MetaR, a global database on metabolic rates of ectotherms

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Abstract

Whole-organism metabolic rate is a key trait for understanding ectotherms' responses to ongoing environmental change. It represents the interface through which organisms interact with their environment and therefore allows for making predictions across various levels of biological organisation. While much of the variation in metabolic rates is explained by body size and temperature, a considerable part of this variation remains unexplained. Lack of standard research practices, data sparsity and insufficient coverage of various taxa limit our capacity to conduct a meaningful synthesis across the Tree of Life; both in the spatial and the temporal dimension. To overcome these limitations, and acquire a better understanding of the evolution of metabolic rates, we created MetaR: which is to date the most comprehensive database on intra- and interspecific variations in ectotherms' metabolic rates. This database currently comprises over 95,000 records covering more than 2,400 species across 16 phyla of ectotherms, encompassing both invertebrates and small and large vertebrates from marine, intertidal, freshwater and terrestrial ecosystems. MetaR also integrates methodological details, which further improves our capacity, on the one hand, to detect ecological, physiological and evolutionary patterns and, on the other hand, to forecast the functional impacts of global environmental changes across the Tree of Life from a metabolic perspective.

Background & Summary

Initiatives developed for centralising and standardising the large body of literature on functional traits offer great potential to achieve a broader understanding of ecological and evolutionary mechanisms occurring in nature[1–4]. One critical aspect is the necessity for an interface facilitating the interaction between organisms and their environment, which is vital for comprehending the repercussions of global environmental changes across various levels of biological organisation, encompassing both aquatic and terrestrial ecosystems. In this sense, whole-organism metabolic rates – usually measured through oxygen uptake, reflect the energy requirements of metabolic processes associated with ATP production during aerobic respiration[5–7]. The metabolic rate of an organism is a key functional trait in physiology, ecology and evolution for understanding ectotherms' responses to ongoing environmental change, and it has important fitness implications for organisms and demography[8–10]. Metabolic rates govern the pace of life; i.e. the rate at which each organism processes energy and materials to grow, reproduce, live and move. Using this fundamental trait therefore allows us to predict most observed ecological processes at the level of organisms, populations, communities and ecosystems[9,11,12].

Body size and body temperature are tightly related to metabolic rates and therefore, not surprisingly, these are two key parameters of the *Metabolic Theory of Ecology* (MTE)[9]. MTE proposes that metabolic rates vary with body temperature and it scales with body mass according to a power relationship with an exponent of around three-quarters[9]. Although the universality of the MTE predictions is debated[13–18], the fact remains that most of the variation in metabolic rates can be explained by differences in body mass and temperature[9,19]. However, even after accounting for these two factors, a considerable amount of intra-individual, and inter-and intraspecific variation remains unexplained. For instance, there is substantial variation (often ∼2-fold, on a $\log_{10}$ scale) across spatial and temporal scales[20], and developmental stages[21], lifestyle and activity levels[22]. The next natural step is to explore which other traits, together with body size and body temperature, can explain this variation. Reconciling the different views of this debate is, however, a serious scientific challenge, that has been exacerbated by the lack of standard research practices, resulting in methodological differences among studies, data sparsity, and insufficient coverage of metabolic data across the Tree of Life. This in turn has limited the establishment of a meaningful synthesis to date[5].

To overcome these limitations, we have created MetaR, the largest database focusing on the metabolic rates of metazoans, with the scope to unveil eco-physio-evolutionary patterns undescribed to date and investigate the impacts of global environmental changes on this central physiological trait. We assembled and curated a large, intra-and-interspecific database on metabolic rates of ectotherms (invertebrates, fishes, amphibians and reptiles), globally distributed across all realms (marine, freshwater, intertidal and terrestrial), climate zones (polar, temperature and tropical), and from the deepest ocean to the highest mountains.

Methods

In reporting and describing our methods, we adhere to the MeRIT guidelines outlined by Nakagawa et al.[23] for enhanced clarity and transparency.

Literature search. Félix P. Leiva (FPL) searched published literature for studies quantifying metabolic rates in invertebrates and vertebrates using various searching methods. We could not follow a step-by-step Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) approach[24] due to barriers to accessing data associated with the use of search engines such as ISI Web of Science and Scopus at the time FPL initiated this project (year 2007). Despite the mentioned limitations, the current version of MetaR far exceeds any other database on this topic in terms of the number of records, metadata, number of articles, and species included, as well as the spatial and temporal coverage of the data available in the literature to date.

