



GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms

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Published in:
Scientific Data

DOI:
[10.1038/sdata.2018.22](https://doi.org/10.1038/sdata.2018.22)

Publication date:
2018

Document version
Publisher's PDF, also known as Version of record

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Citation for published version (APA):
Bennett, J. M., Calosi, P., Clusella-Trullas, S., Martinez, B., Sunday, J., Algar, A. C., ... Morales-Castilla, I. (2018). GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Scientific Data*, 5, [180022]. <https://doi.org/10.1038/sdata.2018.22>

SCIENTIFIC DATA

OPEN Data Descriptor: GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms

Received: 1 March 2017

Accepted: 8 December 2017

Published: 13 March 2018

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How climate affects species distributions is a longstanding question receiving renewed interest owing to the need to predict the impacts of global warming on biodiversity. Is climate change forcing species to live near their critical thermal limits? Are these limits likely to change through natural selection? These and other important questions can be addressed with models relating geographical distributions of species with climate data, but inferences made with these models are highly contingent on non-climatic factors such as biotic interactions. Improved understanding of climate change effects on species will require extensive analysis of thermal physiological traits, but such data are both scarce and scattered. To overcome current limitations, we created the GlobTherm database. The database contains experimentally derived species' thermal tolerance data currently comprising over 2,000 species of terrestrial, freshwater, intertidal and marine multicellular algae, plants, fungi, and animals. The GlobTherm database will be maintained and curated by iDiv with the aim to keep expanding it, and enable further investigations on the effects of climate on the distribution of life on Earth.

Design Type(s)	data integration objective • database creation objective
Measurement Type(s)	heat tolerance • cold tolerance • Acclimatization
Technology Type(s)	data item extraction from journal article
Factor Type(s)	geographic location • biome • Species
Sample Characteristic(s)	Africa • aquatic biome • terrestrial biome • Antarctica • Asia • Europe • North America • Oceania • South America

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Background & Summary

A long-standing challenge in ecology and biogeography is to understand what generates patterns in species diversity and distributions¹. Undertaking this challenge is of increasing importance if we are to manage the effects of global change on biodiversity². The upper and lower temperature limits to performances, sublethal irreversible conditions and molecular degradation are central to determining the geographic distributions and range shifts of species under climate change³. Thus, thermal tolerances limits can be used to evaluate the relative contribution of macrophysiology and macroevolution to generating species diversity gradients in terrestrial, coastal, and marine realms⁴.

Inferring species' thermal tolerance limits based on realized climatic niches can be confounded by non-physiological factors including biotic interactions, dispersal ability, and/or habitat patch size^{5,6}. Studies using experimentally-derived estimates of species' fundamental climatic niches have significantly advanced our knowledge of how species' ranges conform to thermal tolerance limits at land and sea^{7,8} and how thermal physiological traits are asymmetrically conserved through evolution⁹. However, these studies have generally been limited in taxonomic coverage, with only one study focused on trans-realm comparisons⁷.

In order to overcome these limitations and develop unified theories and methodologies on the influence of fundamental thermal niches on the geographic distribution of diversity worldwide and across realms, a comprehensive cross-taxon and cross-realm dataset of thermal tolerance limits is urgently needed. Here we present the GlobTherm database, a large global cross-realm multi-taxon dataset comprising published experimentally-derived species' thermal tolerances for over 2,000 species of multicellular algae, plants, fungi and animals. Experimentally-derived measures of thermal limits provide a direct estimate of relevant aspects of species' fundamental thermal niches^{10,11}. Hence, these metrics overcome many of the confounding factors associated with the currently popular but possibly flawed method of inferring species' thermal tolerance limits from realized geographic niches^{12,13}.

Thermal tolerance limits are highly relevant to key issues in the current ecological literature, including which taxa have realized niches that are closer to their upper physiological tolerances and therefore may be more vulnerable to climate change¹³. The GlobTherm dataset centralizes data-collection efforts across taxon and synthesizes it in a format ready for researchers to use in order to conduct common analyses in macroecology, macroevolution and macrophysiology. While entries describing "thermal ranges" are often available in other databases (e.g. Fishbase, Mammalbase), the estimate of thermal tolerance is often based on distributional data and is not published alongside information on the methodology used to estimate thermal tolerance. GlobTherm is unique in collating experimentally-derived thermal tolerance data, which are independent-and thus comparable-to species' realized ranges.

