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

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Abstract

Tetrapods (amphibian, reptiles, birds and mammals) have become a central model system for global ecology, conservation, and biodiversity science at large. But continuing data gaps, limited data standardisation, and ongoing dynamics of taxonomic nomenclature put constraints on robust integrative research in this group and potentially causes biased inference. Here we combine and harmonise taxonomic, spatial, phylogenetic, and attribute data with phylogeny-based imputation to provide a comprehensive assessment of data gaps and biases across taxa and geographic space. We find that co-missingness in attribute values increased with taxon-level completeness and richness. Prediction of missing attribute values using extensive performance and uncertainty assessment revealed substantial changes to macroecological patterns. These results highlight both the specific biases incurred by non-random data missingness and an important avenue to address them. We provide a comprehensive data resource that includes predictions and address 75 attributes, including body size, activity time, micro- and macrohabitat, geography, environmental preferences, human influence and threat status for all 33,281 tetrapod species covered in recent fully-sampled phylogenies. While there is an obvious need for further data collection and ongoing updates, the presented phylogeny-associated and -informed resource of tetrapod species attributes can support a better representation of undersampled species and their attributes in ecology and conservation.

Introduction

Over the past two decades biodiversity science has seen a dramatic growth in impactful large-scale ecological and conservation research enabled by near-global study systems such as terrestrial vertebrates, or tetrapod (amphibians, reptiles, birds, and mammals). These efforts are usually reliant on datasets spanning wide temporal, spatial, and taxonomic scales [1] that ideally are fully harmonized and well curated. Although terrestrial vertebrates are considered well-known animal groups relative to invertebrates and marine taxa [2,3], significant data gaps remain [4,5]. Consequently, trait-based research on biodiversity conservation, ecology and evolution is often performed with incomplete data.

Because this data missingness is usually highly non-random, i.e. overall trait space is represented unevenly [4], it can have pervasive consequences inference in trait-based research

[6,7] and conservation applications [6,8]. Indeed, available trait data are recognized to be biased towards certain taxa, regions, and traits [4], and often there is co-missingness, i.e. missing values for a given variable are associated with missingness in another [9]. Such congruent or aggregated (as opposed to segregated) patterns in trait data missingness can arise from societal and research preferences towards either charismatic species [3] or taxonomic groups that are easily sampled [6,10], whereas segregated patterns may reveal traits difficult to sample or even underlooked for a given taxonomic group. Documenting which groups show aggregated or segregated data missingness helps to inform strategies of data acquisition and reduce existing biases in trait databases.

While sampled trait data remain limited for many tetrapod species attributes, new methods can help to minimise these data gaps and improve our understanding of biodiversity. Past practices have included the removal of species with missing data or replacement of missing values by observed averages, but these strategies inevitably contribute to reduce statistical power and increase bias [7,9,11]. More recently, the growth in large-scale phylogenetic frameworks have boosted the development of phylogeny-based methods to impute missing values [12–15]. The phylogenetic information can be further combined with available data on other correlated traits to increase the quality of imputed values [16,17]. Among tetrapods, recent large-scale applications of imputation methods include, for example, the use of either phylogenetic regression methods or machine-learning techniques to predict missing values in trait data for amphibians [18,19], 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].

Here we leverage these methodological innovations and combine them with additional data mobilization to provide a comprehensive evaluation and prediction of key ecological attributes of all extant 33,281 tetrapod species covered in recent fully-sampled phylogenies, including 7,238 amphibians [24], 384 chelonians and crocodilians [20], 9,755 squamates and tuatara [25], 9,993 birds [26], and 5,911 mammals [27]. Specifically, we assessed 75 standardised species-level attributes combining a range of sources on taxonomy, body size, activity time, microhabitat, macrohabitat, geography, environmental preferences, human influence, and threat status. As not all species placements in the available phylogenies are yet supported with genetic data, representing one important source of uncertainty in their placement, we also evaluated phylogenetic data gap, i.e. the remaining Darwinian shortfall [28]. We taxonomically harmonised data and fill data gaps with phylogeny-based imputation methods [12–15] for which we verified the performance and remaining uncertainty through extensive validation procedures.

