A phylogeny-informed characterisation of global tetrapod traits addresses data gaps and biases

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Abstract

Tetrapods (amphibian, reptiles, birds and mammals) are model systems for global biodiversity science, but continuing data gaps, limited data standardisation, and ongoing flux in taxonomic nomenclature constrain integrative research on this group and potentially cause biased inference. We combined and harmonised taxonomic, spatial, phylogenetic, and attribute data with phylogeny-based multiple imputation to provide a comprehensive data resource (TetrapodTraits 1.0.0) that includes values, predictions, and sources for body size, activity time, micro- and macrohabitat, ecosystem, threat status, biogeography, insularity, environmental preferences and human influence, for all 33,281 tetrapod species covered in recent fully sampled phylogenies. We assess gaps and biases across taxa and space, finding that shared data missing in attribute values increased with taxon-level completeness and richness across clades. Prediction of missing attribute values using multiple imputation revealed substantial changes in estimated macroecological patterns. These results highlight

biases incurred by non-random missingness and strategies to best address them. While there is an obvious need for further data collection and updates, our phylogeny- -informed database of tetrapod traits can support a more comprehensive representation of tetrapod species and their attributes in ecology, evolution, and conservation research.

Introduction

Over the past two decades biodiversity science has seen a dramatic growth in large-scale research in ecology, evolution, and conservation biology, enabled by near-global coverage for study systems such as terrestrial vertebrates, or Tetrapoda (amphibians, reptiles, birds, and mammals). These efforts usually rely on datasets spanning wide temporal, spatial, and taxonomic scales [1] that ideally are fully harmonised and well curated. Despite terrestrial vertebrates being a relatively well-known animal group when compared to invertebrates and plants [2,3], notable gaps persist across various attributes, including fundamental aspects of species natural history [4,5]. Consequently, trait-based research on biodiversity is often hampered by spatially and phylogenetically incomplete datasets [6–8].

Understanding causes of missingness is instrumental to advancing biodiversity data coverage. For any species attribute, there are observed and unobserved entries, each with a probability of being missing [9]. When all entries, whether observed or unobserved, share the same likelihood of being missing, data are said to be missing completely at random (MCAR). If missingness affects only observed entries, the data is termed missing at random (MAR). For example, a depleted digital scale battery makes weighing subsequent specimens impossible in the field, resulting in MAR data. Data is considered missing not at random (MNAR) when missingness is tied to unobserved entries, indicating a link to the missing values themselves. These three missing mechanisms – MCAR, MAR, MNAR – can lead to different configurations of the invisible fraction of the trait space [9–11].

While some missing mechanisms (e.g., MCAR, MAR) primarily affect a single attribute, the underlying cause behind an attribute MNAR can influence multiple variables, resulting in co-missingness or shared gaps. For instance, a species might lack information on multiple ecological aspects due to being known from only a few specimens with no details on where, when, and how they were found [12]. Similar circumstances apply to rare species or those collected solely through passive sampling techniques (e.g., pitfall traps), leaving ecological data unobserved. Indeed, bias is recognised in the availability of trait data for certain taxa, regions, and traits [4], and missing values for a given variable may be associated with incompleteness in others. Such congruent or aggregated (as opposed to segregated) patterns in trait missingness can arise from societal and research preferences for charismatic species [3], easily sampled taxonomic groups, or accessible geographical regions [6,13]. Conversely, segregated patterns may reveal traits and taxa that are challenging to sample or under-represented.

Despite the continued limitation of sampled data for many attributes in tetrapods, new methods can help to minimise these gaps and improve our understanding of biodiversity. Past practices have included the removal of species with missing data or the replacement of missing values by observed averages, but these strategies may ultimately reduce statistical power and increase bias [7,10,14]. More recently, growth in large-scale phylogenetic analyses has boosted the development of methods to increase the accuracy of imputing missing values [15–18]. Among tetrapods, recent large-scale applications of imputation methods include the use of phylogenetic regression methods and machine-learning techniques to predict missing values in trait data for amphibians [19], reptiles [19,20], birds [19,21], and mammals [19,21,22], as well as to inform threat statuses for data deficient and non-assessed species [20,23,24].

We leveraged a fast and automated multiple imputation technique with additional data mobilisation to provide a comprehensive database and assessment of key ecological attributes

of all extant 33,281 tetrapod species covered in recent fully-sampled phylogenies, including 7,238 amphibians [25], 384 chelonians and crocodilians [20], 9,755 squamates and tuatara [26], 9,993 birds [27], and 5,911 mammals [28]. Our assessment covered standardised species-level attributes for taxonomy, body size, activity time, microhabitat, macrohabitat, ecosystem, threat status, biogeography, insularity, environmental preferences, and human influence. Since not all species have genetic data (representing an important source of the remaining uncertainty about their placements in available phylogenies), we also evaluated completeness in genetic sequences [29]. We pinpointed taxa exhibiting pronounced shared missingness in natural history data to inform new strategies for data acquisition and mitigate biases in trait databases. To enhance database consistency, we taxonomically harmonised data sources and filled gaps using a phylogeny-based multiple imputation method [30–32] for which we verified the performance and associated uncertainty.

We use this gap-filled database to assess the geographic, taxonomic, and trait-related biases and evaluate how their model-based closure supports improved information and biological inference. Due to the biodiversity knowledge paradox – high biodiversity in the tropics [33] but better taxonomic sampling in temperate regions [4,5,34] – we expect larger unsampled fractions in the tetrapod trait space for tropical species. Similarly, the high research capacity (i.e., infrastructure and expertise availability) dedicated to birds and mammals relative to amphibians and reptiles [2,3] contributes to the uneven sampling of trait space [4], likely producing larger biases among historically undersampled taxa. Finally, species biology and sampling methodologies are known to affect detection and collection rates in the field [35–37]. For instance, detectability is typically lower for small- than large-bodied species, and similarly so for nocturnal relative to diurnal taxa [38–40], whereas sampling methodologies often favour the collection and research of species living on the surface compared to fossorial or arboreal groups [34,41–44]. We thus anticipate convergent missingness across trait space in tetrapods, and expect undersampled species to typically be small, nocturnal, and fossorial or arboreal.

Methods

We curated and assembled available databases for global tetrapod groups and used the latest phylogeny-based methods to create the most comprehensive tetrapod attribute dataset to date. While the TetrapodTraits database also covers a wide range of attributes derived from species range maps (see Table S1, Supporting Information), our focus regarding the imputations primarily centred on natural history traits, specifically: body length, body mass, activity time, and microhabitat. Our procedures can be summarised in five general steps: (i) data acquisition, (ii) taxonomic harmonisation, (iii) outlier verification, (iv) taxonomic imputation, and (v) phylogenetic multiple imputation.

Data Acquisition

We compiled species-level attributes regarding taxonomy, body size, activity time, microhabitat, macrohabitat, ecosystem, threat status, biogeography, insularity, environmental preferences, and associated data sources for each tetrapod species (Table S1). We gathered information from several global, continental, and regional databases, and complemented the existing data from published (articles, book chapters, field guides, and monographs) and grey literature (e.g., technical reports, government documents, monographs, theses). We also incorporated unpublished data gathered during fieldwork performed by some of us. To minimise the uneven representation of ecological attributes across clades, we initially identified genera and families whose species did not have available data on body size, activity time, or microhabitat. We then used species belonging to these genera and families to carry out additional online searches on academic platforms (Google Scholar and Web of Science) and included complementary attribute data whenever possible. To improve the chances of finding relevant natural history data [45,46], we conducted these searches using natural history terms in English (e.g., activity time, microhabitat, body size, length, mass, weight),

Portuguese (e.g., tempo de atividade, micro-habitat, tamanho de corpo, comprimento, massa, peso), and Spanish (e.g., tiempo de actividad, microhabitat, tamaño del cuerpo, longitud, masa, peso) along with the respective species scientific name or unique synonyms (see Taxonomic Harmonisation section). When sources were available in other languages, we employed translation tools for inspection (e.g., Google Translate). In our examination of the data sources, we did not use trait values provided solely at the genus level (e.g., mean value per genus).

Briefly, taxonomic data were represented by higher-level taxonomic ranks (Class, Order, Family), scientific name (same spelling as used in recent fully-sampled phylogenies), authority name, and year of description. Three broad natural history traits – body size, activity time, and microhabitat – have been compiled and harmonised across different tetrapod groups. Body size data consisted of information on body length (mm) and body mass (g). Activity time encompassed whether the species was diurnal and/or nocturnal. Cathemeral or crepuscular species were considered as both diurnal and nocturnal. Microhabitat included five categories of habitat use commonly reported in field guides and related literature: fossorial, terrestrial, aquatic, arboreal, and aerial.

Microhabitat categories are not mutually exclusive, meaning that a species can be present in more than one category to represent intermediate microhabitats, such as semifossorial (which involves both fossorial and terrestrial categories) or semiarboreal (which combines terrestrial and arboreal). Exceptionally for birds, we adapted microhabitat data from the EltonTraits database [47], which describes the estimated relative usage for seven types of foraging stratum. To make our definition of microhabitat similar across tetrapod groups, we reduced these seven categories to four by: summing the relative usage of species foraging below the water surface or on the water surface in the aquatic microhabitat; summing the relative usage of species foraging on the ground and below 2m in understorey as terrestrial; summing the relative usage of species foraging 2m upward in the canopy and just above canopy as arboreal. Species with aerial microhabitat were kept as defined in EltonTraits database [47], and no fossorial bird was reported in the later source. We then made binary the relative usage of aquatic, terrestrial, arboreal, and aerial microhabitat using a threshold of 30% to consider a species as typical of a given microhabitat type. In a departure from previous mammal databases that treated fossorial and terrestrial species collectively as 'terrestrial', we have reviewed microhabitat data to consider fossorial life-style separately from terrestrial [22,47].

