**Geographical bias in physiological data limits predictions of global change impacts**

**Running head:** Geographical bias in physiological knowledge

**Keywords:** functional traits, climate, forecasting, interactive effects, meta-analysis, temperature, precipitation, rainfall

**Abstract**

1. Climate affects all aspects of biology. Physiological traits play a key role in mediating these effects, because they define the fundamental niche of each organism.
2. Climate change is likely to shift environmental conditions away from physiological optima. The consequences for species are significant: they must alter their physiology through plasticity or adaptation, move, or decline to extinction. The ability to understand and predict such organismal responses to global change is, however, only as good as the geographical coverage of the data on which these predictions are based.
3. Geographic biases in the state of physiological knowledge have been identified, but it has not been determined if these geographic biases are likely to limit our capacity to predict the outcomes of global change. We show that current knowledge of physiological traits is representative of only a limited range of the climates in which terrestrial animals will be required to operate, because data for animals from only a limited range of global climates have been incorporated in existing compilations.
4. We conclude that geographic bias in existing data sets limits our capacity to predict organismal responses in the vast areas of the planet that are unstudied, and that this geographic bias is a much greater source of uncertainty than the difference between the current climate and the projected future climate. Addressing this bias is urgent to understand where impacts will be most profound, and where the need for intervention is most pressing.

**1. INTRODUCTION**

Physiological traits mediate the responses of species to climate change ([Hoffmann & Sgrò 2011](#_ENREF_27); [Seebacher, White & Franklin 2015](#_ENREF_54)). Physiological information therefore has considerable predictive power for forecasting the responses of species to climate change ([Humphries, Thomas & Speakman 2002](#_ENREF_30); [Kearney & Porter 2009](#_ENREF_36); [Elith, Kearney & Phillips 2010](#_ENREF_22); [Diamond *et al.* 2012a](#_ENREF_18); [Mathewson *et al.* 2017](#_ENREF_42)). However, data accumulated over past decades exhibit a profound spatial bias: more data are available for species from North America, Western Europe, South Africa, and Australia than for species from other regions of the world ([Addo-Bediako, Chown & Gaston 2001](#_ENREF_2); [Chown, Addo-Bediako & Gaston 2002](#_ENREF_15); [Dillon, Wang & Huey 2010](#_ENREF_20); [Clusella-Trullas, Blackburn & Chown 2011](#_ENREF_16); [Seebacher *et al.* 2015](#_ENREF_54)) (Figure 1). The extent to which this spatial bias compromises understanding of global responses to climate change will depend on (1) the extent to which physiological traits differ among species, and particularly whether the sampled species represent species in unsampled environments, and (2) the extent to which the studied environments are representative of unstudied and future environments.

Physiological performance of organisms varies among species living in different environments, because climate is a potent driver of trait evolution ([Chevin, Lande & Mace 2010](#_ENREF_14); [Beaman, White & Seebacher 2016](#_ENREF_7); [Amarasekare & Johnson 2017](#_ENREF_5)). Species from cold environments have relatively high metabolic rates ([Addo-Bediako, Chown & Gaston 2002](#_ENREF_3); [Lovegrove 2003](#_ENREF_40); [Anderson & Jetz 2005](#_ENREF_6); [White *et al.* 2007a](#_ENREF_56)) and are more tolerant of cold ([Addo-Bediako, Chown & Gaston 2000](#_ENREF_1); [Clusella-Trullas *et al.* 2011](#_ENREF_16); [Kellermann *et al.* 2012](#_ENREF_38)) than species from warm environments; species from dry environments have lower rates of water loss ([Addo-Bediako *et al.* 2001](#_ENREF_2); [Portugal *et al.* 2014](#_ENREF_48)) and improved desiccation resistance ([Kellermann *et al.* 2009](#_ENREF_37); [Kellermann *et al.* 2012](#_ENREF_38)) compared to species from more moist environments; and species from stable environments exhibit greater physiological plasticity than those from more variable environments ([Seebacher *et al.* 2015](#_ENREF_54)), although this differs among traits ([Gunderson & Stillman 2015](#_ENREF_25)). Species from understudied regions will therefore be functionally distinct from those from better studied regions, if the regions differ in climate ([Chevin *et al.* 2010](#_ENREF_14); [Marshall & Burgess 2015](#_ENREF_41); [Amarasekare & Johnson 2017](#_ENREF_5)).

