



RESEARCH PAPER

Novel physiological data needed for progress in global change ecology

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Abstract

Studies examining the underlying causes of the distributions of species and their future trajectories under climate change have benefitted from the accumulation of measurements of thermal tolerance across the tree of life. However, gaps in the global coverage of heat-tolerance data for ectotherms persist on four critical fronts. First, most large-scale analyses treat heat tolerance as a fixed species trait despite that population-level variation can equal or exceed cross-species variation. Second, terrestrial non-arthropod invertebrates and aquatic ectotherms other than bony fish have been poorly sampled, particularly in boreal and tropical regions, the Indian Ocean and the mesopelagic-deep ocean. Third, the study of climate impacts on the heat tolerance of terrestrial ectotherms has often neglected the interaction of environmental temperatures with water availability. And fourth, the mechanisms driving the dependence of heat tolerance on oxygen supply-demand remain largely unknown. We contend that filling those data and knowledge gaps requires novel strategies for the ecophysiological sampling of the range of understudied populations and species that occupy the length of climatic gradients globally. Such developments are essential for comprehensively predicting species responses to climate change across aquatic and terrestrial biomes.

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Introduction

Thermal tolerance refers to an organism's capacity to adjust its physiology to changes in environmental tempera-

tures, with 'heat tolerance' and 'cold tolerance' referring to tolerance to high and low temperatures, respectively (Pörtner, 2002). The growing body of measurements of thermal tolerance across the tree of life and the Earth's biomes (Bennett et al., 2018) has become a formidable asset to examine climatic effects on biodiversity (Huey et al., 2012; Somero, 2012), and an active interface linking the fields of ecology and physiology after decades of little cross-disciplinary, large-scale research (Gaston et al., 2009; Huey, 1991).

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Large-scale ecophysiological studies typically investigate patterns of thermal tolerance as a function of climatic, phylogenetic and/or geographic predictors at broad spatiotemporal scales and across multiple species, in which heat tolerance is amply used as the response or an element of composite responses like ‘safety margins’ (Sunday et al., 2014), ‘warming tolerance’ (Deutsch et al., 2008), ‘acclimation response ratio’ (Morley et al., 2019) or ‘thermal sensitivity’ (Bennett et al., 2019) — each entailing its own conceptual nuances. For instance, safety margins measure the difference between the temperature an animal experiences in natural conditions and the maximum temperature it can tolerate in stressful conditions. Overall, species with narrow safety margins should be less tolerant of thermal variation in their environment, and the closer a species lives to its upper thermal limits the higher the chances of experiencing thermal stress.

Large-scale research has resulted in three outstanding hypotheses about clines of thermal traits amongst ectothermic fauna. First, when the availability of thermal refugia is accounted for, marine species show narrower safety margins than terrestrial species, suggesting more frequent extinctions and faster species turnover in the oceans than on land under current and future warming scenarios (Pinsky et al., 2019). Second, terrestrial ectotherms from temperate and tropical latitudes are frequently exposed to air temperatures above their tolerance limits (Lancaster, 2016), leading to the postulate that thermoregulatory behaviour like evaporative cooling (Sunday et al., 2014) and/or access to thermal microrefugia (Suggitt et al., 2018) are obligate strategies for ectotherms to cope with climate warming. And third, heat tolerance is less variable than cold tolerance (Araújo et al., 2013), giving rise to the prediction that heat tolerance has lower evolutionary potential than cold tolerance (Bennett et al., 2021; Hoffmann et al., 2013; Qu & Wiens, 2020). The former body of research rests on a diverse kit of analytical approaches that are commonplace in modern macrophysiological (Chown & Gaston, 2016) and biogeographical (Viole et al., 2014) research.

While sophisticated modelling of macrophysiological data has provided refreshing insights into the dynamics of species ranges, and enabled the formulation of new hypotheses about the mechanisms underlying these dynamics, we highlight that prevailing data gaps must be circumvented to ascertain the generality of observed large-scale patterns in the following major domains:

- (1) Large-scale studies use subsets of the same type of data, namely one estimate of thermal performance per species across hundreds to thousands of taxa with the underlying premise that variation amongst species overrides variation amongst populations and/or intra-specific variation has negligible impacts on overall patterns.
- (2) Heat tolerance is best known for terrestrial vertebrates from temperate regions, and such body of knowledge underrepresents the potential magnitude of variation of heat tolerance through different regions and across the tree of life.

- (3) The study of heat tolerance under climate change has mainly looked at the effects of environmental temperatures despite climate change having multiple, non-independent axes of variation in both aquatic and terrestrial ecosystems.

With a focus on the heat tolerance of ectothermic fauna, we provide a synthetic background on measurements of heat tolerance, then describe the data gaps mentioned above, and highlight the ecophysiological importance of the interaction of environmental temperatures with two other axes of environmental variation: water availability on land and oxygen availability at sea. Throughout, we recommend key areas of future development.

Quantifying heat tolerance

Measurements

Metrics of heat tolerance used in large-scale ecology originate from a long history of physiological experiments undertaken for more than two centuries. Davenport and Castle (1895) pioneered a comprehensive collation of measurements dating back to the physiologist Lazzaro Spallanzani (1787). The first systematic protocols of those measurements were developed in the 1940s (Cowles & Bogert, 1944; Fry et al., 1942) and 1950s (Hutchison, 1961; Lowe & Vance, 1955). These protocols laid the basis of a massive scientific effort surveying thermal tolerance across the Earth, with measurements being assembled into the recently developed global database GlobTherm (Bennett et al., 2018; Fig. 1). This database is the only available quantitative synthesis of the state of knowledge of thermal tolerance across taxa and habitats, and much of our data analysis rests on this resource. Succinctly, GlobTherm (accessed on December 2021) includes heat tolerance for 1631 eukaryotic species, of which 946 are ectotherms, the earliest being published in the mid-20th century (Doudoroff, 1942).