From 2007 to 2016, focusing specifically on invertebrates, FPL used Google Scholar regularly to search for primary articles reporting metabolic rates by using the following keyword combinations: (metabol* OR oxygen consumption OR metabolic rate OR respiration) AND (acidification OR hypoxia OR salinity OR temperature OR scaling) AND (clade names). For clade names, the following terms were employed: "invertebrates" OR "coral" OR "arthropod*" OR "insect*" OR "crustacea*" OR "arach*" OR "echinoderm*" OR "molluscs" OR "gastropod". Measuring oxygen uptake as a proxy for metabolic rates is considered an informative physiological trait for assessing whole-organism performance in response to environmental stressors[25,26]. Therefore, the terms acidification, hypoxia, salinity, and temperature were included in the search due to their potential to cause reductions in the performance or fitness of organisms, especially in the context of global climate change[27,28]. The literature search resulted in >5,000 publications. After a thorough examination of their abstracts and titles, 1,253 full-text articles were downloaded for a more detailed screening.

On the 14 of March 2021, FPL used ISI Web of Science to search for literature on amphibians, reptiles and fishes using a similar combination of Boolean terms as for invertebrates. For amphibians, the following combination was used: (metabol* OR oxygen consumption OR metabolic rate OR respiration) AND (amphibia* or salamander OR caecilian OR siren OR newt* OR frog* OR toad* OR tadpoles). For reptiles the following combination: (metabol* OR oxygen consumption OR metabolic rate OR respiration) AND (reptil* OR crocodile* OR alligator* OR tuatara* OR lizard* OR snake* OR turtle*). For fishes the following combination: (metabol* OR oxygen consumption OR metabolic rate OR respiration) AND (fish*). The search was refined by focusing on specific categories such as zoology, physiology, biology, ecology, biochemistry molecular biology, evolutionary biology, multidisciplinary sciences, environmental sciences, marine and freshwater biology, toxicology, genetics heredity, veterinary sciences, behavioural sciences, endocrinology metabolism, fisheries, biodiversity conservation, respiratory system, and oceanography. The search spanned from 1945 to 2020 and included only primary references. Using this approach, 652 primary references were obtained for amphibians, 1,265 for reptiles, and 5,510 for fishes.

Additionally, in an attempt to supplement this search, FPL compiled references from meta-analyses[29–33], comparative approaches[8,34–41], books[42–45], and literature reviews conducted on various aquatic-living taxa, including crustaceans and molluscs, among others[46–48]. FPL also utilized the list of references of articles that have conducted previous compilations on metabolic scaling[22,40,49,50]. In addition, on June 12, 2020, a list with a total of 348 references was downloaded from FishBase[51]. Many of these references were not possible to access or were not available digitally. Since last verified (December 2023), FishBase had not incorporated additional data on metabolic rates in fishes.

Until January 2024, FPL contacted the corresponding authors requesting additional data related to the estimation of metabolic rates for some articles published between 2001 and 2022, in which it was not possible to extract the data adequately from the figures. In total, 13 researchers responded positively (out of the 62 researchers we contacted) to this request, providing their data. Their names are listed in the acknowledgements section.

All references were imported into Zotero for better management, and the existence of duplicates was checked using the same open-source software. The complete list of literature used in the current version of MetaR is publicly supporting material in the form of a *.ris file (Supplementary Information).

Structure of MetaR. MetaR is a relational database built in Microsoft Access using nested tables. Currently, the database consists of four tables that provide details on the reference, taxonomy, origin, and oxygen uptake of ectotherms. The relational database, maintained and curated for internal control, is shown in the supplementary information and the GitHub repository (https://github.com/felixpleiva/MetaR/blob/main/DB_relationships.md). The data structure undergoes a transformation into a spreadsheet file through a query, encompassing an extensive table of trait records and metadata measured at the individual level, as much as possible.

Data extraction. Combining all the searching methods, FPL screened > 12,775 references, which included primary published, peer-reviewed scientific studies, as well as grey literature, theses, and books. A study was included in our database if the metabolic rate was measured at the individual level in any subspecies, species, or genus of metazoan. Metabolic rates data from various specimens, which were aggregated, were not incorporated into the current database. We attempted to consider the primary reference reporting the data as much as possible. Hence, review articles were also excluded if the data were reported in a previous study. Applying these criteria, we obtained a total of 2,145 papers considered for data extraction.

