of aquatic thermal safety margins. All simulations were performed assuming 4°C of global warming above pre-industrial levels in a specific grid cell (latitude, longitude = -9.5, -69.5; where the highest number of overheating events was predicted), for the most vulnerable species (*Noblella myrmecoides*). Depicted is the variation in daily thermal safety margins (TSM) as density distributions. Negative daily TSMs were recorded as overheating events, and conditions depicted in dark grey reflect the results presented in the manuscript. The number of predicted overheating events is indicated in brackets for each condition.

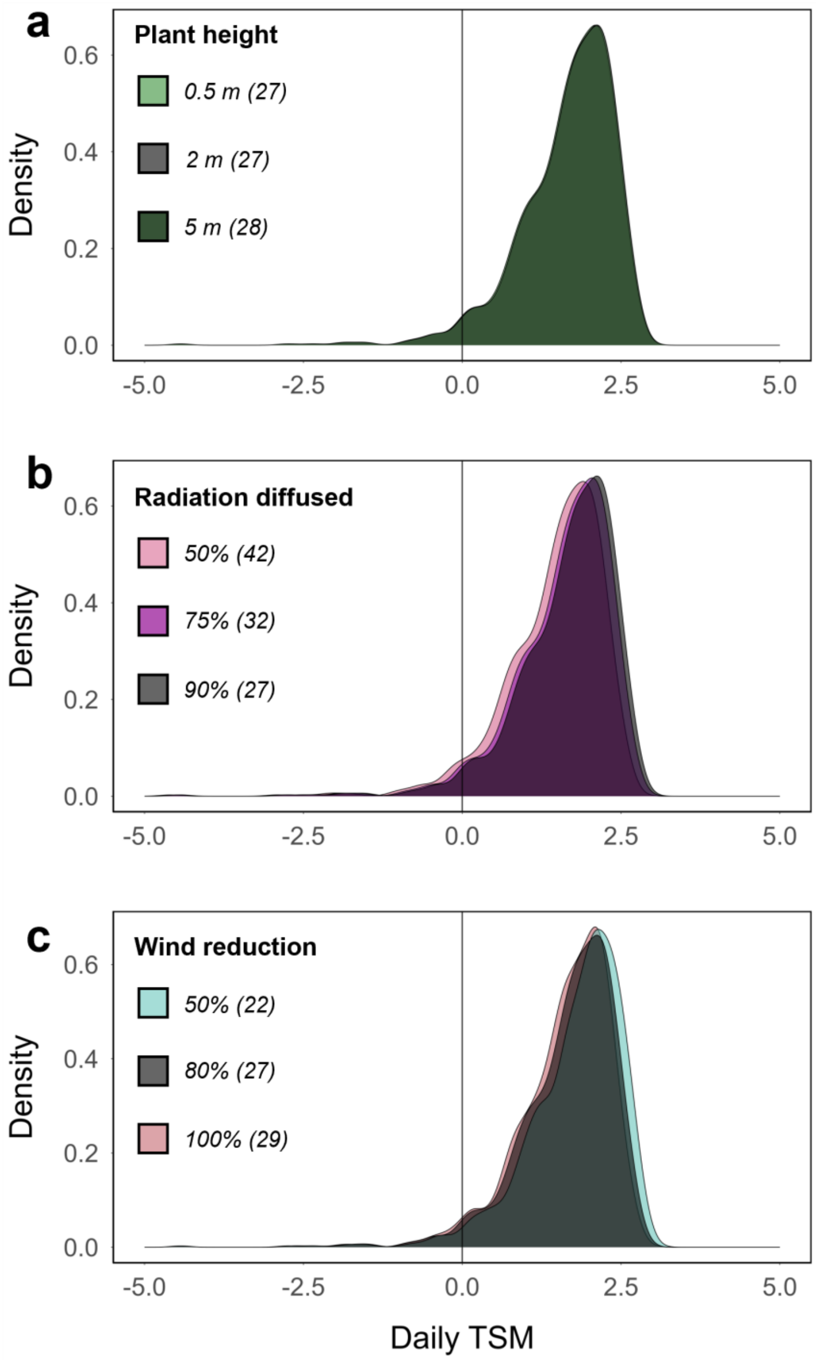


Fig. S11 | Influence of biophysical parameters on the estimation of aquatic arboreal safety margins. All simulations were performed assuming 4°C of global warming above pre-industrial levels in a specific grid cell (latitude, longitude = -9.5, -69.5; where the highest number of overheating events was predicted), for the most vulnerable arboreal species (*Pristimantis ockendeni)*. Depicted is the variation in daily thermal safety margins (TSM) as density distributions according to height of the animal in above-ground vegetation (a), the percentage of solar radiation diffused by vegetation (b) and the percentage of wind reduced by vegetation (c). Negative daily TSMs were recorded as overheating events, and conditions depicted in dark grey reflect the results presented in the manuscript. The number of predicted overheating events is indicated in brackets for each condition.