Methods for measuring heat tolerance in ectotherms can be classified as either static or dynamic — these categories depend on whether test temperatures are kept constant or increased through an experimental assay, respectively. The static method defines heat tolerance as the *time* to death (or the *survival rate* after a predefined time) under constant environmental temperatures, and the dynamic method defines heat tolerance as the *body temperature* at which physiological failure, and possibly death, occur under ramping environmental temperatures (Jørgensen et al., 2019; Lutterschmidt & Hutchison, 1997b) — methodological jargon and concepts associated with heat tolerance are reviewed by Bates and Morley (2020). The dynamic method is currently the preferred option in global studies because it is replicable, can be easily implemented, and has clear biological interpretation (Kingsolver & Umbanhowar, 2018). Accordingly, all heat tolerances in GlobTherm are dynamic estimates (Bennett et al., 2018).

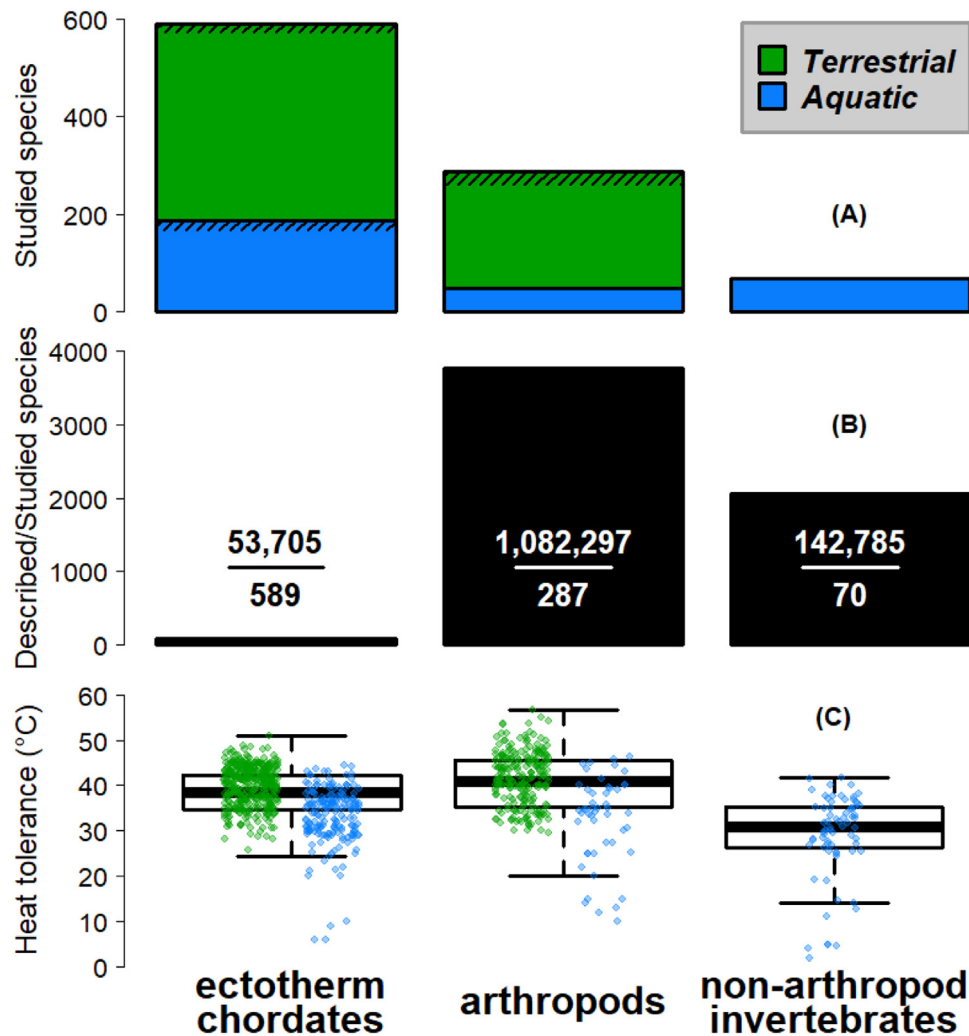


Fig. 1. How much is known and unknown about ectotherm tolerance to high temperatures? The known (A) is the number of ectotherm chordates (vertebrates plus three ascidians) and (arthropod and non-arthropod) invertebrate species for which heat tolerance (critical thermal maxima and upper lethal temperatures) has been quantified according to the database GlobTherm (Bennett et al., 2018) — line texture within bars indicates the number of species for which heat tolerance has been measured in >1 population or experiment. The unknown (B) is the proportion of taxonomically described (upper numbers) to studied (lower numbers) species. The bottom panel (C) shows heat tolerance across species where each dot represents one species included in GlobTherm. Number of described species accessed from www.catalogueoflife.org on 20/03/2020, and ‘aquatic’ refers to species spending their entire life cycle in water. Significance: Terrestrial, chordate and species-level data outnumber aquatic, invertebrate and population-level data, respectively, and upper limits of known thermal tolerance range from ~0 to ~60 °C across species.

The dynamic method broadly comprises a duet of procedural steps. Immediately after capture, or following rearing in the laboratory, specimens are acclimated to a common range of daily temperatures in experimental enclosures for hours to days, depending on the thermal biology of the organism in question. The goal is to remove individual differences in thermal and ecological history and standardize experimental starting temperatures (Brattstrom & Lawrence, 1962; Terblanche et al., 2007). Specimens are then exposed to ramping temperatures, and heat tolerance is quantified as (i) *upper lethal temperature* or the temperature that results in the death of an individual or a proportion of individuals (e.g., 50%, 100%), or (ii) *critical thermal maximum* or the

temperature at which body function is blocked (e.g., cardiac failure, loss of righting response) or shows symptoms of thermal stress like muscular spasms (Bates & Morley, 2020; Lutterschmidt & Hutchison, 1997b). For endotherms, heat tolerance is also often quantified as the *upper critical temperature* of the ‘thermoneutral zone’ at which an organism’s metabolism increases above basal metabolic rates and prompts body-heat dissipation to the environment (Riek & Geiser, 2013).

Ectotherm heat and cold tolerance are characterized as the endpoints of a left-skewed, bell-shaped performance curve centred around a peak demarcating the thermal optimum (Huey & Stevenson, 1979; Sinclair et al., 2016). The

magnitude of this optimum, its associated endpoints, and the overall shape of the thermal performance curve can vary for a range of biological processes such as body growth, aerobic scope, reproduction or locomotion, each process operating at specific temporal scales and tailored to address different research questions (Bozinovic et al., 2020; Kellermann et al., 2019; Kingsolver & Buckley, 2017). From an ecophysiological viewpoint, dynamic measurements of heat tolerance are manifestations of the pathways driving whole-organism failure at molecular, cellular and tissue scales — a form of ‘functional mortality’, which has proved robust for examining large-scale clines of thermal tolerance (Bates & Morley, 2020).