We followed the classification given by the authors for life stages and type of metabolic rate. Rates of oxygen uptake were categorized as routine (RMR), resting, standard (SMR), maximal (MMR), or active based on the terminology used in the original publications, or classified by the definitions proposed by Chabot et al.[52] and Brett[53]. We made several assumptions in our data collection process. When a study reported only body mass or only metabolic rates as an interval, we calculated a mean value based on that interval. If the papers did not specify the type of body mass used (e.g., fresh mass, dry mass, ash-free dry mass) or did not provide procedures for drying the animals, we assumed that the reported mass was fresh mass. Whenever possible, we included this information in the comments. In studies where the authors mentioned the use of freshwater, tap water, or dechlorinated water during the conditions of maintenance, rearing, acclimation, and testing, we assumed a salinity of 0 for all these conditions. Important to mention is that the data points we used represent actual observations and not estimates generated by linear models unless otherwise specified in the legend of figures of the primary references. For instance, some studies included partial residuals for metabolic rate data, and in such cases, those studies were not included in our database. In cases where metabolic rate data were presented graphically but no information was reported in the text or a table, we used the Java program Plot Digitizer, designed for extracting X-Y coordinates from graphs (http://plotdigitizer.sourceforge.net).

Geographical position, depth and elevation of the collection. We harmonized the geographical positions from where the species were collected using the World Geodetic System (WGS84) as the reference geographical coordinate system. The geographic coordinates were converted, if necessary, to decimal degrees, both for latitude and longitude. In various cases, numerous researchers collected animals from different geographical locations, elevations and depths. Despite these specific locations, elevations and depths being explicitly mentioned in the paper, in some articles the authors chose to present the data as a combined dataset, regardless of the various spatial scales at which the data was collected. In these cases, we calculated the mean geographical coordinates, as well as the depth and elevation concerning their respective country, region, province, county, city or locality, as given in the original data sources. For those species for which we could not obtain geographical coordinates from the paper, we used the description of the locality or the geographical reference point mentioned by the authors in the paper. We inspected the spatial distribution of the sites visually and then manually georeferenced them using Google Earth (https://www.google.com/earth/) or GeoNames (https://www.geonames.org/) when the reference point was clearly mentioned (e.g., Isla Chiloé). The details of which approximations were used are described in the respective comments column of the database. When specimens were collected from different locations and mixed during experiments, we chose the central geographical reference within these locations. However, when the locality was treated as a factor distinguishable in the article or its figures or tables, we included these entries independently to make the distinction. As part of a forward search, additional data were sought in case reference was made to another paper describing, for example, animal collection sites or methodological aspects. In such cases, the additional paper was downloaded and used to complement the missing information.

Taxonomy and phylogeny. FPL verified the scientific names of species in the database by manually cross-referencing them with the Open Tree of Life[54,55]. Subsequently, we employed the same taxonomic harmonization procedure outlined by Lenoir et al.[56]. This taxonomic harmonization process consists of three steps: (1) searching for names in the National Center for Biotechnology Information (NCBI) taxonomy database, (2) confirming any taxonomic entities not found in NCBI using the Integrated Taxonomic Information System (ITIS) database, and (3) checking the remaining entities not found in NCBI and ITIS against the Global Biodiversity Information Facility (GBIF) database. In cases where a match was identified, the corrected taxonomic entity underwent the entire procedure again, including verification in NCBI and ITIS, to ensure a reliable taxonomic classification. Ultimately, only names at the species and genus levels were retained for the database, with subspecies aggregated at the species level. The R packages "rgbif v3.7.8"[57] and "taxize v0.9.98"[58] were utilized for this harmonization procedure.

Before gathering information about phylogenetic relationships, the most recent version of our database, as of February 2024, encompassed 2,459 entries representing taxa up to the species and subspecies level. The phylogenetic tree retrieved from the OTL underwent pruning to retain only those species present in our database using the package "rotl"[59]. Entries lacking phylogenetic information or flagged as "incertae_sedis_inherited", "extinct, incertae_sedis, sibling_higher", "hidden" and "unplaced_inherited" were excluded. Consequently, the final count of species in the current version (v1.0.0) of MetaR has been streamlined to 2,287 distinct species, each accompanied by phylogenetic information (Fig. 3).