Macrohabitat data followed the IUCN Habitat Classification scheme v. 3.1 [48]. This scheme describes 17 major habitat categories in which species can occur, and an 18th category for species with unknown major habitat (not included here). We also gathered data on species' major ecosystem (terrestrial, freshwater, and marine). For both macrohabitat and ecosystem, we initially used the *rredlist* package [49] to obtain macrohabitat for 31,740 species, and ecosystem for 32,442 species. Our macrohabitat variables correspond only to the first level of IUCN Habitat Classification scheme. For an additional 1,322 species, we extracted macrohabitat data from relevant literature, bringing the coverage to 33,019 species (99.2% of all species considered). Ecosystem data was extracted from the literature for another 837 species, encompassing 33,279 species and accounting for >99,9% of the total number of species.

We used the *rredlist* package [49] to obtain non-DD assessed status for 29,181 tetrapod species based on IUCN red list v. 2023-1 [50]. For 392 species not available via *rredlist*, we used non-DD assessed statuses matching those described in previous assessments and included in works using the same taxonomy of fully-sampled trees [20,24,26,51]. Data deficient species totalled 2,924 species. We did not find an assessed status for 555 species. To enhance the usability of TetrapodTraits, we also provide the respective IUCN binomials for 32,207 species based on IUCN 2023-1 [50].

To compute spatially-based attributes in TetrapodTraits, we derived expert-based range maps for amphibians [24,48,52], reptiles [20,33,48], mammals [48,52–54], and birds [27,52]. We matched the authoritative expert range maps for each of the tetrapod groups with the corresponding phylogenies and edited species ranges to ensure that they represented the species concept adopted in the corresponding phylogeny. Overall, our verification procedure of the species range maps can be summarised under 10 scenarios: (i) no changes, where species range maps matched directly with binomials in the phylogeny, (ii) synonyms, where species range maps were direct synonyms to binomials in the phylogeny, thus requiring only an updated name, (iii) split, where species range maps needed to be clipped from a parent species, or when parent species needed to have part of their range removed, (iv) lumps, where species range maps needed to be combined with those of other species, (v) new species-1, where no range map was previously available, so we derived ranges based on recent literature, (vi) new species-2, in the absence of any published map, we drew 10 km radius buffer around point occurrence data (including the species type locality), (vii) new species-3, in the absence of point occurrence data, we drew a polygon around nearby geographical features reported in the literature (e.g. boundaries of a municipality or protected area). We used two additional scenarios for extinct species [54] by referencing the natural ranges of either (viii) extant or (ix) extinct species that coexisted with fossil records of the target extinct species. The last scenario refers to (x) domesticated species, which were represented by their natural ranges before domestication. *Homo sapiens* had its range map represented by the overlapping of all range maps. We did not derive range maps for 11 species (1 amphibian, 2 bats, and 8 squamates) because information on their occurrence was either vaguely defined (e.g., continental land mass or very large administrative unit) or completely absent.

Species expert-based maps were used to compute different attributes related to species range and biogeography. We extracted the latitude and longitude centroids of each range map. Range size was measured as the number of 110 × 110 km equal-area grid cells intersected by each species, a spatial resolution that minimises the presence of errors related to the use of expert ranges maps [55–57]. We recorded the presence of a species in a grid cell if any part of the species distribution polygon overlapped with the grid cell. We then computed the proportion of the species range overlapped by each biogeographical realm.

To define if a species was insular endemic or not, we used the literature available [58,59]. We further completed insularity data by registering species whose range maps intersected with minor (< 2 km²) and major islands worldwide. Island vector data was sourced from Natural Earth (www.naturalearthdata.com, [60]) databases, v. 4.1.0 and v. 5.1.1 for minor and major islands, respectively. Species missing range maps were assumed as non-insular based on the collection of type specimens within major continental land masses (e.g., South Asia, South America, West Africa, Madagascar).

Finally, spatially-based attributes associated with environment or human influence were computed as the within-range average value of continuous variables (e.g., annual mean temperature, proportion of urban area) [61–64] weighted by species range occupancy in the cell. All within-range attributes were derived from spatial layers available online [61–64] and are individually described in the Results and Discussion section (see also Table S1).

Taxonomic Harmonisation

The taxonomy of the TetrapodTraits database follows the respective taxonomies of the recent, fully-sampled phylogenies for each of the major tetrapod groups [20,25–28]. The amphibian phylogeny taxonomy [25] follows the 19 February 2014 edition of AmphibiaWeb (http://amphibiaweb.org), with 7,238 species. The phylogeny for chelonians [20] follows the Turtles of the World (8th ed.) checklist [65], with the addition of *Aldabrachelys abrupta* and *Al. grandidieri*, and the synonymisation of *Amyda ornata with Am. cartilaginea*, adding to 357 chelonian species. For crocodilians [20], the taxonomy followed [66], complemented by the revalidation of *Crocodylus suchus* [67] and *Mecistops leptorhynchus* [68], and the

recognition of three *Osteolaemus* species [69,70], resulting in 27 species. The taxonomy of the squamate and tuatara phylogeny [26] follows the Reptile Database update of March 2015 (http://www.reptile-database.org) with 9,755 species. For brevity, we refer hereafter to species in the latter phylogeny as squamates, although we recognise that the tuatara, *Sphenodon punctatus*, is not a squamate. The taxonomy of the bird phylogeny [27] followed the Handbook of the Birds of the World [71], including 9,993 species. Finally, the taxonomy of the mammal phylogeny [28] follows the IUCN [72] with modifications resulting in a net addition of 398 species, bringing the total to 5,911 species.

To maximise data usage from previous compilation efforts, and to ensure coherence among species names and the multiple data sources, we built lists of synonyms and valid names based on multiple taxonomic databases [48,73,74], and extracted the unique synonyms in each taxonomic database. By unique synonym, we refer to a binomial (scientific name valid or not) applied to only one valid name. We then performed taxonomic reconciliation based on four steps:

1. ***Direct match with data sources:*** We directly paired the names of each of the 33,281 species in TetrapodTraits with the potential source of the data. Species-level attributes of closely related species could appear as identical values if the attributes had been extracted from sources in which different species were treated as synonyms. We minimised the inclusion of duplicated values by flagging each taxonomic match between TetrapodTraits and external data sources to ensure that each data entry was made only once.
2. ***Direct match with data source synonyms:*** For the species we were unable to directly match with the data source in step 1, we updated the taxonomy using the list of unique synonyms, and then performed a new matching operation which allowed us to extract and flag additional data whenever possible.
3. ***Direct match with TetrapodTraits synonymies:*** Some data sources may follow more recent taxonomies than those inherited from the fully-sampled phylogenies [20,25–28]. For species without a direct match after step 2, we updated their taxonomy in the TetrapodTraits using the list of unique synonyms and repeated the data extraction and flagging procedures.
4. ***Manual verification:*** For species without a direct match after step 3, we manually searched the specialised taxonomic databases (amphibians [73], reptiles [74], birds [75], and mammals [76]) for potential spelling errors and/or additional synonyms not yet included among our synonym lists. Whenever possible, we updated the taxonomy applied to data sources and then repeated the data extraction and flagging procedure. Species without data after the completion of step-4 were classified as missing data.

Outlier Verification

We implemented two approaches to detect potential inconsistencies in continuous attribute data, body length and body mass, before applying phylogeny-based methods to impute missing values.

1. ***Interquartile Range Criterion:*** Species body length and body mass were $\log_{10}$ transformed and then flagged as outliers if their value were outside the interval defined between $[q_{0.25} - 1.5 \times \mathrm{IQR}]$ and $[q_{0.75} + 1.5 \times \mathrm{IQR}]$, where $q_{0.25}$ and $q_{0.75}$ are respectively the first and third quartiles, and IQR is the interquartile range $[q_{0.25} - q_{0.75}]$.
2. ***Deviation from allometric relationship:*** Although allometric escape is a phenomenon observed in nature, we used interactive scatterplots to flag species with unusual deviations from the expected allometric relationship between body length and mass. We inspected allometric relationships separately for species within each Class, Order, and Suborder.

For species flagged in steps one or two above, we checked body length and/or body mass for validity and corrected these values where necessary. Data entries that could not be confirmed using a reliable source were purged from the database.

Taxonomic Imputation

The global scope of the present database inevitably includes some gaps that are hard to fill, e.g., natural history data for species known only from the holotype or a few specimens [12,77]. Previous studies have addressed this challenge and reduced data missingness by using values imputed at the level of genus or from close-relatives [47]. Although these earlier strategies of 'taxonomic imputation' might artificially reduce variability in attribute values, they are useful for filling gaps in highly conserved attributes, and can ultimately help increase the performance of phylogeny-based imputation methods applied in concert with correlated attribute data [78,79].

We used taxonomic imputations for two cases of missing data in microhabitat: chiropterans, who were considered 'aerial' (66 species), and dolphins and whales who were considered 'aquatic' (5 species). For the remaining tetrapod species, we computed the per-genus proportion of species in each type of activity time (diurnal or nocturnal), microhabitat (fossorial, terrestrial, aquatic, arboreal, aerial), macrohabitat (17 binary variables informing the IUCN Habitat Classification scheme), and ecosystem (terrestrial, freshwater, marine). If a type of activity time, microhabitat, macrohabitat, or ecosystem appeared in at least 70% of species in the genus, we assumed this ecological attribute was also present among species with missing data in the respective genus. Our goal was to reduce missing values in activity time, microhabitat, and macrohabitat for groups with well-known ecologies (observed data available for at least 70% of species) before running phylogeny-based imputation methods. We did not use taxonomic imputation for continuous attributes.