Given that species traits vary with climate, the extent to which current knowledge of functional trait diversity will be useful to predict global responses to climate change will depend on the extent to which studied environments are representative of the full range of current global environments, and the range of environments that organisms will be exposed to in the future. Here we quantitatively evaluate the concordance between the environments for which we have some knowledge of functional traits (“studied environments”) and global current and projected future environments by combining georeferenced trait data from published studies with climate data from recent (1970-2000) and projected future (2041-2060) climatologies. We compare studied environments to randomly chosen current and projected future environments to assess how well our current knowledge is representative of the range of current global environments and future environments.

**2. MATERIALS AND METHODS**

We gathered a total of 5329 spatially explicit measurements of the physiological traits likely to dictate the responses of terrestrial animals to climate change: critical upper and lower thermal limits, supercooling temperature, optimal temperatures for performance, rates of metabolism, patterns of gas exchange, and acclimation capacity (Table 1). The physiological traits we chose as means to identify studied environments define the range of temperatures over which animals can survive (critical upper and lower thermal limits, supercooling temperature), the rates at which they utilise energy and the demands they place on their environment (metabolic rate, which exhibits associations with survival and fitness that vary among environmental and ecological contexts: Boratyński & Koteja 2009; [Pettersen, White & Marshall 2016](#_ENREF_45); [Boyce *et al.* 2020](#_ENREF_11); [Pettersen *et al.* 2020](#_ENREF_46)), their susceptibility to desiccation stress (gas exchange patterns: [White *et al.* 2007b](#_ENREF_57); [Schimpf, Matthews & White 2012](#_ENREF_53)), the temperatures at which functional performance (development, growth, and locomotion) is maximised, and their capacity to compensate physiologically for changes in the thermal environmental (acclimation capacity). The data set includes records for 2637 species, including insects, arachnids, fish, amphibians, reptiles, birds and mammals (Table 1). We drew exclusively upon published compilations with broad spatial or taxonomic coverage ([Anderson & Jetz 2005](#_ENREF_6); [White *et al.* 2007a](#_ENREF_56); [White *et al.* 2007b](#_ENREF_57); [Wiersma *et al.* 2007](#_ENREF_59); [Irlich *et al.* 2009](#_ENREF_32); [Clusella-Trullas *et al.* 2011](#_ENREF_16); [Diamond *et al.* 2012a](#_ENREF_18); [Hoffmann, Chown & Clusella-Trullas 2013](#_ENREF_28); [Portugal *et al.* 2014](#_ENREF_48); [Londoño *et al.* 2015](#_ENREF_39); [Seebacher *et al.* 2015](#_ENREF_54); [Buckley *et al.* 2018](#_ENREF_12); [Bushuev *et al.* 2018](#_ENREF_13); [Naya, Naya & White 2018](#_ENREF_43); [Rohr *et al.* 2018](#_ENREF_51); [Sørensen *et al.* 2018](#_ENREF_55); [White *et al.* 2019](#_ENREF_58)). Spatial bias in existing data is already well documented ([Addo-Bediako *et al.* 2001](#_ENREF_2); [Chown *et al.* 2002](#_ENREF_15); [Dillon *et al.* 2010](#_ENREF_20); [Clusella-Trullas *et al.* 2011](#_ENREF_16); [Seebacher *et al.* 2015](#_ENREF_54)), and our aim was to quantify the extent to which this known bias limits our capacity to forecast responses to climate change.