Data Records

MetaR includes 95,373 records on metabolic rates for 2,459 species across 16 phyla, 58 classes, 220 orders, 780 families and 1,623 genera, ranging from invertebrates to small and large vertebrates from marine, intertidal, freshwater, and terrestrial realms, extracted from primary references published between 1914 to 2022 (Figs. 1-3). Based on studies that reported geographical positions (N = 1,345), most of the studies (> 75 %) incorporated in our database were conducted in the North Hemisphere (1,020 articles, 1,557 species, 52,130 records) compared to the South Hemisphere (343 articles, 566 species, 22,081 records) (Fig. 1).

For each paper, we include up to 95 characteristics associated with metabolic rates, when available. Taxonomically speaking, Arthropoda, Chordata, Mollusca, Echinodermata, Cnidaria, Annelida, Nematoda and Chaetognatha are the main phyla present in this version of MetaR. They contain, respectively, 0.10%, 1.20%, 0.29%, 0.90%, 0.32%, 0.24%, 0.17% and 12.88% of the species described on Earth (https://www.catalogueoflife.org/, accessed on the 22 of March 2024 and considering accepted species only). On the other hand, the phyla Porifera, Ctenophora, Brachiopoda, Nemertea, Rotifera and Gastrotricha, and to a greater extent, Platyhelmynthes and Bryozoa, are underrepresented (Fig. 3). Records on metabolic rates included in this version of MetaR show a range of variation from -7.032 to 4.621 mg O2 h^{-1} ind^{-1}, equivalent to 11.6 orders of magnitude (in $\log_{10}$ scale). The body temperatures at which these rates were measured ranged from -5°C to 47°C. On the other hand, the smallest species included in this version corresponds to the nematode *Plectus palustris*, weighing 0.06 µg of fresh mass, while the largest species corresponds to the green sea turtle *Chelonia mydas*, weighing 142 kg of fresh mass (Fig. 4). All these records were retrieved from more than 1,800 primary references.

We foresee that MetaR will make a substantial scientific contribution by shedding light on the longstanding question of what influences variation in metabolic rates. Despite the widespread coverage, our database reveals evident geographic and taxonomic biases. Notably, Russia, northern Canada, northern Africa, and the tropics lack studies on metabolic rates. On another hand, except Chaetognatha, all other phyla included here are underrepresented, and none of them exceeds 1.2% of the total number of species *per* phyla. Our forthcoming step entails conducting a quantitative and qualitative analysis to map and identify existing knowledge gaps. This analysis will establish a basis for addressing future research questions utilizing the most comprehensive dataset on metabolic rates over the last century.

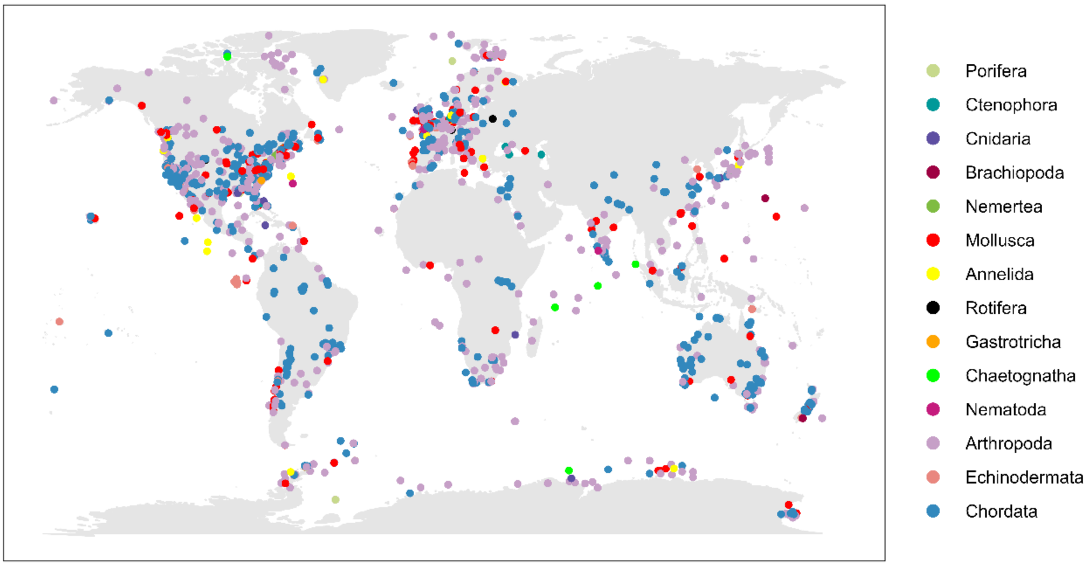

Figure 1. Map illustrating the geographical locations where ectotherms species were collected. Colours define different phyla included in MetaR. The data represent 1,577 unique geographical positions reported in 1,345 studies.