Phylogenetic Multiple Imputation

To minimise missing values and capture their uncertainty, we applied the *mixgb* method [30], a recently developed approach that combines the tree-based algorithm *XGBoost* [80] with predictive mean matching (PMM) [81], a multiple imputation technique. *XGBoost* captures interactions and nonlinear relations among variables, while PMM, alongside subsampling, addresses variability associated with missing data. PMM assigns imputed values to each missing entry based on a group of k donors whose predicted values are the most similar among the observed entries. One donor is then randomly selected, and its observed value is used for imputation [81,82]. The process is repeated m times to produce multiple imputations. When PMM uses a single donor without subsampling, imputations are expected to be identical.

The *XGBoost* does not directly include a phylogenetic tree into its computations. To account for phylogenetic information, we used the phylogenetic covariance matrix of each fully-sampled tree [20,25–28] to derive a set of phylogenetic filters (eigenvectors). We determined the number of phylogenetic filters to retain using the broken stick rule [83]. The selection of phylogenetic filters was performed separately for each tetrapod group and across the subset of 100 trees.

To assess the reliability of imputed data, we initially filtered a subset of species with complete data within each tetrapod group. Then, we randomly partitioned these subsets into 10 folds for cross-validation. In each iteration, one fold was excluded from the training process and used as testing data in subsequent modelling. Continuous variables (body length and body mass) were $\log_{10}$-transformed to reduce skewness, while binary variables represented types of microhabitat (fossorial, terrestrial, aquatic, arboreal, aerial) and activity time (diurnal and nocturnal). Note that microhabitat and activity time types are non-mutually exclusive. For birds only, we complemented the observed attribute data with 10 morphometric traits ($\log_{10}$-transformed) made recently available through the AVONET database [84].

XGBoost places a central emphasis on the tuning of hyperparameters, covering aspects such as learning rates, tree topology, subsampling, weighting, and regularisation [80,85]. Our tuning procedure began with an initial grid search, exploring 1K parameter combinations uniformly draw from specified ranges for five key hyperparameters: learning rate (η) from 0.01 to 0.3, maximum tree depth from 3 to 12, subsample portion of training data from 0.7 to 1, minimum child weight from 0.5 to 1.5, and number of boosting iterations (*nrounds*) from 30 to 1000. For continuous traits, our goal was to minimise the Normalised Root Mean Square Error (NRMSE) in *XGBoost* regression models using the 'reg:squarederror' objective, while for binary traits, we sought to reduce misclassification error in models using the 'binary:logistic' objective. We refined the hyperparameter selection by reassessing model performance with an additional 1K parameter combinations uniformly drawn from the parameter ranges defined by the top 5% of models. The tuning procedure was performed separately for each combination of response variable and tetrapod group. Other *XGBoost* parameters were kept at their default values.

Following hyperparameter tuning, we trained *mixgb* models under the 10-fold cross-validation approach. Each *mixgb* model considered the predictive mean matching with 10 donors, and provided 10 imputations for each missing entry. This process yielded a total of 10K imputed values for each missing entry across the subset of 100 phylogenetic trees (= 10 imputed values × 10 validation folds × 100 phylogenies). In each iteration, we assessed the reliability of imputations using four distinct validation metrics:

1. ***Pearson correlation:*** computed between imputed and observed values for continuous attributes (body length and body mass).
2. ***Regression slope:*** computed between imputed and observed values, where slope values > 1 indicate overestimation, and a slope < 1 indicates the underestimation for continuous attributes (body length and body mass).
3. ***Normalised Root Mean Square Error (NRMSE):*** computed for continuous attributes (body length and body mass), with lower values indicating higher accuracy [86].
4. ***Accuracy:*** measured the proportion of correctly classified entries, computed for binary categories representing microhabitat (fossorial, terrestrial, aquatic, arboreal, aerial) and activity time (diurnal and nocturnal).

Computations were carried out in R version 4.2.3 using the *mixgb* [30], *ape* [87], *gmodels* [88], *hydroGOF* [89], and *stats* [90] packages. The availability of the 10K imputed values per missing entry per species are reported under Data Availability.

We recognise that this section does not constitute a comprehensive investigation into the impacts of proportion of missing data and the degree of shared missingness on imputation performance. Delving into this aspect is beyond the scope of the present study and is an area for future research. For further details on mechanisms of data missingness, see [91]. Instead, our goal is to illustrate the utility of multiple imputation to uncover directional bias in natural history data.

Patterns of Shared Missing Data

We assessed co-occurrence patterns in missing data across species using the 'checkerboard score' (C-score; [92]), which is less prone to type II errors than other co-occurrence metrics computed under a null model approach [93]. The C-score was based on a binary presence-absence matrix (PAM) of species (columns) and missing attributes (rows). These attributes were represented by five binary variables informing the absence of observed values in body length, body mass, activity time, microhabitat, and threat status. Missing data in threat status were represented by Data Deficient (DD) or non-assessed species. We computed the C-score using individual PAMs for each genus and family with at least two species, and each pairwise combination of attribute variables, following recommendations by [94].

To verify whether an observed C-score differed from the value expected by chance, we built a null distribution of C-score values using a randomisation algorithm in which attribute completeness (rows sums) remained fixed while the probability of showing missing attribute values was considered equal for all species. Null distributions were built for each individual PAM using 10K iterations with a burn-in of 500. We then computed the standardised effect-size (SES) of the C-score and associated p-values and identified the pairwise attribute combinations with an aggregated (SES C-score < 0 and $p < 0.05$) or segregated (SES C-score > 0 and $p < 0.05$) co-occurrence pattern of missing data per taxa. Computations were performed using the *EcoSimR* [95] package in R.

Patterns and Biases in Imputed Traits

If certain parts of the multivariate attribute space are missing, the inclusion of imputed values may fill such 'invisible fractions' and change emergent attribute properties per taxon or geographical assemblage (e.g., average value, geometric mean, proportion or prevalence of a certain category). But changes in attribute property per taxon can also arise from the inclusion of biased imputed values [78], since imputation errors can increase either with the percentage of missing data or when multiple attributes are imputed simultaneously [15,78,79]. To verify how the inclusion of imputed values affected attribute patterns per taxon, we calculated the per-genus and per-family relative change in attribute property after adding imputed values.

Initially, we extracted the median (for continuous traits, body length and body mass) or the mean (for binary traits, categories of activity time and microhabitat) value per missing attribute across 10K imputations. We then computed attribute properties per-genus, -family, and -assemblage using (i) observed data only, and (ii) the combined dataset of observed and imputed data. For continuous attributes, we used the geometric mean due to its lower sensitivity to outliers and fluctuations in the median position value. For binary attributes, we computed the mean based on two scores derived from microhabitat and activity time categories: verticality (0 = strictly fossorial, 0.25 = fossorial and terrestrial, 0.5 = terrestrial or aquatic, 0.75 = terrestrial and arboreal, and 1 = strictly arboreal or aerial) and nocturnality (0 = strictly diurnal, 0.5 = cathemeral or crepuscular, 1 = strictly nocturnal). Relative change in attribute property was expressed as the ratio of attribute property obtained with the combined dataset to attribute property with the observed data only. We subtracted the relative change from 1 to centre it around zero:

$$Relative\ Change = 1 - (Attribute\ Property_{obs+imp} / Attribute\ Property_{obs})$$

Positive values of relative change indicate the proportional increase in attribute property after inclusion of imputed values, whereas negative values show the opposite. We used the R function *tree.merger* of the *RRphylo* package [96] to build a tetrapod super tree by combining the available global phylogenies for amphibians [25], chelonians and crocodilians [20], squamates [26], birds [27], and mammals [28]. The full tetrapod tree topology was only used for visualisation purposes. In the presence of severe data limitations (e.g., very low completeness, highly uneven sampled data, and lack of inter-correlated attributes), the relative changes in attribute properties could arise due to estimation errors instead of representing unsampled fractions of the attribute space. We therefore used Kruskal-Wallis tests to assess whether the relative increase or decrease of attribute properties differed with respect to the number of simultaneously imputed attributes.

Results and Discussion

TetrapodTraits offers insights into species-level attributes related to taxonomy, body size, activity time, microhabitat, macrohabitat, ecosystem, geography, environmental preferences, and threat status of tetrapod species (Table S1). Compilation efforts of previous works have significantly benefited TetrapodTraits, with these major data sources contributing to 68% of the natural history data entries. Additional information, whether compiled or revised from

original sources (e.g., field guides, taxonomic revisions, and species descriptions), accounted for 14.2% of data entries, and imputed values represented 18.1% of the natural history information (Fig. 1). In total, data acquisition involved the scanning of more than 3,400 references, including previously published databases. Imputation performance demonstrates high overall effectiveness across all tetrapods (Figs S1-S3), particularly for body mass (average Pearson correlation coefficient, r = 0.950, range = 0.692–0.973) and body length (r = 0.933, range = 0.585–0.976). Average accuracy is also high for activity time (0.880, range = 0.625–0.886) and microhabitat (0.897, range = 0.742–0.891). The number of observed, taxonomically imputed, or phylogenetically imputed data entries per tetrapod group are reported in Table S2, Supporting Information.

Data Completeness

Our assessment of data gaps focused on five attributes with considerable missing data: body length, body mass, activity time, microhabitat, and threat status. Across these five attributes, we observed complete species-level data for 43% of tetrapod species (n = 14,321), 36.9% of genera (n = 1,883), and 22.4% of families (n = 116). No genus or family showed zero completeness for these five attributes combined. The lowest completeness levels were among attributes related to body length (75.6%), activity time (77.1%), body mass (79.7%), and microhabitat (95.3%, Table S2). While assessed threat status was available for 98.3% of tetrapod species, this number decreased to 89.5% when DD species were treated as missing data (Fig. 2).