We use this combined dataset to assess the geographic, taxonomic, and trait-related biases imposed by existing data gaps and how their model-based closure supports improved information and biological inference. Because of a biodiversity knowledge paradox – the high biodiversity over tropics [29] but better sampling in temperate regions [4,5,30] – we expect larger unsampled fractions of the tetrapod trait space for species occurring in tropical than temperate regions. Similarly, the high research capacity (i.e., infrastructure and expertise availability) towards birds and mammals relative to amphibians and reptiles [2,3] contribute to the uneven sampling of trait space [4]. We expect larger biases in trait data among historically less sampled taxa. Finally, species' biology and sampling methodologies are known to affect species detection and collection rates in the field [31–33]. For instance, species detectability can be lower for small- than large-bodied species, and similarly so for nocturnal relative to diurnal species [34–36], whereas sampling methodologies often favour the collection and research of terrestrial and semi-terrestrial species [37–41]. We thus expect some convergent missingness across the tetrapod trait space, with undersampled species being typically small-sized, nocturnal, and fossorial or arboreal.

Methods

We reviewed available databases on global tetrapod groups and used the latest phylogeny-based methods to create the most comprehensive tetrapod attribute dataset to date. Our database includes various fields that track data sources and imputation techniques, which we collectively refer to as 'attributes', along with trait data. Our procedures can be summarised in five general steps: (i) data acquisition, (ii) taxonomic harmonisation, (iii) outlier verification, (iv) taxonomic imputation, and (v) phylogenetic imputation. Details on the validation of our predictions and imputation performance are available in the Supplementary Information.

Data Acquisition

We compiled 75 species-level attributes on taxonomy, body size, activity time, microhabitat, macrohabitat, threat status, geography, environmental preferences, and associated data sources for each tetrapod species. We gathered information available in several global, continental, and regional databases, and complemented the existing data by inspecting the published (articles, book chapters, field guides, and monographs) and grey literature (e.g., technical reports, government documents, monographs, theses), besides incorporating unpublished data gathered by us. To minimise the uneven representation of ecological attributes across clades, we identified genera and families whose species did not have data on body size, activity time, or microhabitat. We then used species belonging to such genera and families to feed additional online searches through academic platforms (Google Scholar and Web of Science) and included complementary attribute data whenever possible. We did not use the imputations available at the genus level in the data sources we examined.

Briefly, taxonomic data were represented by taxonomic ranks, authority name, and year of description. Body size data consisted of information on body length (mm) and body mass (g). Activity time informed if the species was diurnal and/or nocturnal. Cathemeral or crepuscular species were considered as both diurnal and nocturnal. Microhabitat informed five categories of habitat use commonly reported in field guides and related literatures: fossorial, terrestrial, aquatic, arboreal, and aerial. Microhabitat data for birds were adapted from the EltonTraits database [42], which described the estimated relative usage for seven types of foraging stratum. We reduce these seven categories to four by: summing the relative usage of species foraging below water surface or on water surface in the aquatic microhabitat; summing the relative usage of species foraging on the ground and below 2m in understory as terrestrial microhabitat; summing the relative usage of species foraging 2m upward in canopy and just above canopy as arboreal microhabitat. Species with aerial microhabitat were kept as informed in EltonTraits database [42], 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 the threshold of 30% to consider a species as typical of a given microhabitat type.

Some attributes in the Tetrapod Traits database were derived from expert-based range maps for amphibians [18,43,44], reptiles [20,29,43], mammals [43–45], and birds [26,44]. We matched the authoritative expert range maps for each of the tetrapod groups with the corresponding phylogenies and edited species ranges to ensure they represented the species concept adopted in the corresponding phylogeny. Overall, the verification procedure for species range maps can be summarised in eight 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, requiring therefore only an updated name, iii) no range, where extinct and domesticated species in the phylogeny did not need a range map, iv) 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, vi) lumps, where species range maps needed to be lumped back with another species range, vii) new species, where there was no available range map and ranges were drawn from other literature sources or a minimum convex polygon with a buffer needed to be drawn around type localities, and viii) *de Novo* species whose ranges needed to be removed because they were not in the phylogeny.