Methods

From November 2015 until October 2016, data were compiled from published experimental estimates of upper and lower temperature tolerance limits following the protocols established by Clusella-Trullas¹⁴. Measures of thermal tolerance that allow the greatest across taxon coverage were targeted; these included (i) critical (threshold) and (ii) lethal temperatures. (i) Critical temperatures mark the loss of key ecological functions, such as locomotion, ability to gain nutrition, or maintain basal metabolism (as per thermal neutral zone TNZ for endotherms) and are measured with critical thermal maximum (CTmax) or minimum (CTmin), and TNZ or reduced by a predefined amount (i.e. 50%, CT50). (ii) At lethal temperatures mortality occurs in whole individuals or part thereof i.e. leaf die back to a predefined percentage (commonly measured as lethal temperature 100% (LT100) or 50% measured as LT50) after a fixed duration of time. For studies in which data were presented graphically and not stated as text, values were extracted using Plot digitizer software, version 2.0¹⁵. Species names and taxonomy were standardized into the National Center for Biotechnology Information (NCBI) taxonomic system using 'taxize' package¹⁶ in the statistical program R¹⁷.

The protocol was as follows. JMB searched for published articles, books and thesis using the following search terms: 'critical thermal maximum', 'critical thermal minimum', 'upper thermal tolerance', 'lower thermal tolerance', 'thermal tolerance breadth', 'heat tolerance', 'cold tolerance', 'upper lethal temperature limit', 'lower lethal temperature limit', 'thermal tolerance window', 'species temperature tolerance', 'thermo-neutral zone', and 'frost resistance' in Google Scholar (see Table 1 (available online only)). JMB then examined the abstracts and methods sections of the manuscripts to determine if they complied with our selection criteria. When insufficient information on experimental methods or sampling locations was provided within the publication, the authors were contacted to request additional information. Measures of thermal tolerance were only recorded if methodology and sampling locations were provided (either in the manuscript or by the author). When reviews were found in the literature search that complied with our data quality requirements, the cited papers or authors attributed were located and the data extracted from these original sources when possible. A total of 567 studies were found to provide data of a high enough quality to be included in the dataset, out of the thousands of candidate studies.

Species phenotypes are intrinsically plastic. In particular, thermal limits show a considerable level of plasticity among different life stages and/or populations of a same species living along temperature gradients associated with latitude. To make the estimates of species thermal limits in the dataset comparable, only estimates from study specimens in their later life stages were used, i.e. eggs, larvae,

seeds, gametes etc. were all excluded from the present form of our dataset. When multiple estimates for a species' thermal limits were available, to standardize methodologies between estimates as much as possible, priority was given to estimates that had the greater share of the following attributes with more weight given to attributes in the following order: (1) thermal limits measured using more common metrics, i.e. CTmax and CTmin over LT50, LT50 over LT100, and LT100 over super cooling point (SCP) (with the exception of mammals and birds for which all data were TNZ and algae where lethal measures were given preference due to the inconstancy among the methods used to determine critical measures in these taxa) (2) estimates of upper and lower thermal limits in the same population; (3) field-fresh specimens over acclimated specimens and acclimated specimens over those in long-term captivity; (4) whole individuals over part specimens, (i.e. tree branches); (5) measurements taken during active seasons and phases (i.e., diurnal during the day and overnight for nocturnal species); (6) measurements with larger sample sizes (7) measurements taken from fasted individuals over fed; (8) mean measures over median (due to the paucity of the latter); (9) the loss of righting response and/or locomotion over the onset of spasms (OS) as the end point of CTmax and CTmin in ectothermic animals (due to the rarity of OS); and (10) estimates with stronger supporting information including location, ramping rate (rate of temperature increase) and acclimation temperature. In all cases, these criteria lead to the selection of a single study that optimized comparability between species measures. Despite such precautions variations in the methods used between studies will add some random error to the estimates, however our methods should not bias the error in any one direction¹⁴.

Data were excluded if measurements were taken from individuals bred for commercial purposes, such as agriculture, aquaculture, or the pet trade, to reduce confounding issues associated with artificial selective history. Individuals held in managed populations i.e., zoos, university laboratory populations and botanical gardens or those bought from wild life traders were only used if we were able to insure the animals were not of a commercial origin. If this information was not provided in the manuscript i.e. if the location of their original wild capture/collection was not given the authors were contacted before a study was included.

Data Records

This database includes thermal tolerance metrics for 2,133 species of multicellular algae, plants, fungi, and animals in 43 classes, 203 orders and 525 families from marine, intertidal, freshwater, and terrestrial realms, extracted from published studies (Data citation 1, and Figures 1 and 2). The data presented here are available in both Excel and text formats in the Data Dryad (Data citation 1). Updates to the data and metadata will be curated through the iDiv data portal (<https://idata.idiv.de/>). For example, in the future it is planned to include intraspecific variation in the dataset, to provide multiple estimates of thermal tolerance limits for a given species. Where, estimates determined using the best possible methods will be more highly ranked.