Across geographic assemblages, missingness of body length showed large variation, with Neotropical and Afrotropical species presenting the lowest completeness (Fig. 3A). The low spatial variability in attribute completeness for body mass, activity time, microhabitat, and assessed threat status (Fig. 3B–E) reveals that species with missing data are mostly narrow-ranged [4], which can limit the influence of these gaps in assemblage-level patterns. Of the 6,233 species missing at least two of the five attributes (body length, body mass, activity time, microhabitat, and threat status), 77.3% occurred in 10 or fewer 110 × 110 km equal-area grid cells. If we restrict missing data to three or more attributes, then 87% of species filtered occur in ≤10 grid cells. The completeness of genetic data in the fully-sampled trees of tetrapods [20,25–28] also showed high variation in spatial coverage (Fig. 3F), with the Afrotropical and Indomalayan realms emerging with the highest shortfall in genetic data [29]. Overall, our findings help illustrate that geographical patterns in data coverage can be strongly influenced by data for wide-ranged species.

Patterns of Shared Missing Data

We found non-random co-occurrence patterns in data gaps for 15.5% of the pairwise attribute combinations at the genus-level and for 37% at the family-level. Almost all non-random co-occurrence patterns showed aggregation of missing values, that is, missing data was shared among multiple attributes for the same species, particularly among squamates and amphibians (Fig. 4A). This supports the perspective that amphibians and squamates are the least researched tetrapod classes [2,3,34]. In our examination of shared gaps between threat status and other attributes, we found higher co-missingness in several tetrapod genera representative of leaf litter-dwelling (*Craugastor*, *Eleutherodactylus*, *Lerista*, and *Pristimantis*), fossorial and semifossorial (*Atractus*, *Crocidura*, and *Tantilla*), and arboreal or scansorial (*Cyrtodactylus*, *Dendroica*, and *Sphaerodactylus*) species. These findings indicate the uneven sampling coverage of attribute space within certain clades.

Aggregated data gaps were more common among species-rich clades with a lower proportion of missing data (Figs 4 and S9). That is, shared gaps were strongest in species-rich and well-sampled taxa, particularly in those holding many species known only from their type locality or holotype [77,97]. About 80% of the genera and 66% of families within the top 50 taxa in shared gaps include ‘lost taxa’, species that have not been reliably observed in >50 years but are not yet declared extinct [12]. While the rediscovery of ‘lost’ species is somewhat common

[97], their absence in attribute databases will not be easily filled through field observations [98]. The data gaps resulting from these poorly-known species often prevent their inclusion in trait-based research, potentially harming biogeographical research and conservation practice.

Biases Uncovered by Imputation-Based Gap Filling

We found that the use of imputations to fill gaps resulted in substantial changes in aggregate attribute properties and the insights they could support. These changes occurred in both directions (increasing and decreasing values) and were strongest in continuous attributes (body length and body mass). After the inclusion of imputed values, the average attribute value per genus decreased in 6.1% of the attribute-genus combinations and increased in 5.4% of these combinations. At the family-level, after the inclusion of imputed attributes, 16.3% of the attribute-family combinations showed an increase in the average values whereas 19.4% decreased (Figs 5 and S15).

Changes in attribute properties at the level of geographic assemblages revealed substantial alterations in average body size in tropical regions (Fig. 6A-F). Such differences are mostly absent in more temperate regions, reflecting the dedicated mobilisation and the resulting large availability of natural history data throughout North America, Europe, and Asia [2,4,99]. Average nocturnality of tetrapod assemblages tended to increase strongly after the inclusion of imputed values, pointing to a global knowledge bias from lack of observed attribute data (Fig. 6H-I), particularly for squamates and to a lesser extent, amphibians (Figs S10-S14). We attribute this to both the low detectability of nocturnal species [39,40] and to the general lack of data for tropical regions where nocturnal species predominate [100]. Changes in average verticality were less pronounced across tetrapod assemblages (Fig. 6K-L), which is somewhat expected given the relatively high completeness of microhabitat data.

Although imputation biases can increase in the absence of additional correlated attributes [78], we found no relationship between the number of imputed attributes and changes in attribute averages after imputation-based gap-filling (Fig. S16). That is, changes in average attributes were not higher in genera and families that included species with multiple missing attributes. Moreover, changes in average attributes were either mostly unrelated to shared gaps (Fig. S17) or occurred in opposite directions, with low shared gaps leading to greater changes.

Broadly, we found that the magnitude of change in average attributes from imputation-based gap-filling was associated with both completeness and richness (Figs S18-S20). Those taxa and assemblages with great incompleteness and with fewest species saw the most pronounced changes in average attribute values. Lower attribute completeness creates more opportunities for variation in attribute space after imputation-based gap-filling, whereas low species richness can enhance the importance of imputed values in the sample. Future research replacing imputed values with empirical data will reveal the accuracy of these estimates over time.

TetrapodTraits – a comprehensive, imputation informed attributes database

The full phylogenetically coherent database we developed, TetrapodTraits, is being made publicly available to support a range of research applications in ecology, evolution, and conservation and to help minimise the impacts of biased data in this model system. The database includes 24 species-level attributes linked to their respective sources across 33,281 tetrapod species. Entries across this database show at least 98% of completeness after the inclusion of imputed values. Specific fields clearly label data sources and imputations in the TetrapodTraits (Table S1), while additional tables record the 10K values per missing entry per species.

1. **Taxonomy –** includes 8 attributes that inform scientific names and respective higher-level taxonomic ranks, authority name, and year of species description. Field names:

Scientific.Name, Genus, Family, Suborder, Order, Class, Authority, and YearOfDescription.

2. **Phylogenetic tree –** includes 2 attributes that notify which fully-sampled phylogeny contains the species, along with whether the species placement was imputed or not in the phylogeny. Field names: TreeTaxon, TreeImputed.

3. **Body size –** includes 7 attributes that inform length, mass, and data sources on species sizes, and details on the imputation of species length or mass. Field names: BodyLength_mm, LengthMeasure, ImputedLength, SourceBodyLength, BodyMass_g, ImputedMass, SourceBodyMass.

4. **Activity time –** includes 5 attributes that describe period of activity (e.g., diurnal, fossorial) as dummy (binary) variables, data sources, details on the imputation of species activity time, and a nocturnality score. Field names: Diu, Noc, ImputedActTime, SourceActTime, Nocturnality.

5. **Microhabitat –** includes 8 attributes covering habitat use (e.g., fossorial, terrestrial, aquatic, arboreal, aerial) as dummy (binary) variables, data sources, details on the imputation of microhabitat, and a verticality score. Field names: Fos, Ter, Aqu, Arb, Aer, ImputedHabitat, SourceHabitat, Verticality.

6. **Macrohabitat –** includes 19 attributes that reflect major habitat types according to the IUCN classification, the sum of major habitats, data source, and details on the imputation of macrohabitat. Field names: MajorHabitat_1 to MajorHabitat_10, MajorHabitat_12 to MajorHabitat_17, MajorHabitatSum, ImputedMajorHabitat, SourceMajorHabitat. MajorHabitat_11, representing the marine deep ocean floor (unoccupied by any species in our database), is not included here.

7. **Ecosystem –** includes 6 attributes covering species ecosystem (e.g., terrestrial, freshwater, marine) as dummy (binary) variables, the sum of ecosystem types, data sources, and details on the imputation of ecosystem. Field names: EcoTer, EcoFresh, EcoMar, EcosystemSum, ImputedEcosystem, SourceEcosystem.

8. **Threat status –** includes 3 attributes that inform the assessed threat statuses according to IUCN red list and related literature. Field names: IUCN_Binomial, AssessedStatus, SourceStatus.

9. **RangeSize** – the number of 110×110 km grid cells covered by the species range map.

10. **Latitude** – coordinate centroid of the species range map.

11. **Longitude** – coordinate centroid of the species range map.

12. **Biogeography –** includes 8 attributes that present the proportion of species range within each biogeographical realm. Field names: Afrotropic, Australasia, IndoMalay, Nearctic, Neotropic, Oceania, Palearctic, Antarctic [101].

13. **Insularity –** includes 2 attributes that notify if a species is insular endemic (binary, 1 = yes, 0 = no), followed by the respective data source. Field names: Insularity, SourceInsularity.

14. **AnnuMeanTemp –** Average within-range annual mean temperature (Celsius degree). Data derived from CHELSA v. 1.2 [62].

15. **AnnuPrecip –** Average within-range annual precipitation (mm). Data derived from CHELSA v. 1.2 [62].

16. **TempSeasonality –** Average within-range temperature seasonality (Standard deviation × 100). Data derived from CHELSA v. 1.2 [62].

17. **PrecipSeasonality –** Average within-range precipitation seasonality (Coefficient of Variation). Data derived from CHELSA v. 1.2 [62].

18. **Elevation –** Average within-range elevation (metres). Data derived from topographic layers in EarthEnv [61].

19. **ETA50K –** Average within-range estimated time to travel to cities with a population >50K in the year 2015. Data from [64].

20. **HumanDensity –** Average within-range human population density in 2017. Data derived from HYDE v. 3.2 [63].

21. **PropUrbanArea –** Proportion of species range map covered by built-up area, such as towns, cities, etc. at year 2017 [63].

22. **PropCroplandArea –** Proportion of species range map covered by cropland area, identical to FAO's category 'Arable land and permanent crops' at year 2017 [63].

23. **PropPastureArea –** Proportion of species range map covered by cropland, defined as Grazing land with an aridity index > 0.5, assumed to be more intensively managed (converted in climate models) at year 2017 [63].

24. **PropRangelandArea –** Proportion of species range map covered by rangeland, defined as Grazing land with an aridity index < 0.5, assumed to be less or not managed (not converted in climate models) at year 2017 [63].