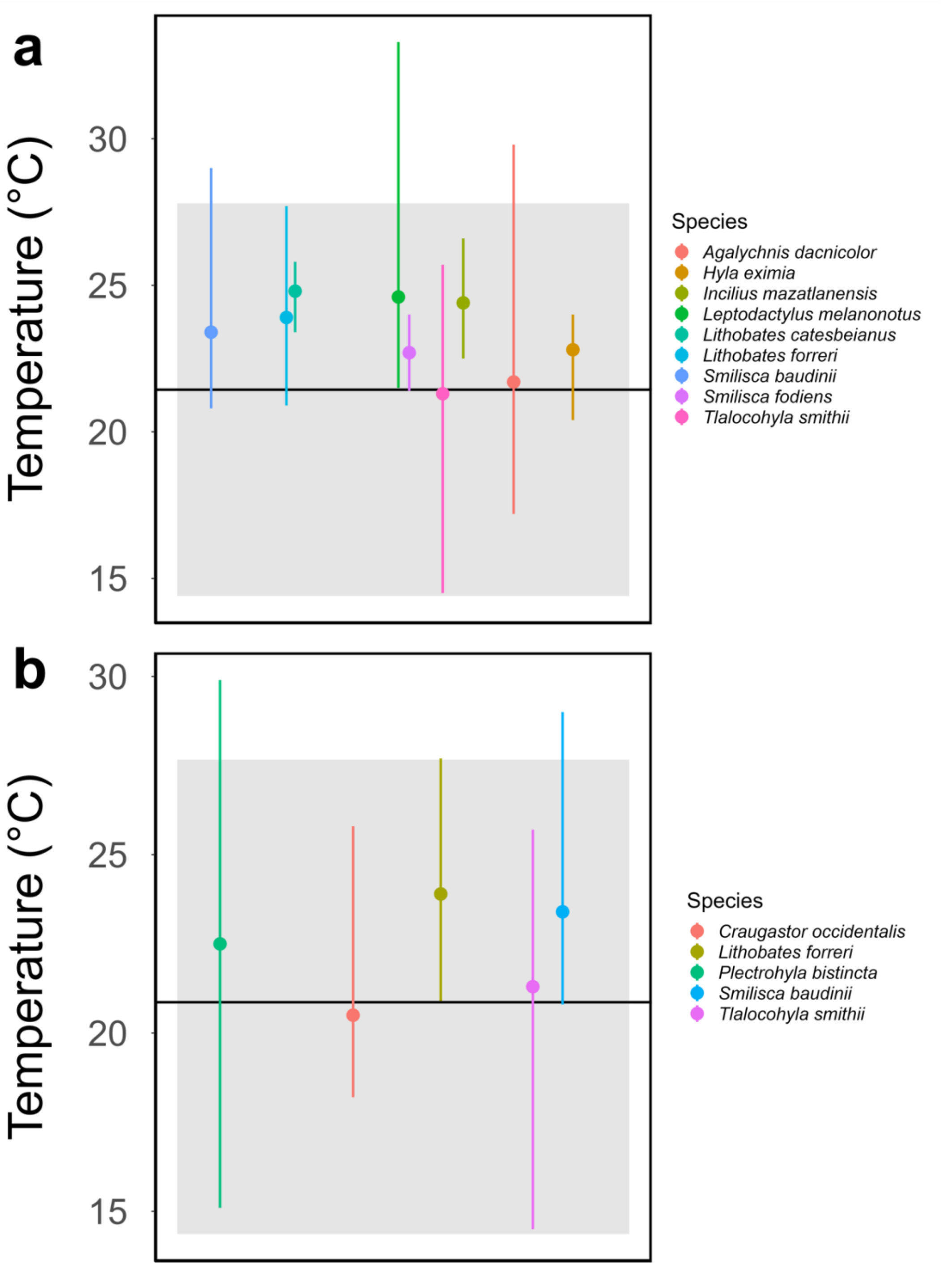


Fig. S12 | Validation of operative body temperature estimations. Terrestrial operative body temperatures estimated from biophysical models were compared to field body temperatures recorded around Tepic (21.48° N, -104.85° W; panel a) and El Cuarenteño (21.45° N, -105.03° W; panel b) between June and October of 2013/2015, for 11 species of frogs[5]. The range of hourly operative body temperatures predicted from our models are presented by the grey boxes and the mean by the black horizontal line. The mean (point) and range (bars) of field body temperatures recorded for each species are presented in colour.

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