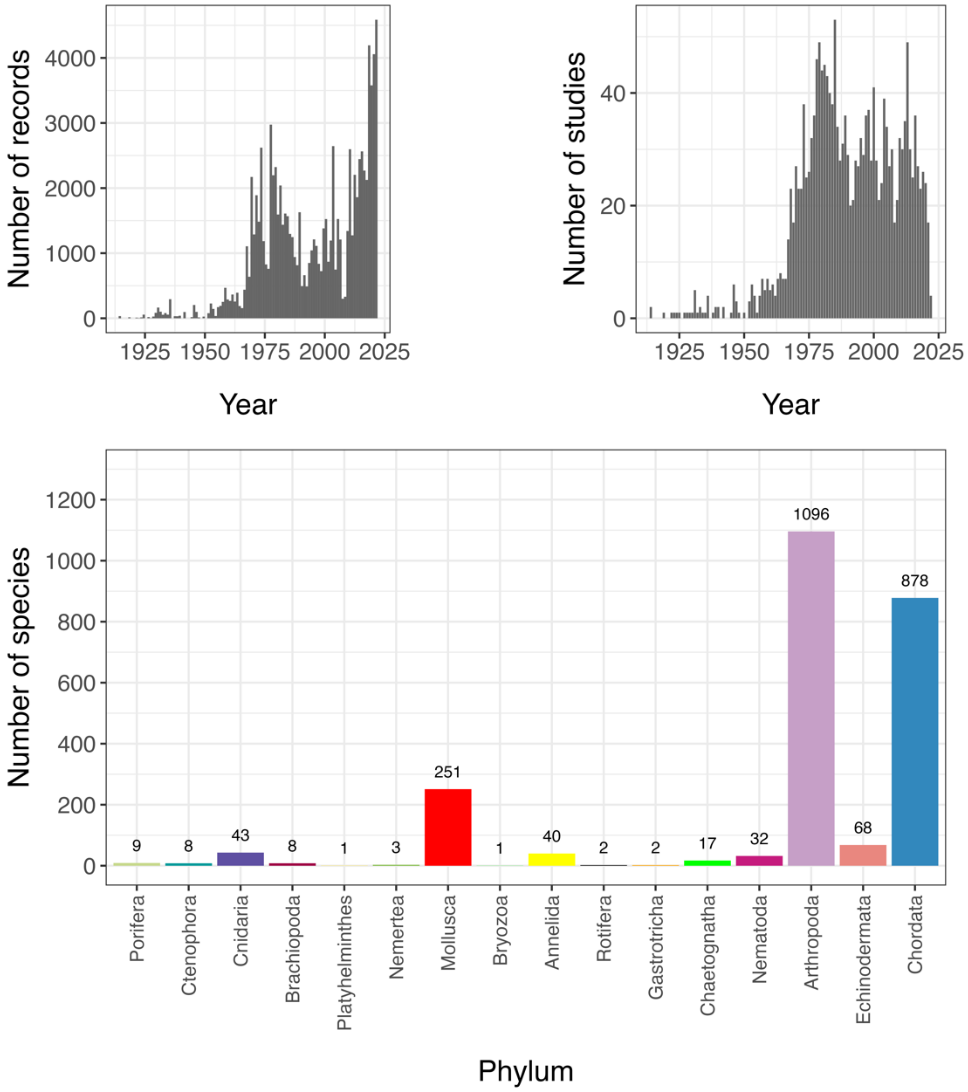

Figure 2. (a) Total number of records, (b) studies along the years (from 1914 to 2022) and (c) number of species by Phylum included in MetaR. The colour-coded bars match the ones used in Figure 1 to represent different phyla.