Conclusion

The growth in mobilised attribute data over the last several decades has enabled significant progress and increased geographic and taxonomic generality for global studies in comparative biology [102–104], macroevolution [105], macroecology [106], and conservation [107–109]. Despite the richness of available data, research outcomes and their interpretation often remained constrained by non-randomly missing data [6,8,79], and by the lack of standardisation across data dimensions (trait, phylogenetic, spatial) and data sources [110]. We show a clear latitudinal bias in the sampling of genetic data, with limited availability of genetic samples towards the Equator. In concert with taxonomic updates [111,112], these issues have imposed significant limits on multi-taxon investigations and global biodiversity synthesis [113–115]. We documented remaining global data gaps for key traits and then used imputation to fill these gaps, revealing the biases in our knowledge due to the missingness of attribute data. By using phylogeny-based imputation methods in concert with inter-related ecological attributes, we uncovered the hitherto invisible part of attribute space. Our findings confirmed the predominance of attributes that share missing data and provide a comprehensive assessment of gaps and biases across tetrapod groups.

Attributes predictions for species with missing data brought to light key correlates and allowed us to identify the significant consequences these gaps can have for inference. For instance, larger body size has been related to both high species detectability [38,39,42] and discovery probability [116–118], larger research effort and public interest [34,44,119,120], increased availability of assessed status [121,122], and better data sampling. Despite the

difficulties associated with researching large-sized species – e.g., high sensitivity to disturbances [123,124], lower abundance [125,126], challenges with collection or transport – the presence of multiple data biases towards small-sized species confirm the struggle of biodiversity scientists to accurately characterise the smallest organisms and the lower tail of size distributions in nature.

Biodiversity knowledge shortfalls are also clearly related to activity time and microhabitat. Nocturnal species often show lower detectability [39], and typically are less researched [44] and underassessed with respect to threat status [121], which helps explain why diurnal species are more likely to have activity time data. In addition, the higher detectability of terrestrial than arboreal or fossorial species via standard sampling methods [41,42] can lead to less biased occurrence data [127] and more research effort [34,44]. Although foraging stratum may constrain certain aspects of our biodiversity knowledge, verticality has a limited influence on the availability of microhabitat data.

Attribute imputations can be limited and biased [78,79]. For tetrapods generally and this study specifically, these concerns were minimised by the already substantial taxon-specific datasets and by the gap-oriented mobilisation of additional data. We had to impute all four focal attributes (body length, body mass, activity time, and microhabitat) in only 186 tetrapod species (<0.25%). No family or genus had the four focal attributes missing in all species. Two important diagnostics offered strong support for the robustness of our attribute predictions. First, there was no association between the number of imputed attributes and changes in average attributes after imputation-based gap-filling (Fig. S16). Second, there was no positive association between shared gaps in attribute data and changes in average attribute values (Fig. S17). We encourage researchers to consider how assumptions and uncertainty of any imputed data might affect downstream use and interpretation. However, for many tetrapod research cases, including species with imputed data is preferable to wholesale exclusion of data-limited species.

We have demonstrated that even for Tetrapoda, a central model system in biodiversity science, our ecological knowledge attribute data are lacking consistently across certain types of traits, taxa, and regions. Through careful imputation, we discovered that these gaps have led to attribute distributions with strong geographical and taxonomic biases. We expect that our approach and likely our general insights regarding biodiversity knowledge shortfalls will transcend taxa and systems. The consequences of biased data can percolate through trait-based metrics and comparative analyses, and may ultimately mislead research on functional diversity [8,19,128], extinction risk [6,21,129], and ecogeography [130–132]. The new phylogeny-based attribute database we have constructed can help minimise the impact of biased data and support new avenues of research in tetrapod conservation, ecology, and evolution.

Supporting Information

The Supporting Information includes Tables S1-S2 and Figures S1-S20.

Code Availability

The TetrapodTraits database and R-code used for data validation will be made available on vertlife.org and GitHub upon acceptance for publication.

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Competing interests

The authors declare no competing financial interests.

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Figure Legends

Figure 1. Relative contribution of major data sources to natural history information in TetrapodTraits. For improved readability, only sources containing data entries for at least 500 species are shown. Boxes labelled 'Other sources' encompass combined information not included within major data sources, often compiled from field guides and taxonomic-specific literature for tetrapod species.

Figure 2. Attribute data coverage (completeness) of tetrapod species by family. Colour rings show the proportion of species with observed attributes in each tetrapod family for the five attributes with the lowest completeness. Phylogenetic relationships shown are simply the family-level topology of tetrapod families. Darker colours indicate higher completeness.

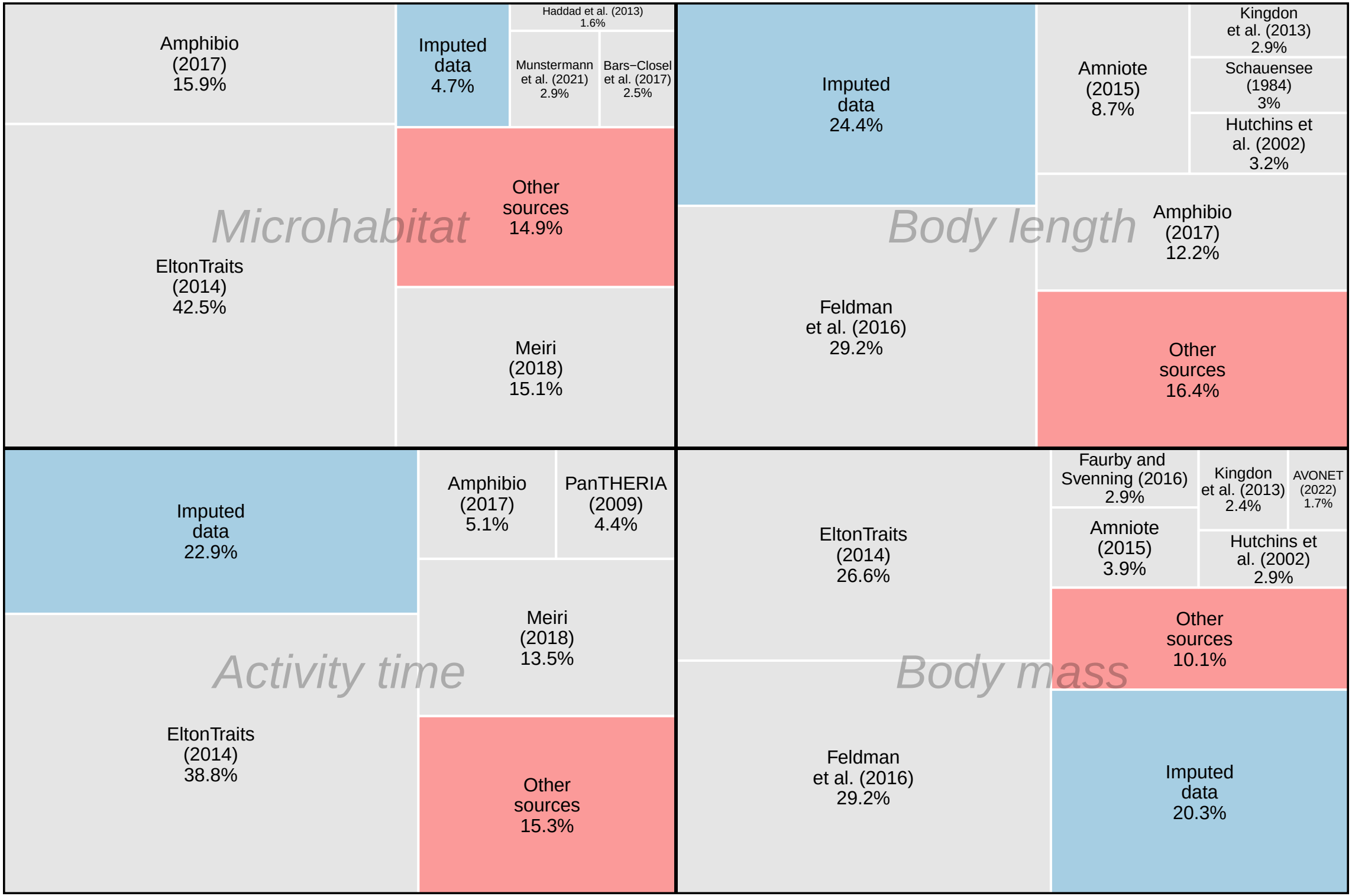
Figure 3. Average data completeness across tetrapod assemblages. Proportion of species with observed values for: (A) body length, (B) body mass, (D) activity time, (E) microhabitat, (G) assessed threat status, (H) phylogenetic data, (J) attribute set, i.e., the average pattern for maps depicted in ABDE, and (K) the complete database, i.e., average pattern for maps depicted in ABDEGH. Maps show grid cell assemblages of 110 × 110 km size in an equal-area projection. Latitudinal plots (C, F, I, L) show the average values of these cells across latitudes. Colour ramps followed Jenks' natural breaks classification. See Figs S4-S8 for spatial patterns of attribute completeness for each tetrapod group.