Species-level data: gaps and improvements

The average estimate of ectotherm heat tolerance across the tree of life captured by GlobTherm (Bennett et al., 2018) represents a single population of a species of terrestrial vertebrate from a temperate climate. Indeed, ectotherm heat-tolerance data in this database (comprising critical thermal maxima and lethal temperatures) are positively biased towards large ectothermic vertebrates from temperate regions, reflecting similar clustering across the whole ecological literature (Hughes et al., 2021; Taheri et al., 2021; Titley et al., 2017). Taxonomically, 62% of estimates in GlobTherm are from chordate species, while 30% and <8% represent arthropods and non-arthropod invertebrates (Fig. 1B). When compared to the total number of described species, such bias becomes strikingly obvious since heat tolerance has been measured in one of every 91 described species of chordate ectotherms as opposed to only one of every 3800 and 2100 described arthropod and non-arthropod invertebrate species, respectively (Fig. 1B). Geographically, a total of 25% and 65% of heat-tolerance traits of ectothermic species have been obtained from tropical (–23.5 South to 23.5° North) and temperate regions (23.5 to 66.5° North/South), respectively, with only 10% of data originating from boreal and polar latitudes (Bennett et al., 2018). And habitat-wise, only 32% of the ectothermic species contributing heat-tolerance estimates to GlobTherm spend their entire life cycle in aquatic environments (Fig. 1A and C), with marine outnumbering freshwater estimates (Bennett et al., 2018). This proportion is even smaller in published comparisons of ectotherm safety margins between the marine and terrestrial realms (Pinsky et al., 2019). In fact, there are few, if any, studies of heat tolerance for most invertebrate phyla comprising obligate marine species.

All eukaryotes are unable to complete their life cycle at temperatures beyond 60 °C (Oren, 2019), and a major revision of that absolute threshold of thermal tolerance is unlikely, with only hydrothermal vent worms known to prefer temperatures above 40 °C (Girguis & Lee, 2006). However, expanding the taxonomic coverage of species-level heat-tolerance data (see Chown & Gaston, 2016), primarily

for terrestrial non-arthropod invertebrates and aquatic ectotherms other than bony fish, should provide a comprehensive global picture of the cross-species variation of heat tolerance and how the latter responds to climatic variation in terrestrial relative to aquatic habitats. The ability to capture global patterns of physiological traits also requires further data-collection efforts being directed to the parts of the planet where thermal tolerance across ectothermic species has been poorly surveyed, namely the boreal stretch of Canada and Russia, the African and Asian tropics, the Indian Ocean and the poles (Bennett et al., 2018), and the entire mesopelagic and deep ocean. These include some of the world’s most thermally extreme areas. So, measurements of thermal traits of understudied or neglected species from those regions under such circumstances are critical to understand thermal-trait plasticity and behavioural and genetic adaptations to climate extremes at regional to global scales. These novel efforts are all the more important as comparing climate-driven poleward or latitudinal shifts in global species distributions across continents is bound to miss multidirectional climate impacts within regions in terrestrial (Heikkinen et al., 2020; Seabra et al., 2015; Taheri et al., 2016; VanDerWal et al., 2013) and marine ecosystems (Helmut et al., 2002; Lathlean et al., 2014; Rilov et al., 2019).

Population-level data: why more matters

More data of species-level thermal traits will continue to refine global patterns of species responses to climate change. We argue, nevertheless, that ascertaining the biological realism of estimated patterns, and developing a mechanistic understanding of the drivers governing them, must be boosted by the collection of population-level heat-tolerance data over the full geographical distribution of individual species, because species operate in thermally-dynamic geographic spaces (Sears et al., 2016). A salient feature of GlobTherm is that >90% of thermal-tolerance measurements have been obtained from a single experiment and/or study population per species (Bennett et al., 2018; Fig. 1A). This data format restricts the analysis of thermal performance to a single data point per species. However, each of those data points (species) has a biologically meaningful variance and, if accounted for, it could largely determine the magnitude and uncertainty of thermal-tolerance estimates. When applied to models predicting climate change effects on species distributions, such variance can lead to substantially different projections (Valladares et al., 2014). Indeed, thermal traits within ectothermic species can vary at multiple spatiotemporal scales in aquatic and terrestrial habitats (Clusella-Trullas & Chown, 2014; Garland & Adolph, 1991), thus altering measured ectotherm responses to climate change (Bennett et al., 2019; Sinclair et al., 2016; Valladares et al., 2014). For instance, intra-specific variation in heat tolerance of Iberian lizards can be up to 4 °C amongst different populations (Herrando-Pérez et al., 2019; Fig. 2A). A 4 °C