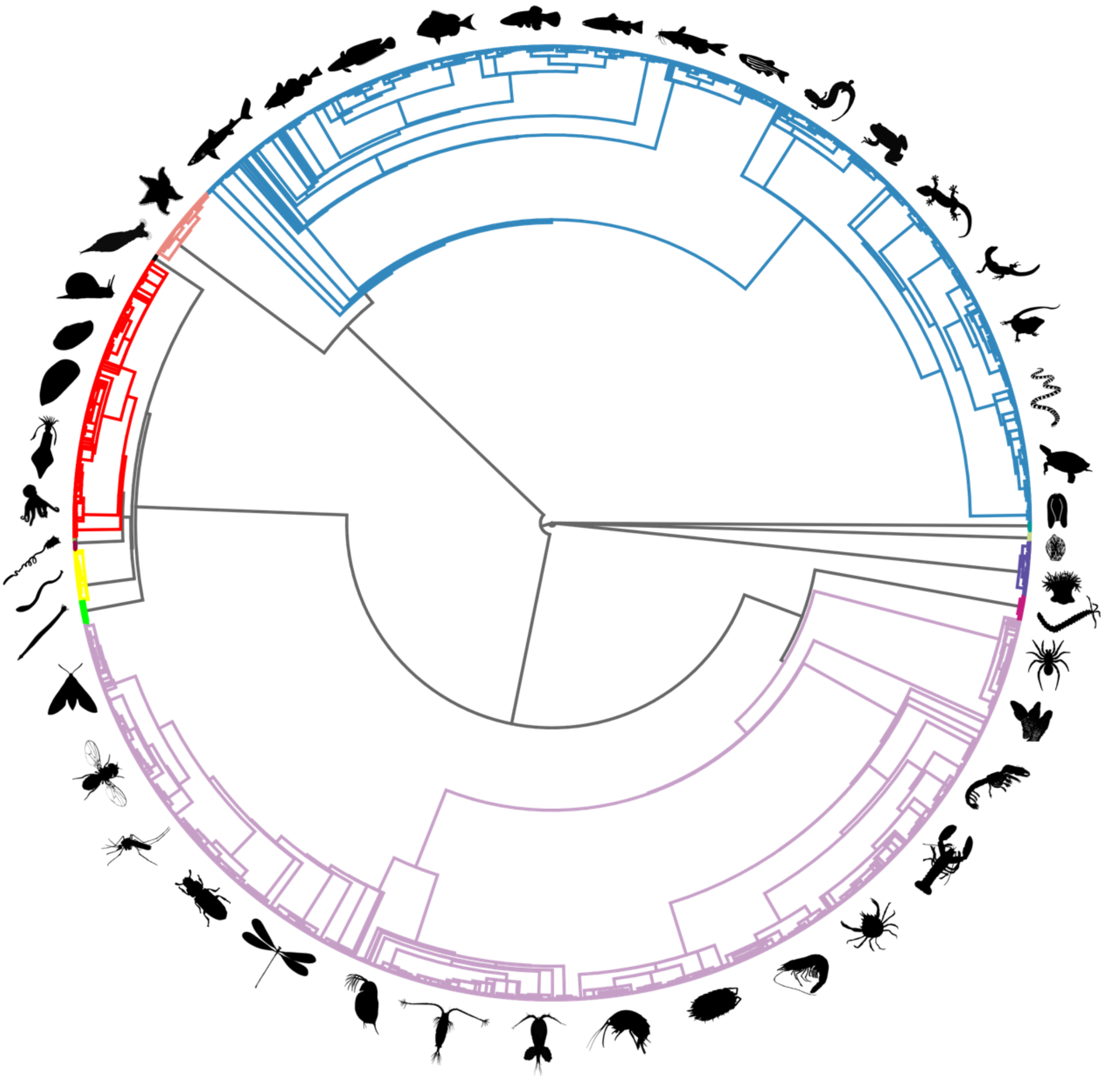

Figure 3. Phylogenetic tree showing the relationships among the 2,287 ectotherms species included in the current version of MetaR and for which we have phylogenetic information from the Open Tree of Life. Dots are colour-coded to match the ones used in previous figures to represent different phyla. The tree is plotted using the R package "*phytools*"[60]. Silhouettes are available for reuse on PhyloPic (www.phylopic.org) under the Public Domain Dedication 1.0 license.