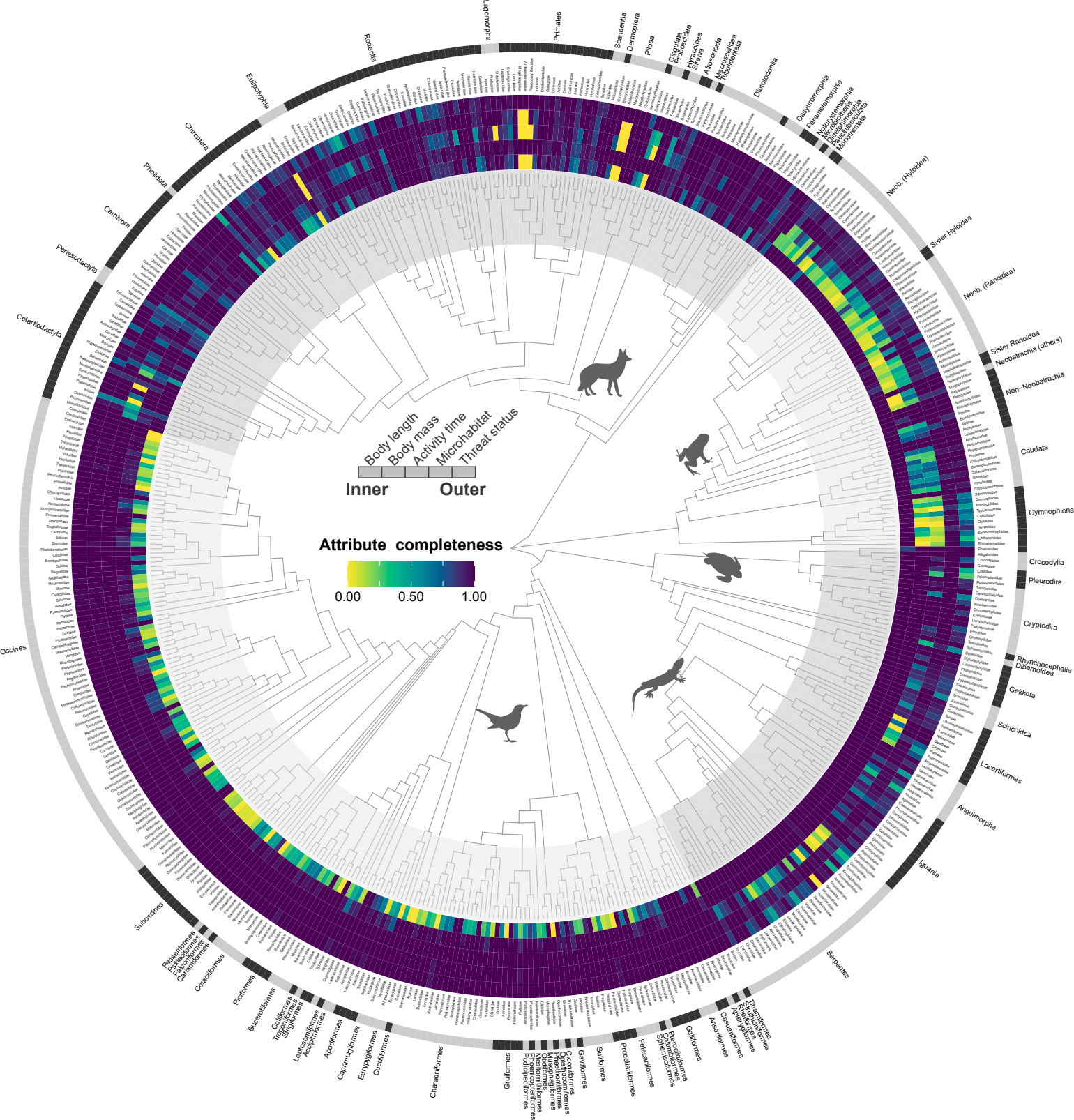
Figure 4. The top 50 tetrapod genera with the most pronounced patterns of shared data gaps. For each genus, the aggregation metric equals the median value of the standardised effect-size (SES) of the C-score metric computed across (A) all pairwise attribute combinations among the five focal traits; and (B) all attribute pairs involving threat status. Grey numbers on the left side of each panel indicate the species richness per genus. See Fig. S9 for aggregation patterns computed at the family-level.

Figure 5. Changes in family-level attributes values after imputation-based gap-filling. For continuous attributes (BL, body length; BM, body mass), relative change in attribute property quantifies the proportional change in the geometric mean attribute per genus. For

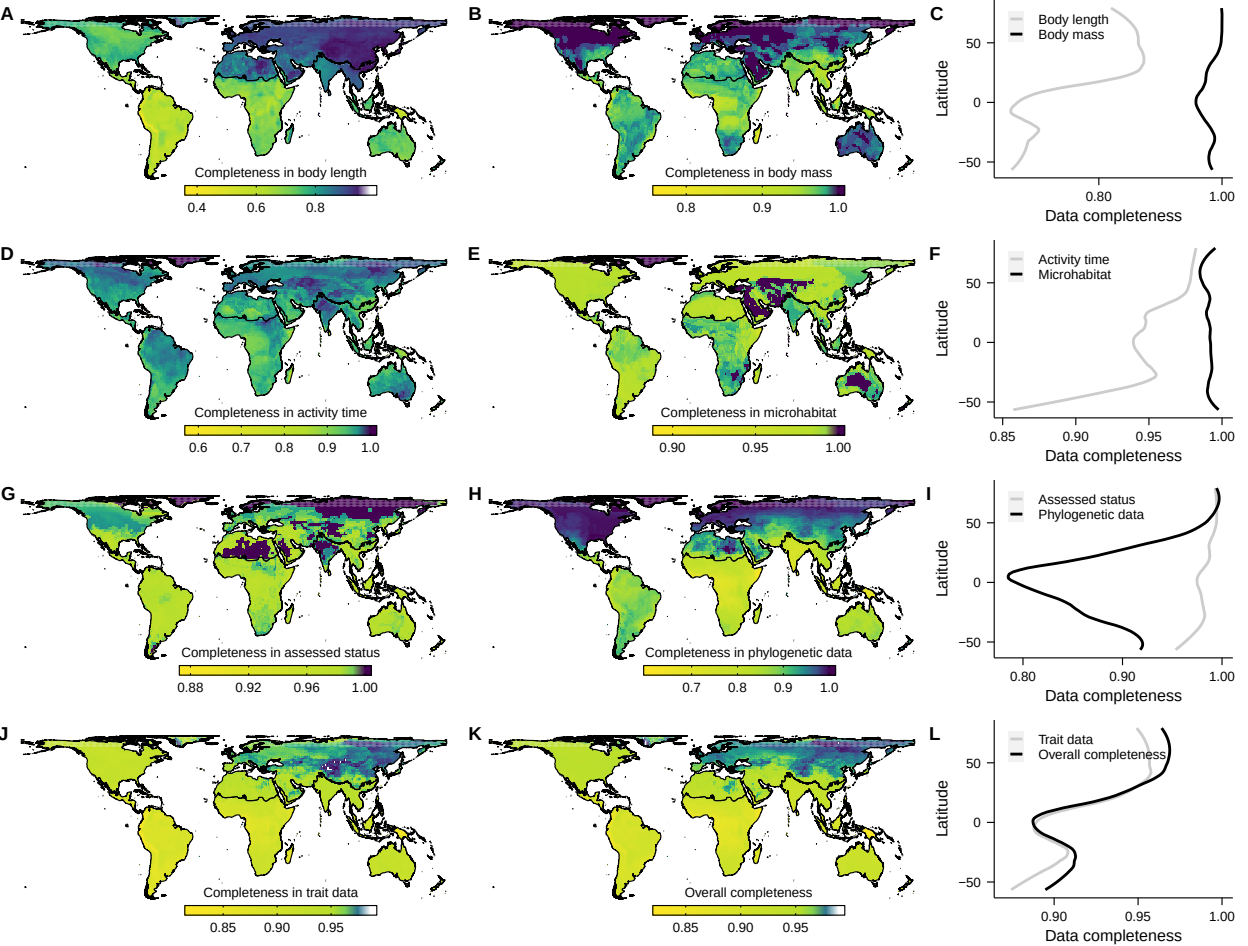
binary attributes (types of activity time and microhabitat), relative change in attribute property measures the change in mean species nocturnality (Noct) and verticality (Vert) scores. The inset donut chart denotes the proportion of genera (inner donut) and families (outer donut) by category of attribute change. The y-axis of histograms is square-rooted to improve readability.