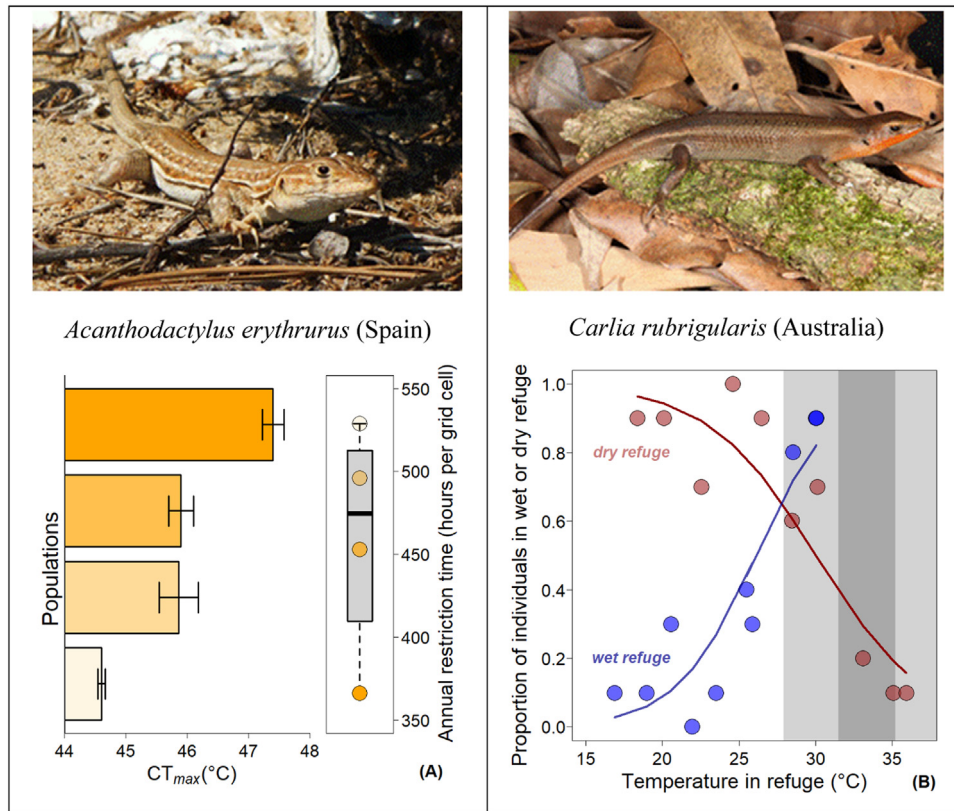


Fig. 2. Intra-specific variability in heat tolerance and thermo-hydropregulatory behaviour. Barplots (A) show critical thermal maxima (mean $CT_{max} \pm SE$, $N = 5$ to 7 lizards per population, estimated as the temperature at which the body-righting response is lost) of four Spanish populations of the spiny-footed lizard (*Acanthodactylus erythrurus* from, top to bottom bars, Doñana National Park, Los Santos, Alpedrete and Aranjuez), and boxplot shows restriction times (grid cell = $25 \times 25 \text{ km}^2$) predicted via a biophysical model over the full Iberian distribution of the species iteratively computed after assuming that the species' CT_{max} be represented by the CT_{max} of only one of the four populations (Herrando-Pérez et al., 2020b). Lines (B) show the proportion of 10 red-throated skinks (*Carlia rubrigularis*) choosing dry or wet refuges after 16 h through a sequence of experimental assays at 10 different air temperatures from 18 to 36 °C (Pintor et al., 2016). Red and blue lines separate logistic fits using the temperature at a dry or wet refuge as predictor, respectively. Grey shading indicates the range of median (dark) and 25% and 75% quartiles (light) of the environmental temperatures preferred by individuals (120 substrate temperatures per assay measured), respectively. Significance: (lizard) Prediction of climate impacts depend on what population is chosen to represent a species' heat tolerance. The higher the population's CT_{max} , the lower the predicted species' restriction time, with 450 h of restriction time totalling 64 seven-hour days without diurnal activity; (skink) thermal performance responds to the interaction of air temperature and moisture. The higher the temperature, the lower the choice of dry refuge, with individuals showing avoidance of the dry refuge well before reaching preferred substrate temperatures. Photos: Salvador Herrando-Pérez (lizard) and Conrad Hoskin (skink).

variation in heat tolerance across 8° of latitude in the Iberian Peninsula is a substantial physiological shift, amounting to 40% of the cross-species variation in heat tolerance (38 to 48 °C) that has been modelled for tens of squamate reptiles from the entire temperate zone of the Northern Hemisphere (23.5 to 66.5° North) (Pinsky et al., 2019; Sunday et al., 2014). This kind of observations supports the view that different populations, potentially representing distinct lineages within a species, engage in local-adaptation strategies (see next section). Accounting for variation in thermal tolerance amongst lineages is a robust, albeit expensive, approach to characterize the thermal niche of a species (Martin et al., 2020; Smith et al., 2019).

Intra-specific variation in heat tolerance can be expected to buffer species exposure to moderate climate change if at least some populations have higher tolerance to temperature

extremes, wider safety margins or warming tolerance, or stronger acclimation response ratios than others across the distributional range of species. Therefore, thermoregulatory behaviour (Sunday et al., 2014) and/or access to thermal microhabitats (Suggitt et al., 2018) might be obligate strategies for survival but *only* for the subset of populations that have the lowest thermal tolerance and/or are experiencing the strongest impacts of climate change within the distribution of a species. Local extirpation of single populations, driven by thermal stress, should be more common in response to sudden (short-term, often localized) events of extreme climate. In contrast, long-term (gradual, often widely spatially spread) climate shifts might drive homogenization of the heat tolerance between populations (*via* plastic or adaptive shifts) at a pace dictated by climate-change velocity and population acclimation and generation time

(Bennett et al., 2019). The debate about the relative role of short-term versus long-term climatic variation in shaping patterns of heat tolerance and extinction risk is not new (Chown et al., 2003; Feder, 1987), but remains to be comprehensively tested by comparing thermal-tolerance responses across populations within the distribution of species. Without enough large-scale population-level data, simulation of traits offers the possibility of making theoretical predictions using intra- and inter-specific trait variation (Valldares et al., 2014).

A preliminary analytical step would be to quantify the relative magnitude of intra-versus inter-specific variation in heat tolerance across as many taxa as possible. Addressing such a question requires the invigoration of experimental work across broader environmental gradients focusing on intra-specific trait variation for non-model species and the compilation of available population-level thermal traits in a comprehensive dataset. GlobTherm does document 21 aquatic and 43 terrestrial ectothermic species with multiple population measurements of heat tolerance, despite ultimately filtering and reporting one per species. Empirical measurements of intra-specific variability in heat tolerance are far more common than reported by GlobTherm, and have accumulated steadily since the 1970s in the form of studies of ectothermic species in aquatic (e.g., Brattstrom, 1970; Morley et al., 2012; Schulte, 2007) or terrestrial (e.g., Bozinovic et al., 2014; Buckley et al., 2015; Hertz et al., 1979) habitats (e.g., Manis & Claussen, 1986). Such vast corpus of data remains scattered across multiple (often low-impact) ecological and physiological journals and papers, and proves somewhat cryptic to searches using key words in mainstream primary-literature databases in English (e.g., *Scopus*, *Web of Science*). An initiative following the former path of action is the new database of amphibian heat tolerances (Pottier et al., 2022). These authors show that, through a comprehensive literature review in five databases and seven languages, the number of species with measured heat tolerances increases from 113 (GlobTherm, 20 data sources in English) to 616 (213 data sources), including 1 to 163 measurements per species (mean = $5 \pm 13SD$), with prevailing data gaps from Africa, Asia and high latitudes as in GlobTherm.