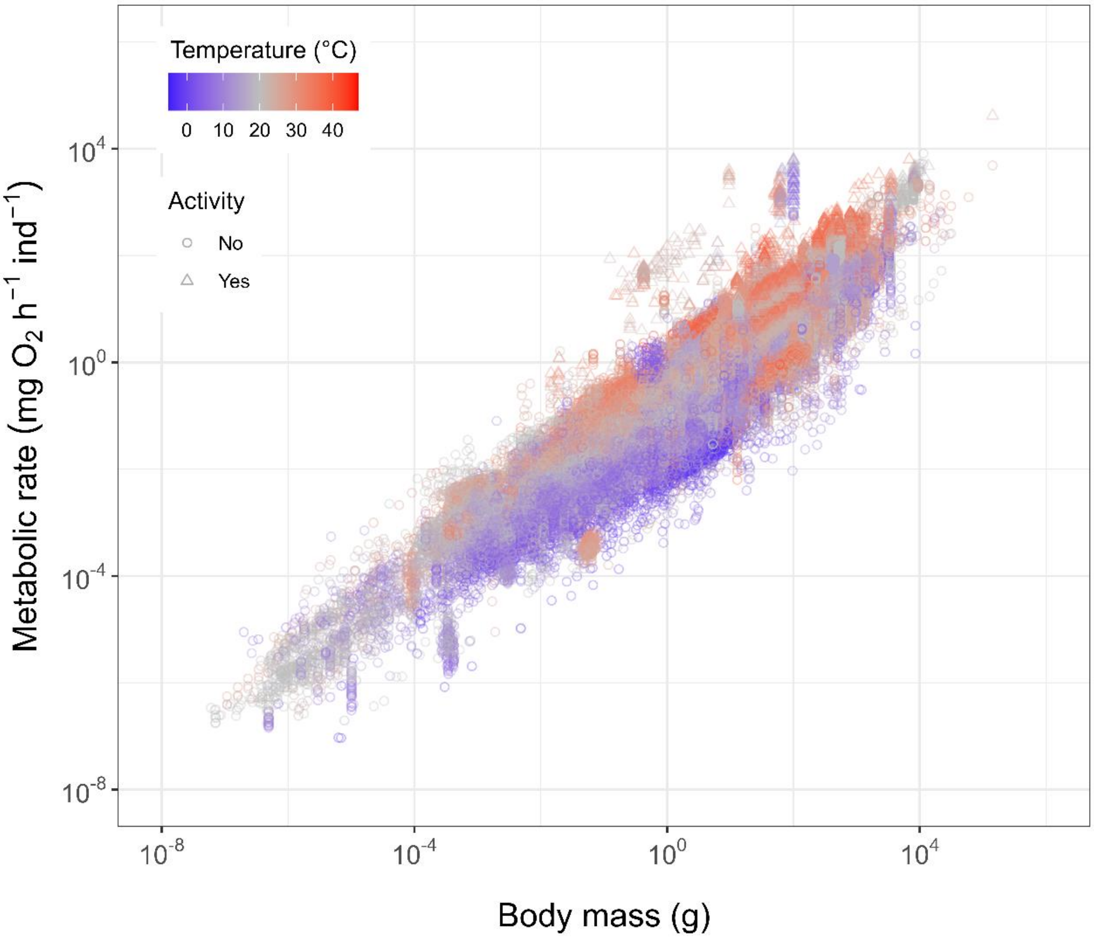

Figure 4. Scaling of metabolic rates with body mass using data gathered from ectotherms species across various geographical locations and realms. Measurements were conducted under diverse experimental conditions, encompassing factors such as temperature, oxygen levels, salinity, pH, CO_2, photoperiod, humidity, and food type. Additionally, observations were recorded across different sexes, life stages, and activity levels, including standard, routine, resting, minimum, and basal metabolic rates, as well as active, field, flight, maximum, and swimming activities. Coloured points represent the measurement temperature range from -5°C to 47°C, illustrating the breadth of metabolic rate variation captured in MetaR.

Technical Validation

We have established a procedure to examine inconsistencies in our database, covering both discrete and continuous variables. We methodically detect, assess, and rectify potential inconsistencies and deviations in metabolic rate data. Specifically, these inconsistencies and deviations were evaluated in the well-known biological pattern of allometric scaling. FPL fitted a $\log_{10}$-$\log_{10}$ ordinary least square model between body size and metabolic rate and then calculated z-scores for the residuals of this model. These scores measure the extent of deviations from the mean, facilitating the identification of potential outliers or significant variations within the dataset based on a predefined, random threshold of 2.5. Once potential outliers were identified, the corresponding entries were examined, and any record that seemed inconsistent was rechecked against the source. Other steps included verifying the accuracy of the names of discrete variables and their units. All of these steps and potential corrections were implemented before the release of this database (v1.0.0).

Usage Notes

The most recent versions of the MetaR database will be accessed and downloaded from the GitHub repository (https://github.com/felixpleiva/MetaR). When citing MetaR in a manuscript, users should indicate the exact version they used, together with this data paper. Explicitly specifying the version is crucial when utilizing the data to guarantee the reproducibility of any subsequent analyses and, if possible, citing the primary references gives credit to the original publications used to build this database.