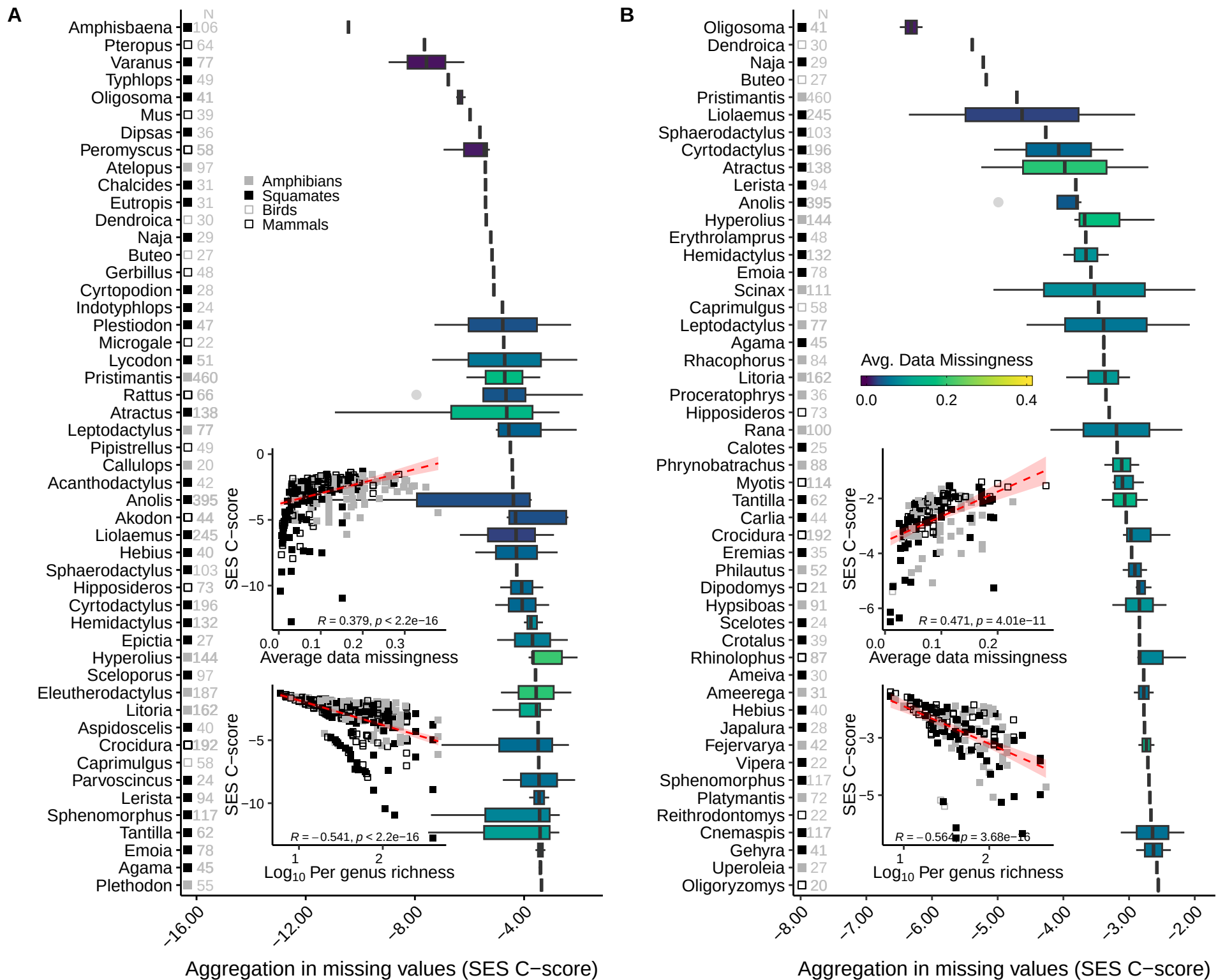
Figure 6. Changes in average attribute per tetrapod assemblage after imputation-based gap-filling. For each grid cell, maps show the average species attribute value and respective relative change in attribute value after inclusion of imputed values for (A-C) body length, (D-F) body mass, (G-I) nocturnality, and (J-L) verticality. Body length and body mass were $\log_{10}$ transformed before computations. Grey cells indicate assemblages without species with imputed values. See Figs S10-S14 for patterns of attribute change for each tetrapod group.

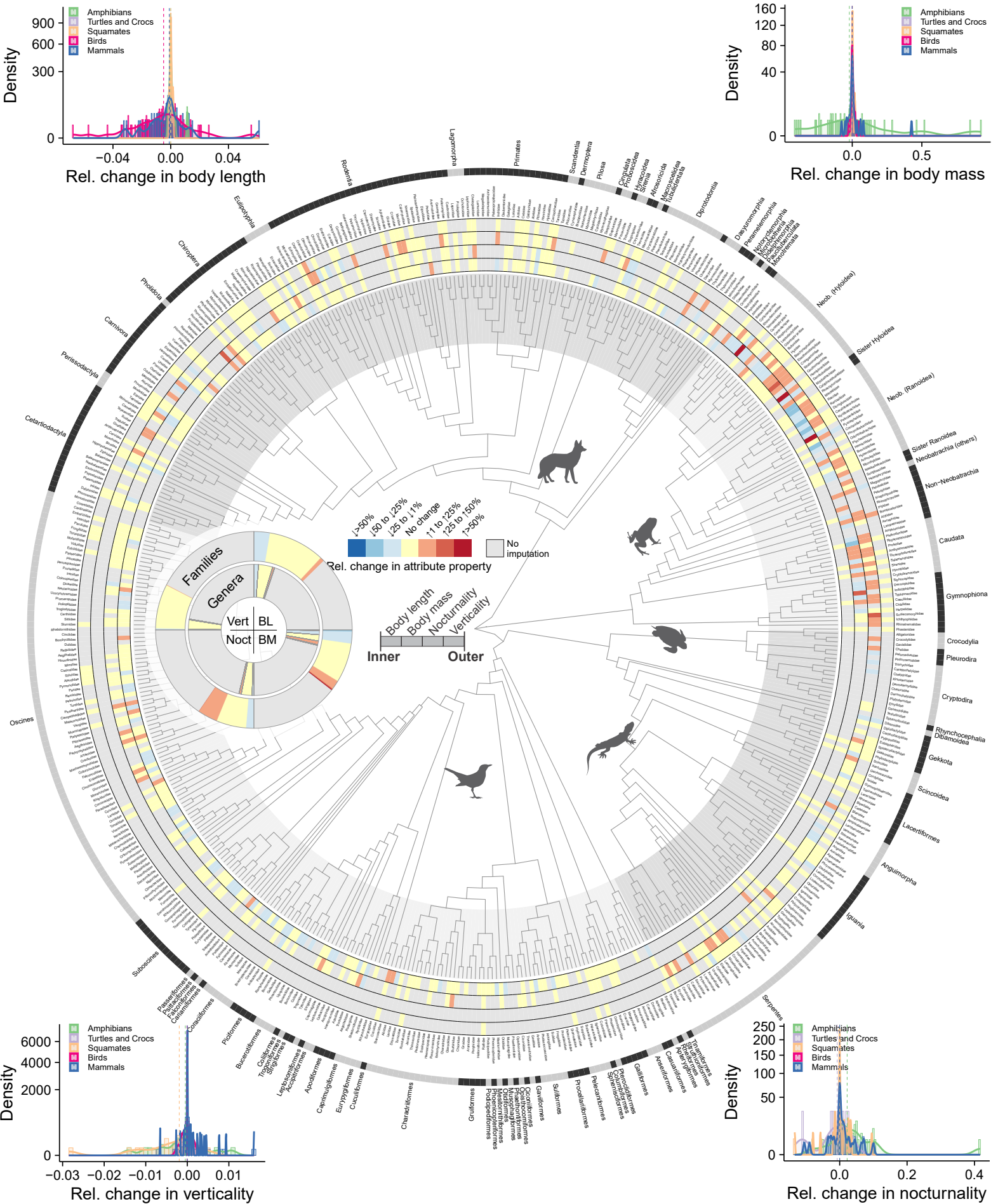

Microhabitat
Amphibio (2017) 15.9%
Imputed data 4.7%
Haddad et al. (2013) 1.6%
Munstermann et al. (2021) 2.9%
Bars−Closel et al. (2017) 2.5%
Other sources 14.9%
EltonTraits (2014) 42.5%
Meiri (2018) 15.1%
Body length
Imputed data 24.4%
Amniote (2015) 8.7%
Kingdon et al. (2013) 2.9%
Schauensee (1984) 3%
Hutchins et al. (2002) 3.2%
Amphibio (2017) 12.2%
Feldman et al. (2016) 29.2%
Other sources 16.4%
Activity time
Imputed data 22.9%
Amphibio (2017) 5.1%
PanTHERIA (2009) 4.4%
Meiri (2018) 13.5%
EltonTraits (2014) 38.8%
Other sources 15.3%
Body mass
EltonTraits (2014) 26.6%
Faurby and Svenning (2016) 2.9%
Kingdon et al. (2013) 2.4%
AVONET (2022) 1.7%
Amniote (2015) 3.9%
Hutchins et al. (2002) 2.9%
Other sources 10.1%
Feldman et al. (2016) 29.2%
Imputed data 20.3%