Further ecophysio-prospection: how to do it

More data, of course, implies more funding. Funders will, however, not be captivated by simplistic messages of the kind ‘let’s study everything’. Instead, deciding whether taxonomic, geographic and habitat gaps in heat-tolerance data should be filled, at a rate proportional to the relative functional diversity of the different phylogenetically related groups, does rely on more ecophysiological sampling within and across those groups. For instance, in monitoring global biodiversity, marine biologists have proposed stratified sampling by rates of biological activity, so deeper habitats

should be sampled at lower spatial and temporal resolution than shallower habitats (Costello et al., 2018), and biogeographers also advocate for stratifying spatial samples to cover the full breadth of environmental space that species are expected to occupy using theoretical (model-based) expectations (Araújo & Guisan, 2006). With increasing cuts in research budgets, these proposals should be evaluated against the cost-benefit outcomes that they might bring for the protection and sustainable exploitation of biodiversity and ecosystem services (Canessa et al., 2015).

How to tailor sampling stratification to collect novel ecophysiological data at the relevant spatial scales will require a gap analysis involving (i) reviewing the state of knowledge about the causes of heat-tolerance variation across species and environments, (ii) pinpointing prevailing data biases in light of the major drivers of such variation, and (iii) providing guidelines on what understudied groups (lineages, populations, species) and regions should be prioritized for sampling. Those guidelines might not necessarily ally with recommendations to monitor biodiversity because low-diversity ecosystems, like those in high altitudes or deep waters, often contain specialized forms of thermal adaptation and performance that cannot be ignored to understand large-scale ecophysiological patterns.

Prevailing challenges

We here emphasize three challenges that would need to be considered when conducting large-scale analysis of thermal tolerance using assembled data. A first challenge is the frequent lack of intra-specific measurements in large, compiled datasets. Such a lack includes underrepresentation of different populations (see above) but also different life stages. For example, Bennett et al. (2018) explain “... to make the estimates of species thermal limits in the [GlobTherm] dataset comparable, only estimates from study specimens in their later life stages were used”. But heat tolerance varies through the ontogeny of species with massive implications in their thermal biology and adaptive strategies (Buckley & Huey, 2016; Dahlke et al., 2020; Refsnider et al., 2019). For instance, many insects alternate aquatic and terrestrial thermal environments and/or exploit different microhabitats through their life history (Kingsolver et al., 2011), juvenile stages might have more plastic thermal limits than adult stages (Weaving et al., 2022), and those stages more sensitive to climatic variation should set the biogeographic boundaries of species (Bowler & Terblanche, 2008). A critical question is how restricting analysis to adult stages would affect the conclusions of studies using these data? More specifically, what information is being lost by ignoring early-development stages and how relevant it is for the question being asked? A second challenge is the usual lack of consideration of variation in acclimation treatments of individuals prior to the experimental assays used to measure heat tolerance. Merging data points, including various acclimation

treatments, removes or masks the thermal history of those individuals and of the populations and species they belong to. However, previous exposure to high temperatures can increase heat tolerance to future events of thermal stress (Giomi et al., 2016; Kellermann et al., 2017; Olsen et al., 2021) and individuals can use this information to modulate their activity and behaviour through the life cycle (daily, seasonally, annually) anticipating future stressing conditions (Bernhardt et al., 2020). Finally, a third challenge accrues from discrepancies in acclimation temperatures, ramping rates, experiment duration and body indicators of stress that can introduce noise in thermal assays (Camacho & Rusch, 2017; Carilo Filho et al., 2022; Lutterschmidt & Hutchison, 1997a; Rezende et al., 2014; Terblanche et al., 2011). The extent to which such procedural variance compromises the comparability of heat-tolerance data in large-scale studies, drawing upon repositories of physiological data, has not been assessed in detail as “...there is no way for [database] users to identify the confounding methodological issues in the original study designs” (Bates & Morley, 2020). Only the new database of amphibian heat tolerances (Pottier et al., 2022) includes estimates for different life stages, and exclusively accepted studies reporting acclimation temperatures and, importantly, the temperatures experienced in their habitat by the animals prior to capture and the date of capture — so the native thermal environment of the population might be inferred.

Across the board, the inclusion of (i) metrics of heat tolerance for different life stages and (ii) technical details about the protocols of measurement of thermal tolerance should be ideally considered in updates of databases, such as GlobTherm, or in new data repositories (see Pottier et al. 2022) tailored for large-scale studies. Moreover, novel experimental protocols for measuring heat tolerance, which incorporate thermal history, without jeopardizing comparability amongst individuals, populations and species, constitute a worthwhile endeavour.

Aquatic and terrestrial ecosystems under climate change

How terrestrial versus aquatic (particularly marine) organisms respond to climate change has received considerable attention in the last decade (Blowes et al., 2019; Burrows et al., 2011; Pinsky et al., 2019; Steele et al., 2018; Sunday et al., 2012). Those efforts have voiced authoritative calls that both realms share many functional processes (Mokany et al., 2010; Webb, 2012), and that integrating their study should promote the progress of ecology (Duarte, 2007) and the design of coordinated actions to deal with climate impacts on biodiversity (Menge et al., 2009; Richardson & Poloczanska, 2008). Ecologists examining large-scale ecophysiological patterns have acted on those calls and, time and again, shown a consistent absence of correlation of heat

tolerance with latitude and large-scale climatic predictors on land (Deutsch et al., 2008; Hoffmann et al., 2013; Sunday et al., 2014). Those correlations, however, have been statistically supported in the sea (Sunday et al., 2011) and, similarly, for cold tolerance in both realms (Araújo et al., 2013; Hoffmann et al., 2013). All the latter studies have mostly used data assembled from the literature, most if not all of which are now compiled in the GlobTherm dataset, and are based on single-point estimates of species heat tolerance (as response) and mean temperature averages (as predictor).