We provide MetaR with several metadata related to the experimental determination of metabolic rates. This allows users to incorporate such information to test the robustness of conclusions emerging from their analyses, but also to filter data based on their specific requirements. Given the versatility of the structure of our database, as well as the variety of metadata present in it, we have included many columns of information regarding maintenance, rearing, acclimation, and testing conditions. Many of the studies manipulated single or multiple combinations of environmental factors, such as temperature, oxygen, salinity, carbon dioxide, pH, humidity, photoperiod or measuring different types of metabolic rates at different life stages and sexes. MetaR contains all these data, which means users should pay special attention to filtering the data of interest that allows them to address their specific questions. Some studies use the term "acclimation" to refer to various aspects. For example, it may denote the maintenance of animals in the laboratory, exposure to environmental conditions before experiments, or during acclimation to the respirometry chamber. Special attention was given to avoid misinterpretations of the experimental design by incorporating such information into the corresponding column. For each paper included in MetaR, there is, for instance, a column designated for maintenance temperature, rearing temperature, acclimation temperature, and testing temperature. This applies to all other environmental factors, such as oxygen, salinity, carbon dioxide, pH, humidity, photoperiod and food type. Important to note is that many of these columns correspond to an expansion of the guidelines provided by Killen et al. al.[61] for aquatic respirometry, which is also applicable to terrestrial respirometry. In addition, many studies simply report the means in tables or figures. When this was the case, we also took the sample size and the associated error for the respective measure of central tendency so that it could be used for meta-analytic approaches. In an effort to help MetaR users filter and download a subset of data of interest, we have developed an R script for this purpose. This R code is customizable, including options to calculate mean values and to select data based on taxonomic entities and relevant covariables, such as swimming speed, which could in addition serve as a metric for studies in thermal performance. Additionally, the R code allows the inclusion of primary references that, as much as possible, should be cited when appropriate.

Initially, all units of metabolic rates were converted to mg O_2 h^{-1} ind^{-1} (milligram of oxygen *per* hour *per* individual). To increase the reuse of MetaR and facilitate comparisons, we also transformed metabolic rates from mg O_2 h^{-1} ind^{-1} into units of concentration (mmol O_2 h^{-1} ind^{-1}), volume (mL O_2 h^{-1} ind^{-1}) and energy (Joules). We attempted to include rates of oxygen uptake (O_2) as much as possible. However, in cases where only rates of carbon dioxide production (CO_2) were measured, these were converted to rates of O_2 uptake by dividing the CO_2 produced by 0.85, which represents a respiratory exchange ratio based on the intermediate value between the use of lipids (0.7) and carbohydrates (1) as an energy substrate[6]. All body sizes were converted to fresh body mass in grams using appropriate conversion factors[8,62–66].

Code Availability

All materials, including the database, R code, and supplementary content, are licensed under the Attribution-NonCommercial-NoDerivatives 4.0 International license (CC BY-NC-ND 4.0). This license requires that reusers give credit to the creator. It allows reusers to copy and distribute the material in any medium or format in unadapted form and for noncommercial purposes only. The MetaR project is hosted and maintained on a GitHub repository (https://github.com/felixpleiva/MetaR) and will be assigned a DOI on Zenodo. This repository comprises files containing: 1) the database, 2) metadata, 3) a list of references and 4) a customizable R code. MetaR is under embargo until the 30 of June 2025 but will become open to the community afterwards, and users must refer to this data paper when utilizing the resource as well as the repository. We strongly suggest, if possible, citing the original articles that contributed a substantial proportion to the database. We also would appreciate it if users would bring to our attention errors or ambiguous values found in the database. MetaR will be updated as needed with new studies, as well as any identified errors will be corrected following the standard of the Semantic Versioning Specification (SemVer, https://semver.org/).

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Author contributions

Félix P. Leiva conceptualised the idea for this study and led all aspects related to the creation and implementation of MetaR over the last 17 years. Specifically, he is responsible for creating the structure of the database and ensuring its referential integrity, data entry and data curation and has led the writing of the manuscript. Félix P. Leiva created all figures with inputs from Wilco C.E.P. Verberk, Piero Calosi, Enrico L. Rezende and Felix C. Mark. All authors edited the manuscript and gave their approval for publication.

Competing interests

The authors declare no competing financial interests.

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