For each trait record, we first extracted associated data for mean annual temperature, total annual precipitation, the standard deviation of annual temperature and the coefficient of variation of annual rainfall from recent (1970-2000) climatologies with 10 arc-minute resolution ([Fick & Hijmans 2017](#_ENREF_24)). Data for annual precipitation were log10(x + 1) transformed, and the global range of values for each climate variable was scaled to fall between 0 and 1. Next, we assessed the distribution of potential future climates, by generating 5329 randomly selected locations (i.e., the same size as the empirical data set) around the globe, using the ‘dismo’ v1.3-3 ([Hijmans *et al.* 2013](#_ENREF_26)) package in R v4.0.3 ([R Core Team 2020](#_ENREF_49)), and extracted climate data for these locations. This process of generating 5329 randomly selected locations and associated climate data was repeated 1000 times to yield 1000 “sets” of randomly selected locations and climates.

We also extracted climate projections (CMIP Phase 6) of mean annual temperature, total annual precipitation, the standard deviation of annual temperature, and the coefficient of variation of annual rainfall for the year 2050 (average for 2041-2060) at 10 arc-minute resolution based on 8 global climate models (BCC-CSM2-MR, CanESM5, CNRM-CM6-1, CNRM-ESM2-1, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MRI-ESM2-0) under the Shared Socio-Economic Pathway 2-4.5 scenario ([Eyring *et al.* 2016](#_ENREF_23)). Data for annual precipitation were log10(x + 1) transformed, and all future climate projections were scaled using the data ranges for the 1970-2000 climatologies. We then extracted 125 sets of 5329 random locations for each of the 8 models (1000 sets in total). For each of the 1000 sets, we report the mean value, the range, and the 95% confidence interval estimated using the 2.5th and 97.5th percentiles.

We next estimated four-dimensional hypervolumes ([Blonder *et al.* 2014](#_ENREF_8); [Blonder *et al.* 2018](#_ENREF_9)) for the empirical data set of 5329 data locations ("studied environments"), and for the 1000 randomly generated data sets of 5329 random locations ("random environments"), using the *hypervolume* function of the ‘hypervolume’ package v 2.0.12. Hypervolumes are characterised by *n* axes that constitute an *n*‐dimensional Euclidean space, from which a geometrical shape can be defined and used to describe the size, position and geometry of the system ([Blonder *et al.* 2014](#_ENREF_8); [Blonder *et al.* 2018](#_ENREF_9)). The hypervolume concept was introduced by [Hutchinson (1957)](#_ENREF_31) to describe the range of environments that permit a species to exist, with axes corresponding to environmental factors that affect organismal performance ([Holt 2009](#_ENREF_29)). Here we estimate hypervolumes that describe the range of environments occupied by species that have been studied to date, as well as for the environments available to species at present and in the future, with axes corresponding to measures of the mean and variability of temperature and precipitation. A hypervolume can also be described as a probability distribution over these axes, which can be used to create a geographic suitability map based on a set of input climatologies and the probability density function within the hypervolume ([Blonder *et al.* 2018](#_ENREF_9)).

 We then quantified the discordance between the current climate at studied environments, and the current or future climates at random environments. Discordance was determined by calculating the proportion of the hypervolume of studied environments that falls outside of the hypervolume of the random environments, and vice versa, using the *hypervolume\_overlap\_statistics* function. A null expectation for discordance between hypervolumes was generated by comparing 1000 pairs of random four-dimensional hypervolumes, each generated using 5329 random locations. On average, discordance between randomly generated hypervolumes within a pair was 6.8% (range: 3.6 – 15.4%; 95% CI: 4.3%, 11.8%) of the total hypervolume.

Finally, we calculated a geographic suitability map by projecting the four-dimensional hypervolume for current environments onto the 1970-2000 climatology, and onto each of the eight future climate projections, to visualise the extent to which our existing knowledgebase is applicable to the current and future global range of environments. This was achieved using the *hypervolume\_project* function.