In contrast to cold tolerance, heat tolerance could be functionally tuned to small-scale climatic gradients that can go unnoticed by large-scale studies mostly using coarse climatic data and single-species estimates of heat tolerance (Herrando-Pérez et al., 2020b). For example, cold tolerance drives the breadth of amphibian thermal tolerance at large spatial scales, while heat tolerance does so locally (Pintanel et al., 2022). Therefore, climatic effects on ectotherm heat tolerance might not be weaker but simply more challenging to detect on land than in the sea. Not surprisingly, if heat tolerance strongly responds to local environmental variation, the population (local data) chosen to represent the heat tolerance of a given terrestrial ectothermic species can result in widely divergent downstream predictions under climate change — in cross-taxa studies using the thermal tolerance of one population per species over regional to global scales (Herrando-Pérez et al., 2019; Fig. 2A). This area of enquiry represents one additional major reason why the collection of population-level data is urgently needed (see previous section).

The drivers of biodiversity patterns are indeed more complex (shaped by more environmental variables) on land (Gagné et al., 2020). Broadly, aquatic ectotherms balance body temperatures (through convective and conductive heat transfer) with water much faster than terrestrial ectotherms do with air (Angilletta, 2009), and submerged seascapes are much more thermally homogeneous and present fewer physical barriers for adult and larval dispersal than terrestrial landscapes for any given latitude (Antão et al., 2020; Steele et al., 2018). Such environmental differences tally well with mounting evidence that marine species are tracking large-scale thermal and ecosystem shifts (e.g., predators following their prey as the latter track climate change) faster than their terrestrial counterparts, thus resulting in faster re-structuring of communities (Antão et al., 2020) and faster distributional (Lenoir et al., 2020) and phenological (Poloczanska et al., 2013) change in the sea. These results lead to the untested prediction that, with less opportunity for finding thermal refuges, heat tolerance might be subjected to stronger adaptive forcing in marine organisms (Bennett et al., 2019). Unfortunately, statements about climatic effects might fall in contradiction when different groups are examined. For instance, marine fish species appear to be more vulnerable to climate change than terrestrial species (Pinsky et al., 2019), while the opposite holds for marine invertebrates (Morely et al., 2019). Empirical evidence for whether using population-level data would correct this problem is lacking.

The ecophysiological comparison between terrestrial and marine ecosystems epitomizes the data biases presented in the previous section because of the dearth of data collected for aquatic ecosystems (Bennett et al., 2018; Fig. 1). Foremost, air- and water-breathing organisms must cope with contrasting dimensions of climate change with key research areas awaiting development (Garcia et al., 2014; He & Silliman, 2019). In the following two subsections, we highlight and discuss those data gaps relative to, arguably, the two major environmental factors interacting with environmental temperature and thermal tolerance across populations and species, namely water availability on land and oxygen supply-demand at sea.

Water in terrestrial ecosystems

Water (both liquid and vapour) distribution plays a particularly critical ecological role for terrestrial species as they must find water resources to survive — a problem rarely faced by aquatic fauna spending their entire life under water. Terrestrial fauna must deal with climate anomalies, extremes and seasonality in the atmosphere, all of which manifest themselves through a complex interaction between temperature and precipitation regimes in space and time (Garcia et al., 2014). However, terrestrial ecology maintains a major focus on studying the effects of environmental temperatures on organismal fitness under climate change (Herrando-Pérez et al., 2020a), exemplified in the multiple mathematical formulations of safety margins, which only include environmental temperatures (Pinsky et al., 2019; Sinclair et al., 2016; Sunday et al., 2014). In contrast, large-scale ecological studies that include precipitation predictors are much rarer (Herrando-Pérez et al., 2020a and references therein); and these often fail to acknowledge that water resources can be partitioned based on budgets of rainfall, humidity, and dietary and drinking water, with each budget affecting the thermal performance of terrestrial ectotherms in diametrically different fashions (Kearney et al., 2018; Pirtle et al., 2019). The pioneering mechanistic models using thermal tolerance to characterize the behaviour (Porter et al., 1973) and the distributional limits (Porter & Tracy, 1983) of ectotherms already encapsulated the interplay of temperature with water, food and gas exchanges. Those seminal approaches have evolved to dynamic energy budget models that incorporate microclimatic modelling and behavioural thermoregulation (Kearney & Porter, 2020) and tie energetics to growth, development and reproduction (Kearney et al., 2010; Kearney, 2021). Energy budget models, therefore, offer a solid mechanistic framework to incorporate population-level ecophysiological data (see previous section), and should gain realism by factoring in temperature in combination with water-related environmental predictors.

From first principles, the response of terrestrial ectotherms to climatic variation should be shaped by a combination of strategies that provide secure access to water resources and a

safe thermal environment (O'Brien, 2006). Hydric and thermal body balances are indeed functionally interlinked through a range of physiological and behavioural mechanisms (Pirtle et al., 2019; Rozen-Rechels et al., 2019) and beg for the conceptual replacement of 'thermoregulation' by 'thermohydroregulation' (Rozen-Rechels et al., 2019). Examples of this interplay abound. For instance, lizard heat tolerance can differ by 3 to 4 °C if animals are deprived of drinking water relative to individuals having access to food and water or water alone, hence adding further population-level variation in thermal performance (Herrando-Pérez et al., 2020a). Terrestrial ectotherms prefer colder over warmer refuges under water restriction (Rozen-Rechels et al., 2020) but wetter over drier refuges if temperatures increase (Pintor et al., 2016; Fig. 2B), and switch from shaded/forest to open/agricultural habitat as precipitation augments (Frishkoff et al., 2016; Ryan et al., 2016). Moreover, precipitation can drive species' adaptive shifts more strongly than air temperature on land (Siepielski et al., 2017). Unsurprisingly, water-temperature climate interactions modify extinction scenarios determined by climate warming alone (Bonebrake et al., 2018; Cahill et al., 2013; McCain & Colwell, 2011) and should be integrated to comprehensively assess the ecological effects of climate change in the face of increasing drought (Trenberth et al., 2013), aridification (Park et al., 2018) and expansion of drylands (Marvel et al., 2019) regionally and globally.