Technical Validation

JMB gathered the data from published and peer-reviewed scientific studies. The differences among experimental methods, observers, and pre-conditions (i.e. season and capture locations) are known to generate some variance in the estimates of species temperature tolerance. Information relating to experimental methods were recorded alongside the thermal tolerance limits to enable data users to incorporate these parameters in data analyses and approaches for methods validation of data. Provision of such metadata also enables users to filter data based on their specific needs and research questions.

In particular, the experimental methods used to determine the lethal temperature for algae and the upper boundary of the thermal neutral zone (UTNZ) for mammals and birds may have an effect on the quality of the estimate. We provide the temperature intervals between lethal measurements for algae and information on the quality of the regression used to estimate the UTNZ for mammals and birds (for more information on each column in the dataset please see Table 2 (available online only)). Similar to other assessments of the quality of published UTNZ measures^{18–20} we found that only ~50 % of the literature compiled contained valid estimates i.e., evidence that the boundary of the UTNZ was reached in the experiment.

The dataset has a wide global spatial coverage (Figure 1), though clear geographical data gaps do exist, for example, in central Africa, Russia, India, parts of Canada and in the deep ocean. The data gaps present in this study are unfortunately common as they represent locations that are either hard to access due to geography (i.e. northern Canada and Russia, deep ocean, the tropics), or where scientific literature is difficult to access due to language and related citation indexing barriers²¹. The distribution of the data across realms reflects the distribution of known species on Earth, where ~80% of macroscopic species live on land (most being insects) compared to 15% in the ocean (showing however the greatest phyla difference) despite the much larger area and volume, and 5 % in freshwater^{22,23}. The dataset contains approximately 0.20% of plants²⁴, 0.72 % of algae²⁵, 0.00024 % of insects²³, 0.55% of fish²⁶, 3.33% of reptiles²³, 6.01% of mammals²⁷, 1.86% of birds²⁷ currently described. Taxonomically, Chordata are over-represented in our data set, while algae, plants, and, to a greater extent, invertebrates, are underrepresented given their greater contribution to the world's total number of species. In sum, the GlobTherm dataset reflects both geographic and taxonomic bias in sampling of thermal tolerances, which

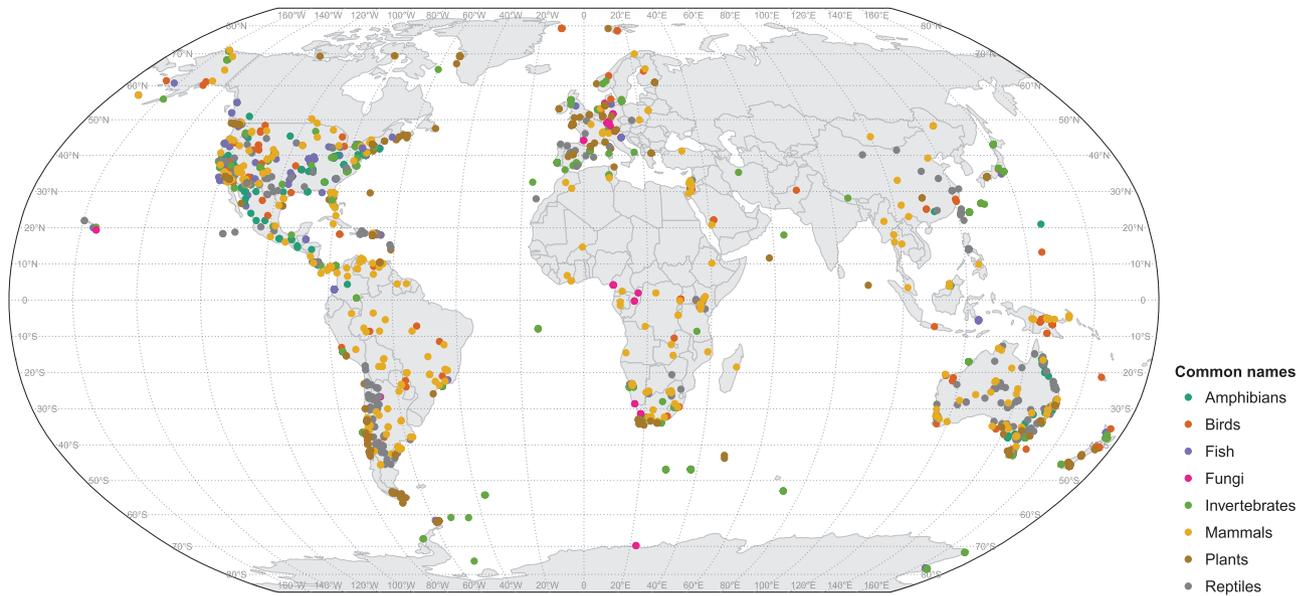


Figure 1. A map illustrating the geographic location at which experimental species were collected. Points are colored according to the common name in which the species belongs including fungi, plants, algae, invertebrates, fish, amphibians, reptiles, birds and mammals.