**3. RESULTS**

Studied environments exhibit a profound spatial bias (Figure 1). A mean of 3.2% (range: 2.0 – 4.8%, 95% CI: 2.4%, 4.2%) of the hypervolume describing the studied environments fell outside of the hypervolume describing the randomly selected current environments. Based on comparison of 95% CIs, this is significantly less than expected by chance, presumably because of the inclusion of a small number of studies that each intensively sample a small number of sites (e.g. [Londoño *et al.* 2015](#_ENREF_39); [Bushuev *et al.* 2018](#_ENREF_13)). A mean of 85.9% (range: 84.9 – 86.7%, 95% CI: 85.2%, 86.7%) of the hypervolume describing randomly selected current environments fell outside of the hypervolume describing the studied environments, which is significantly more than expected by chance.

A mean of 4.8% (range: 3.6 – 6.4%, 95% CI: 4.0%, 5.7%) of the hypervolume describing the studied environments fell outside of the hypervolume describing the randomly selected future environments, which is not significantly different from that expected by chance. A mean of 85.0% (range: 84.4 – 85.6%, 95% CI: 84.4%, 85.6%) of the hypervolume describing randomly selected future environments fell outside of the hypervolume describing the studied environments, which is significantly more than expected by chance.

Projections of the studied environment hypervolume onto current (Figure 2a) and projected future (Figure 2b) climatologies revealed strikingly similar patterns. In both cases, the geographic suitability maps exhibit regions with near zero suitability score (probability density) estimates, indicated that large regions of the surface have climates that are not encapsulated by studied environments.

**4. DISCUSSION**

Our analysis confirms that the studied environments exhibit a profound spatial bias (Figure 1), and that the environments from which physiological data were obtained represent just a subset of the range of predicted future climates. These findings are significant because current knowledge of physiological traits is used to predict the impact of climate change ([Diamond *et al.* 2012b](#_ENREF_19); [Duarte *et al.* 2012](#_ENREF_21); [Janion-Scheepers *et al.* 2018](#_ENREF_33); [Pinsky *et al.* 2019](#_ENREF_47)), but this knowledge is derived from species living in environments that are not representative of many current and predicted future environments (Figure 2).

Many of the regions that are not represented by the studied environments are at high latitude (e.g. Antarctica and Greenland), but there are also significant data-poor expanses elsewhere, including the Saharan and Sahel regions of Africa, parts of the Andes, the northmost regions of north America, and much of Eurasia except western Europe and south-east Asia (Figure 2). A surprising point of distinction between the maps of geographic (Figure 1) and environmental (Figure 2) coverage is that although the tropics are in general rather poorly sampled (Figure 1), environmental coverage through this region is nearly complete (Figure 2). Projections of the climate data from studied environments onto current (Figure 2a) and future (Figure 2b) climates are strikingly similar, suggesting that the major source of uncertainty is not derived from the difference between current and future climates, but instead arises from our poor understanding of animals from many geographic regions of the world (Figure 1 and 2). The responses of animals from unstudied environments to future conditions are difficult to predict, because they may have trait values, including capacities for trait plasticity, that differ in systematic but currently unknown ways from the species that have so far been studied.

In recent years it has become clear that the effects of environmental stressors are typically interactive, such that the response to multiple stressors can be greater or less than the additive combination of the individual effects ([Crain, Kroeker & Halpern 2008](#_ENREF_17); [Alton & Franklin 2017](#_ENREF_4)). Yet the vast majority of assessments of climate change risk consider only a single stressor ([Kaunisto, Ferguson & Sinclair 2016](#_ENREF_35); [Rosenblatt & Schmitz 2016](#_ENREF_52); [O'Brien *et al.* 2019](#_ENREF_44)), and most broad-scale studies of the effect of climate on functional traits test only for additive effects, though there are exceptions ([White *et al.* 2007b](#_ENREF_57); [Naya *et al.* 2018](#_ENREF_43)). Extrapolation from our current knowledge base to predict the outcomes of climate change will be challenging, because predictions are required for animals that live in environments with combinations of environmental conditions that have not yet been studied.