The integration of thermohydroregulation in large-scale studies calls for three major areas of development: (i) terrestrial thermal microrefugia might be available but hydrically inhospitable (Scheffers et al., 2014). Consequently, theoretical expectations of microthermal buffering of extinction risk of terrestrial ectotherms might be underestimated (González-del-Pliego et al., 2020) and must be reassessed by considering whether the hydro-thermal properties of microrefugia expand or wane the thermal niche of species; (ii) theoretical developments proposing a pace-of-life syndrome, whereby thermal performance and thermoregulatory behaviour covary along a thermal continuum (Goulet et al., 2017), seems functionally incomplete and novel research needs to address the mechanisms by which behaviour should covary with physiology along 'hot-cold' and 'dry-wet' axes of environmental change; and (iii) experimental research quantifying the relative effects of environmental temperatures and water availability on the variability of thermal tolerance across the distribution of individual species is sorely needed, and scaling up experiments to broad spatial scales remains a pressing endeavour in ecology as a whole.

Oxygen in aquatic ecosystems

In aquatic ecosystems, the imbalance between oxygen supply and demand is exacerbated by low oxygen solubility and stratification at high temperatures (Breitburg et al., 2018; Rabalais et al., 2010). These phenomena have been

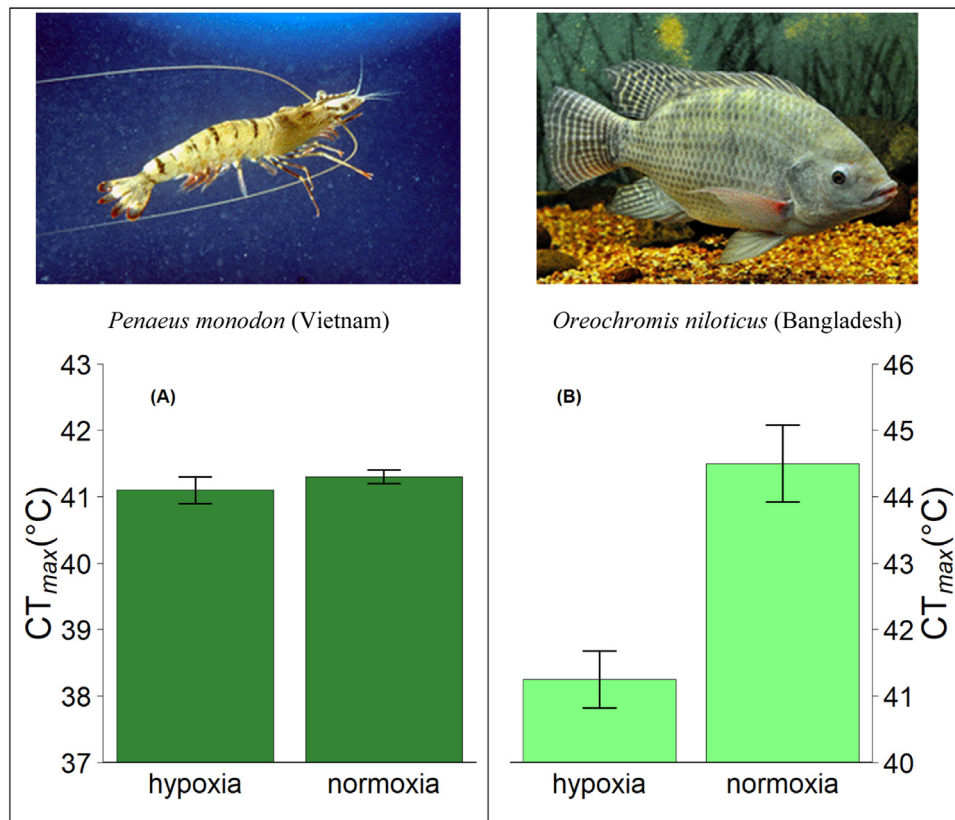


Fig. 3. Heat tolerance under experimental hypoxia and normoxia. Barplots show mean critical thermal maxima ($CT_{max} \pm SE$) quantified as the water temperature causing heart failure in the giant tiger shrimp (A: *Penaeus monodon*, $N = 8$ per treatment) (Ern et al., 2015) or loss of balance in the Nile tilapia (B: *Oreochromis niloticus*, $N = 5$) (Islam et al., 2020) obtained from fishery stocks in Can Tho (Vietnam) and Mymensingh (Bangladesh), respectively. Significance: Only the tilapia experiment provides an element of empirical support for the ‘oxygen- and capacity-limited thermal tolerance’ hypothesis as heat tolerance decreases in response to low oxygen availability. Photos: CSIRO Marine Research (shrimp) and Germano Roberto Schüür (fish).

intensifying deoxygenation under ongoing marine warming (Keeling et al., 2010; Li et al., 2020; Rabalais et al., 2010; Schmidtke et al., 2017), thereby creating additional metabolic constraints to dispersal for marine organisms (Deutsch et al., 2015). As temperatures rise, oxygen demand could outpace the physiological ability to supply oxygen to tissues in ectotherms, leading to reduced ‘aerobic scope’ (Halsey et al., 2018: the capacity to increase the aerobic metabolic rate above maintenance levels) for locomotion, growth and reproduction, and setting thresholds of heat tolerance (Fry & Hart 1948, Pörtner 2010, Fig. 3). Such postulate, under the so-called ‘oxygen- and capacity-limited thermal tolerance’ (OCLTT) hypothesis, suggests that physiological oxygen-supply mechanisms (i.e., ventilation and cardiac output) are working at their maximum capacity when body temperature reaches CT_{max} , even at rest and in normoxia (atmospheric oxygen partial pressure $PO_2 = 21$ kPa). According to OCLTT, at CT_{max} aerobic scope should be abolished, atmospheric PO_2 should become the critical PO_2 below which even resting oxygen demand cannot be supported (Claireaux & Chabot, 2016; Rogers et al., 2016), and any additional decrease in PO_2 should further reduce heat tolerance

resulting in whole-organism physiological failure (Farrell, 2016; Pörtner et al., 2017).