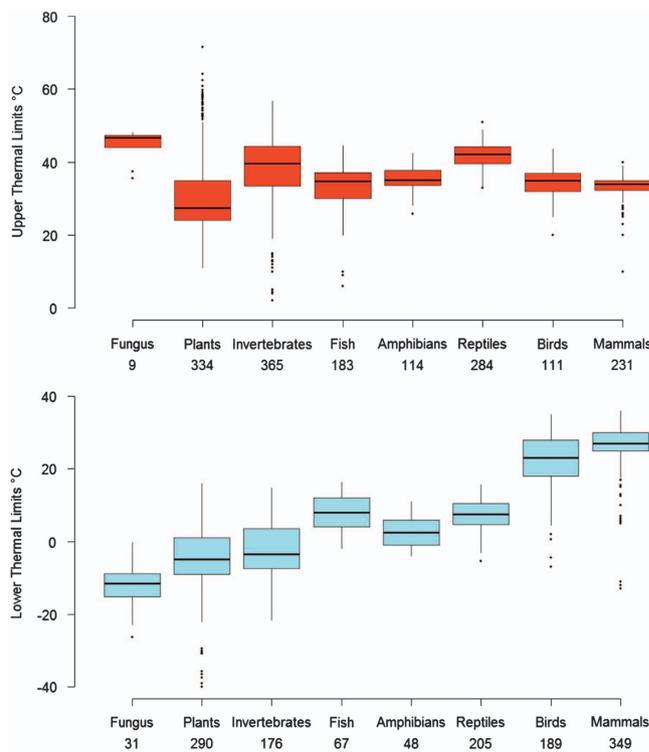


Figure 2. Boxplot of the mean upper and lower thermal limits for fungi, plants, algae, invertebrates, fish, amphibians, reptiles, birds and mammals, the total number of records for each group shown below. Upper thermal tolerance is shown in red and lower thermal tolerance in blue, whiskers show the maximum and minimum quartiles.

may ultimately help identifying gaps and guiding subsequent efforts in documenting the thermal physiology of life on Earth.

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Data Citations

- Bennett, J. M. *et al.* *Dryad Digital Repository* <http://doi.org/10.5061/dryad.1cv08> (2017).

Acknowledgements

This paper is a joint effort of the working group sWEEP and an outcome of a workshop kindly supported by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118). J.M.B. was supported by an sDiv postdoctoral fellowship to conduct this work. We would like to thank the many authors and institutions that provided additional information. I. M.-C. is currently supported by a postdoctoral fellowship funded by the University of Alcalá.

Author Contributions

J.M.B. collected all the data, contributed to the development of the data collection protocol, and led the data analysis and writing of the manuscript. P.C., contributed to the development of the data collection protocol and assisted in the writing of the manuscript. S.C.T., contributed to the development of the data collection protocol, assisted in the literature search and assisted in the writing of the manuscript. B.M. assisted in the literature search and in the writing of the manuscript. J.S. contributed to the development of the data collection protocol, assisted in the literature search and assisted in the writing of the manuscript. A.C.A. contributed to drafts of the manuscript. M.B.A. assisted in the writing of the manuscript. B.A.H. contributed to drafts of the manuscript. S.K. contributed to drafts of the manuscript. I.K. contributed to drafts of the manuscript. C.R. contributed to drafts of the manuscript. L.R. contributed to drafts of the manuscript. A.S. contributed to drafts of the manuscript. F.V. assisted in the writing of the manuscript. MAOT conceived the idea of developing the database, was a principle investigator on the

project and contributed to the writing of the manuscript. I.M.C. conceived the idea of developing the database, was a principle investigator on the project and contributed to the writing of the manuscript.

Additional Information

Tables 1 and 2 are only available in the online version of the paper.

Competing interests: The authors declare no competing financial interests.

How to cite this article: Bennett, J. M. *et al.* GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Sci. Data* 5:180022 doi: 10.1038/sdata.2018.22 (2018).

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