The recognition of geopolitical biases in epidemiology led to the formulation of specific strategies to redress this bias ([Jones *et al.* 2008](#_ENREF_34)), and recent work has proposed strategies to overcome spatial biases in conservation research ([Reboredo Segovia, Romano & Armsworth 2020](#_ENREF_50)). We suggest that a similar effort is necessary to understand where the impacts of climate change will be most profound, and where conservation efforts will be most necessary. Expansion of data compilations to include the non-Anglophone literature would be a useful first step, followed by efforts to measure species from regions with climates that are not represented in the existing data (Figure 2).

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**FIGURE 1** The spatial distribution of functional trait knowledge, visualised as the number of data values within 250 km of each grid cell at 1 arc minute resolution.



**FIGURE 2** Geographic suitability maps depicting the congruence between the climate at studied locations and at (a) current and (b) future global environments. Suitability scores (probability densities) near zero indicate locations with climates that are poorly represented by the climates at studied locations; higher suitability scores indicated locations with climates that are well represented by studied locations. (a) estimates of the four-dimensional hypervolume describing the current climates for studied environments projected onto current (1970-2000) global climatologies. (b) Suitability score estimates of the four-dimensional hypervolume describing the current climates for studied environments projected onto future climatologies (CMIP Phase 6) for the year 2050 (average for 2041-2060) under the Shared Socio-Economic Pathway 2-4.5 scenario, averaged over 8 global climate models (BCC-CSM2-MR, CanESM5, CNRM-CM6-1, CNRM-ESM2-1, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MRI-ESM2-0). Four-dimensional hypervolumes were constructed using data for mean annual temperature, total annual precipitation, the standard deviation of annual temperature, and the coefficient of variation of annual rainfall.

**TABLE 1**. Summary of the traits for which data were compiled, and the distribution across major taxonomic groups. Note that the total number of records is larger than the total number of species, because data are available for more than one trait for some species.

 acc CTmax CTmin DGC FMR FT\_FA MMR RMR T.LL T.UL Topt\_d Topt\_g Topt\_l n.species
Actinopterygii 137 0 0 0 0 0 0 0 0 0 0 38 22 65
Amphibia 32 923 0 0 0 0 0 0 0 0 0 0 74 260
Arachnida 24 0 0 0 0 0 0 0 0 0 4 4 5 13
Aves 0 0 0 0 190 0 64 460 0 0 0 0 0 539
Insecta 4 678 85 76 0 428 0 91 273 155 120 77 21 1018
Mammalia 0 232 277 0 112 0 0 458 0 0 0 0 0 606
Reptilia 34 0 0 0 142 0 0 0 0 0 0 0 89 136
Total 231 1833 362 76 444 428 64 1009 273 155 124 119 211 2637

acc: acclimation capacity ([Seebacher *et al.* 2015](#_ENREF_54))

CTmax: critical thermal maximum (°C)

CTmin: critical thermal minimum temperature (°C)

DGC: Discontinuous gas exchange characteristics ([White *et al.* 2007b](#_ENREF_57)), which are related to fitness ([Schimpf *et al.* 2012](#_ENREF_53)).

FMR: Field metabolic rate (kJ day-1)

Tsc: Supercooling point (°C) and an indication of freezing tolerance (FT) or freeze avoidance (FA)

RMR: Resting metabolic rate (kJ day-1)

T.LL: Lower lethal temperature (°C)

T.UL: Upper lethal temperature (°C)

Topt\_d: Optimum temperature for development (°C)

Topt\_g: Optimum temperature for growth (°C)

Topt\_l: Optimum temperature for locomotion (°C)