Within the OCLTT’s conceptual framework, extinction or dispersal to cooler latitudes by marine and terrestrial ectotherms in response to climate warming should be driven by a weakening of aerobic performance (Dahlke et al., 2020; Pörtner et al., 2017; Pörtner & Knust, 2007). The OCLTT hypothesis and associated predictions have, however, been ferociously criticized due to methodological caveats in measuring aerobic scope (Clark et al., 2013) and lack of conceptual and terminological consistency (Jutfelt et al., 2018). Most importantly, many ectotherms do not show an optimum of aerobic scope, nor display oxygen-limited thermal maxima (Ern et al., 2016; Verberk et al., 2016), nor modify thermal preferences in varying oxygen conditions (Camacho et al., 2018). Instead, some species increase their aerobic scope as body temperatures reach thermal limits (reviewed by Lefevre 2016, Schulte 2015), while others have reduced aerobic scope despite increasing oxygen supply (Seibel & Deutsch, 2020), suggesting that mechanisms other than oxygen supply determine thermal maxima.

These contradictory results could be reconciled by considering active, rather than resting, metabolic oxygen requirements. Maximum values of temperature and oxygen tolerance measured at rest are often well outside the values experienced by a species in its native habitat, apparently widening the window of physiological tolerance to buffer the potential effects of climate change on marine species (Boardman & Terblanche, 2015; Sunday et al., 2014; Verberk et al., 2016). However, physiological oxygen supply in ventilatory and/or cardiovascular systems has evolved to support active metabolism at prevailing environmental PO_2 irrespective of temperature (Seibel & Deutsch, 2020). This is so because extreme temperatures and PO_2 values are less likely to result in adaptive changes; instead, natural selection should act on the window of aerobic scope (typically $\times 3$ the resting rate) expressed under prevailing temperature and oxygen ranges (Deutsch et al., 2020). In this context, supposed ‘thermal bottlenecks in the life cycle’ (e.g., larval stages in fish, Dahlke et al. 2020) might simply indicate that some stages require less aerobic scope than others. Consequently, most species seem not to be protected by substantial safety margins but, instead, must engage in acclimation, adaptation or migration for survival in response to any decline in oxygen and/or rise in temperature beyond native environmental ranges (Deutsch et al., 2020).

Rather than the prevailing debate on whether the dependence of heat tolerance on aerobic scope is a universal principle, a more fertile ground would be to address three areas of development: (i) no study has quantified whether oxygen-heat tolerance correlations are weaker or stronger for particular habitat characteristics and species traits like contrasting capacities for oxygen extraction and transport (see Verberk and Bilton 2013). In fact, it has been proposed that, in normoxic conditions, it is no more difficult for water breathers to obtain oxygen than it is for air breathers (Seibel & Deutsch, 2020), though the former have to face hypoxia more often than the latter, more so with climate change (Keeling et al., 2010; Rabalais et al., 2010); (ii) large-scale analysis of multiple species assemblages mostly relies on metabolic measurements made for animals in a resting state across a limited temperature range, and can gain biological realism by incorporating performance metrics under sustained activity. Those include the maximum metabolic rate and its oxygen dependence (Claireaux & Chabot, 2016; Killen et al., 2017), as already conceived by the earliest experimental frameworks on the subject (Fry & Hart, 1948); and (iii) the interplay of heat tolerance with aerobic performance is known for only a small fraction of the ocean’s biodiversity (Deutsch et al., 2020), and varies intra-specifically across different magnitudes of hypoxia (Ern et al., 2016; Kamalam et al., 2019; Regan & Richards, 2017) and temperature (e.g., seasonally or latitudinally, Clarke & Johnston, 1999; Dell et al., 2011). Therefore, the study of this interplay would benefit from considering its spatiotemporal variation over the distributional range of individual species, including environmental gradients through which variation in oxygen

and/or temperature peaks, particularly altitude (DuBois et al., 2017), depth (Cau et al., 2018) and eutrophication (Gomez Isaza et al., 2020).

Concluding remarks

Progress in ecology is intertwined with the ability to test inferences about climate change and its effects on species distributional changes, abundances, adaptation capacity and extinctions, and how they resolve into model-enabled forecast statements in the years to come (Ladle et al., 2004; Urban, 2019). However, concerns have been raised that improvements in theoretical sophistication gained from increasing power of computational models have yet to be translated into an improved mechanistic understanding of how ecosystems actually work (Mouquet et al., 2015). In simple words, “...all models are wrong, the practical question is how wrong do they have to be to not be useful” (Box & Draper, 1987), and insufficient data are bound to limit the realism of the models and inflate the user’s perception of performance. Recommending ‘more data’ to promote research progress (our tenet) will be uninspiring to many. More so because, given growing habitat destruction, overexploitation and species extinctions, halting or delaying management and conservation actions conditional on gathering more information seems a costly trade-off (Schiermeier, 2018). However, this trade-off exists and begs for more integration of empirical and experimental research with modelling developments (Seidl, 2017).

In light of forecasts of severe future-climate change scenarios in combination with other environmental threats to biodiversity (Bonebrake et al., 2019; Brook et al., 2008; Hof et al., 2011; Simmons et al., 2021; Strona & Bradshaw, 2022), large-scale measurements of thermal traits could help inform proposed guidelines of global monitoring of biodiversity (Hochkirch et al., 2020) and the technological coordination needed to realize those guidelines (Dornelas et al., 2019). Without additional funding incentives, ecophysiological research will remain centred on the relatively biodiversity-poor temperate zone where research capacity is currently concentrated, while moving forward will require prioritizing research on the poorly studied animal groups, habitats biogeographical regions of the planet. After all, funders and the scientific community alike should appreciate that improved resolution of global-ecology research ultimately depends upon generating new biological measurements in the good old-fashioned way: going into the field, capturing individuals and doing thermal assays. Large-scale ecological studies absolutely rely on local and empirical research. Having said that, we underline that global efforts to compile and analyse ecophysiological data for global change ecology have already been massive and a trade-off will always exist between data breadth and depth. The greater the breadth, the lower the depth — it is hard to circumvent this reality.

Data accessibility

Figure 1: Data taken from Bennett et al., (2018); Figure 2A: Data taken from Herrando-Pérez et al., (2020b); Figure 2B: Data taken from Pintor et al., (2016); Figure 3A: Data taken from Ern et al., (2015); Figure 3B: Data taken from Islam et al., (2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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