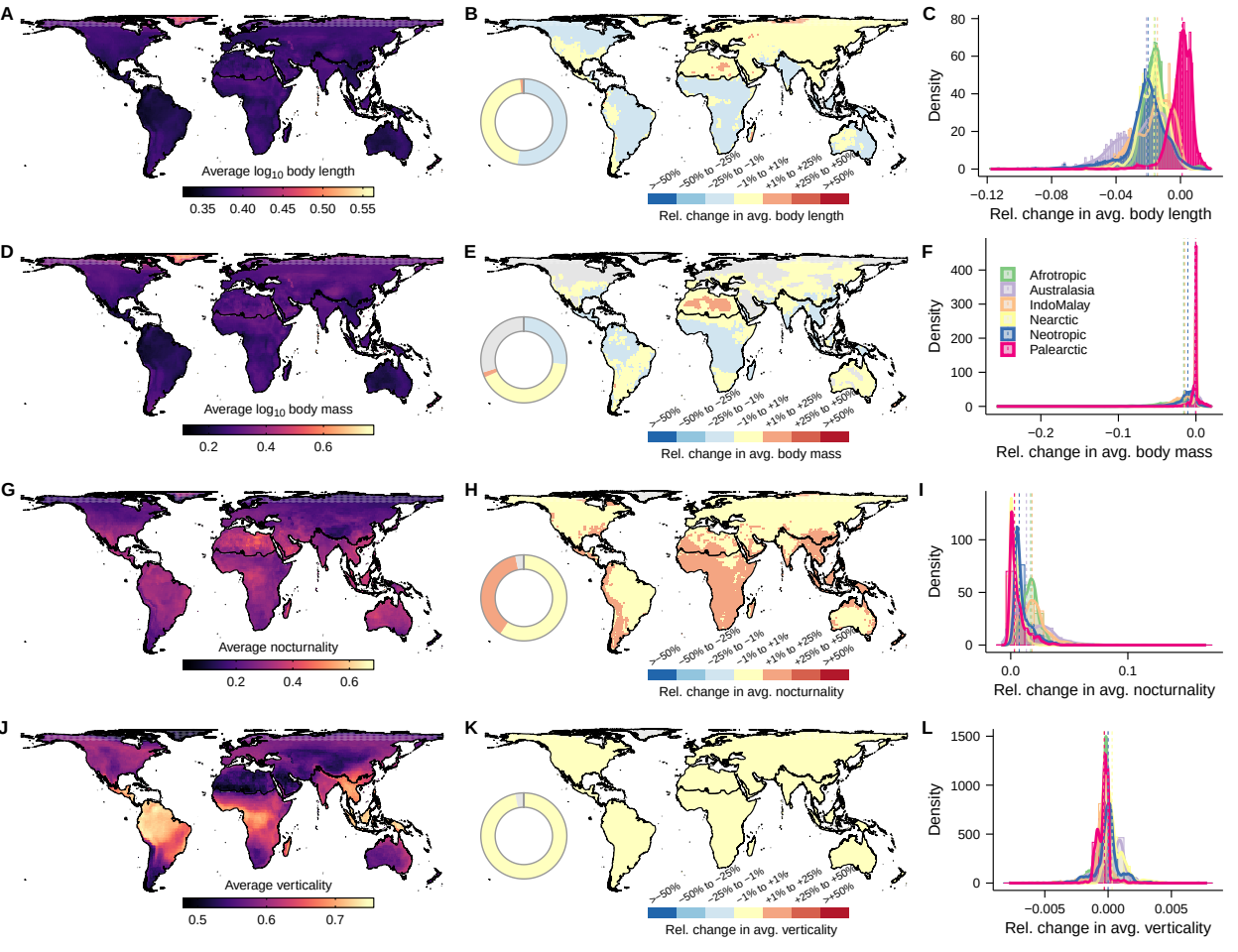
Body length
Body mass
Activity time
Microhabitat
Threat status
Inner
Outer
Attribute completeness
0.00
0.50
1.00
Lagomorpha
Primates
Scandentia
Dermoptera
Pilosa
Cingulata
Proboscidea
Hyracoidea
Sirenia
Afrosoricida
Macroscelidea
Tubulidentata
Diprotodontia
Dasyuromorphia
Peramelemorphia
Notoryctemorphia
Microbiotheria
Didelphimorphia
Paucituberculata
Monotremata
Neob. (Hyloidea)
Sister Hyloidea
Neob. (Ranoidea)
Sister Ranoidea
Neobatrachia (others)
Non−Neobatrachia
Caudata
Gymnophiona
Crocodylia
Pleurodira
Cryptodira
Rhynchocephalia
Dibamoidea
Gekkota
Scincoidea
Lacertiformes
Anguimorpha
Iguania
Serpentes
Thamiformes
Strutiformes
Rheiformes
Apteryiformes
Casuariformes
Anseriformes
Galliformes
Pterocliidiformes
Columbiformes
Sphenisciformes
Pelecaniformes
Procellariiformes
Suliformes
Gaviiformes
Ciconiiformes
Phoenicopteriformes
Podicipediformes
Gruiformes
Charadriiformes
Cuculiformes
Eurypygiformes
Caprimulgiformes
Apodiformes
Leptosomiformes
Accipitriformes
Strigiformes
Trogoniformes
Coliiformes
Bucerotiformes
Piciformes
Coraciiformes
Cariamiformes
Falconiformes
Psittaciformes
Passeriformes
Suboscines
Oscines
Cetartiodactyla
Perissodactyla
Carnivora
Pholidota
Chiroptera
Eulipotyphla
Rodentia


A
Completeness in body length
0.4
0.6
0.8
B
Completeness in body mass
0.8
0.9
1.0
C
Body length
Body mass
Latitude
50
0
−50
0.80
1.00
Data completeness
D
Completeness in activity time
0.6
0.7
0.8
0.9
1.0
E
Completeness in microhabitat
0.90
0.95
1.00
F
Activity time
Microhabitat
Latitude
50
0
−50
0.85
0.90
0.95
1.00
Data completeness
G
Completeness in assessed status
0.88
0.92
0.96
1.00
H
Completeness in phylogenetic data
0.7
0.8
0.9
1.0
I
Assessed status
Phylogenetic data
Latitude
50
0
−50
0.80
0.90
1.00
Data completeness
J
Completeness in trait data
0.85
0.90
0.95
K
Overall completeness
0.85
0.90
0.95
L
Trait data
Overall completeness
Latitude
50
0
−50
0.90
0.95
1.00
Data completeness


A
N
Amphisbaena 106
Pteropus 64
Varanus 77
Typhlops 49
Oligosoma 41
Mus 39
Dipsas 36
Peromyscus 58
Atelopus 97
Chalcides 31
Eutropis 31
Dendroica 30
Naja 29
Buteo 27
Gerbillus 48
Cyrtopodion 28
Indotyphlops 24
Plestiodon 47
Microgale 22
Lycodon 51
Pristimantis 460
Rattus 66
Atractus 138
Leptodactylus 77
Pipistrellus 49
Callulops 20
Acanthodactylus 42
Anolis 395
Akodon 44
Liolaemus 245
Hebius 40
Sphaerodactylus 103
Hipposideros 73
Cyrtodactylus 196
Hemidactylus 132
Epictia 27
Hyperolius 144
Sceloporus 97
Eleutherodactylus 187
Litoria 162
Aspidoscelis 40
Crocidura 192
Caprimulgus 58
Parvoscincus 24
Lerista 94
Sphenomorphus 117
Tantilla 62
Emoia 78
Agama 45
Plethodon 55
Amphibians
Squamates
Birds
Mammals
SES C−score
R = 0.379, p < 2.2e−16
Average data missingness
R = −0.541, p < 2.2e−16
Log10 Per genus richness
−16.00
−12.00
−8.00
−4.00
Aggregation in missing values (SES C−score)
B
N
Oligosoma 41
Dendroica 30
Naja 29
Buteo 27
Pristimantis 460
Liolaemus 245
Sphaerodactylus 103
Cyrtodactylus 196
Atractus 138
Lerista 94
Anolis 395
Hyperolius 144
Erythrolamprus 48
Hemidactylus 132
Emoia 78
Scinax 111
Caprimulgus 58
Leptodactylus 77
Agama 45
Rhacophorus 84
Litoria 162
Proceratophrys 36
Hipposideros 73
Rana 100
Calotes 25
Phrynobatrachus 88
Myotis 114
Tantilla 62
Carlia 44
Crocidura 192
Eremias 35
Philautus 52
Dipodomys 21
Hypsiboas 91
Scelotes 24
Crotalus 39
Rhinolophus 87
Ameiva 30
Ameerega 31
Hebius 40
Japalura 28
Fejervarya 42
Vipera 22
Sphenomorphus 117
Platymantis 72
Reithrodontomys 22
Cnemaspis 117
Gehyra 41
Uperoleia 27
Oligoryzomys 20
Avg. Data Missingness
0.0
0.2
0.4
SES C−score
R = 0.471, p = 4.01e−11
Average data missingness
R = −0.564, p = 3.68e−16
Log10 Per genus richness
−8.00
−7.00
−6.00
−5.00
−4.00
−3.00
−2.00
Aggregation in missing values (SES C−score)



Amphibians
Turtles and Crocs
Squamates
Birds
Mammals
Density
Rel. change in body length
Rel. change in body mass
Rel. change in verticality
Rel. change in nocturnality
Rel. change in attribute property
↓>50%
↓50 to ↓25%
↓25 to ↓1%
No change
↑1 to ↑25%
↑25 to ↑50%
↑>50%
No imputation
Families
Genera
Vert
BL
Noct
BM
Body length
Body mass
Nocturnality
Verticality
Inner
Outer
Lagomorpha
Primates
Scandentia
Dermoptera
Pilosa
Cingulata
Proboscidea
Hyracoidea
Sirenia
Afrosoricida
Macroscelidea
Tubulidentata
Diprotodontia
Dasyuromorphia
Peramelemorphia
Notoryctemorphia
Microbiotheria
Didelphimorphia
Paucituberculata
Monotremata
Neob. (Hyloidea)
Sister Hyloidea
Neob. (Ranoidea)
Sister Ranoidea
Neobatrachia (others)
Non-Neobatrachia
Caudata
Gymnophiona
Crocodylia
Pleurodira
Cryptodira
Rhynchocephalia
Dibamoidea
Gekkota
Scincoidea
Lacertiformes
Anguimorpha
Iguania
Serpentes
Rodentia
Eulipotyphla
Chiroptera
Pholidota
Carnivora
Perissodactyla
Cetartiodactyla
Oscines
Suboscines
Passeriformes
Psittaciformes
Falconiformes
Cariamiformes
Coraciiformes
Piciformes
Bucerotiformes
Coliiformes
Trogoniformes
Strigiformes
Leptosomiformes
Accipitriformes
Apodiformes
Caprimulgiformes
Eurypygiformes
Cuculiformes
Charadriiformes
Gruiformes
Podicipediformes
Phoenicopteriformes
Mesitornithiformes
Mesophagiformes
Musophagiformes
Phaethontiformes
Opisthocomiformes
Ciconiiformes
Gaviiformes
Suliformes
Procellariiformes
Pelecaniformes
Sphenisciformes
Columbiformes
Pterocliformes
Galliformes
Anseriformes
Casuariformes
Apterygiformes
Rheiformes
Struthioniformes
Tinamiformes


A
Average log10 body length
0.35 0.40 0.45 0.50 0.55
B
>−50% −50% to −25% −25% to −1% −1% to +1% +1% to +25% +25% to +50% >+50%
Rel. change in avg. body length
C
Density
Rel. change in avg. body length
D
Average log10 body mass
0.2 0.4 0.6
E
Rel. change in avg. body mass
F
Afrotropic
Australasia
IndoMalay
Nearctic
Neotropic
Palearctic
Rel. change in avg. body mass
G
Average nocturnality
0.2 0.4 0.6
H
Rel. change in avg. nocturnality
I
Rel. change in avg. nocturnality
J
Average verticality
0.5 0.6 0.7
K
Rel. change in avg. verticality
L
Rel. change in avg. verticality