We measured range size as the number of 110 × 110 km equal-area grid cells intersected by each species. This spatial resolution was selected because it minimises the presence of errors related to the use of expert ranges maps [46–48]. Presence of a species in a grid cell was recorded if any part of the species distribution polygon overlapped with the grid cell. We then computed spatially-derived attributes as the within-range average value of continuous variables (e.g., annual mean temperature, proportion of urban area) weighted by species range occupancy in the cell, or as the proportion of the species range occupied by levels of categorical variables (e.g., proportion of the species range overlapped by each biogeographical realm). All within-range attributes were derived from spatial layers available online [49–52] and individually described in the Results and Discussion section. We did not derive range maps for species with uncertain geographic distribution, which refers to those with reported occurrences only at the level of administrative units (e.g., country, state) without precise location information.

Species macrohabitat data followed the IUCN Habitat Classification scheme v. 3.1 [43]. Briefly, the IUCN scheme describes 17 major habitat categories in which species can occur, besides an 18th category for species with unknown major habitat. We used the *rredlist* package [53] to obtain macrohabitat data directly from IUCN for 31,464 species (94.5% of all species herein considered). Our macrohabitat variables correspond only to the first level of IUCN Habitat Classification scheme. Other 157 species had macrohabitat data extracted from pertinent literature. We also used the *rredlist* package [53] to obtain non-DD assessed status for 28,885 tetrapod species based on IUCN red list v. 2021-3 [43]. For other 286 species, we used non-DD assessed statuses matching those informed in previous works using the same taxonomy of fully-sampled trees [18,20,25,54]. Data deficient species totalled 3,476 species. We did not find an assessed status for 646 species. Overall, the data acquisition involved the inspection of more than 2,600 references (Table 1). Full description of attributes and extra details on all sources consulted for each species are provided in the Results and Discussion section.

Taxonomic Harmonisation

The taxonomy of the Tetrapod Traits database followed the respective taxonomies of the recent, fully-sampled phylogenies for each of the major tetrapod groups [20,24–27]. The amphibian phylogeny taxonomy [24] followed the 19 February 2014 edition of AmphibiaWeb (http://amphibiaweb.org), with 7,238 species. The phylogeny for chelonians [20] followed the 8th ed. Of the Turtles of the World checklist [55], with the addition of *Aldabrachelys abrupta* and *Al. grandidieri*, and the synonymisation of *Amyda ornata with Am. cartilaginea*, adding up to 357 chelonian species, whereas for crocodilians [20], the taxonomy followed [56], complemented by the revalidation of *Crocodylus suchus* [57], *Mecistops leptorhynchus* [58], and recognition of three *Osteolaemus* species [59,60], resulting in 27 species. The taxonomy of the squamate and tuatara phylogeny [25] followed the Reptile Database update of March 2015 (http://www.reptile-database.org) with 9,755 species. For brevity, we hereafter refer to species in the later phylogeny as squamates, although we recognise that the tuatara, *Sphenodon punctatus*, is not a squamate. The taxonomy of the bird phylogeny [26] followed the Handbook of the Birds of the World [61], including 9,993 species. Finally, the taxonomy of the mammal phylogeny [27] followed IUCN [62] with modifications, and included 5,911 species.

To maximise the data usage from previous compilation efforts, and to ensure coherence among species names and the multiple data sources, we built lists with synonymies and respective valid names based on multiple taxonomic databases [43,63,64], and extracted the unique synonyms within 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 a taxonomic reconciliation based on four steps:

1. ***Direct match with data sources:*** scientific names between the Tetrapod Traits (33,281 species) and each potential data source were directly paired. However, species-level attributes of close-related species may show identical values if extracted from earlier sources that treated different species as synonymies. To minimise the inclusion of duplicated values among the species-level attributes, we flagged each taxonomic match between the Tetrapod Traits database and external data sources to use each data entry only once.
2. ***Direct match with data source synonymies:*** species without a direct match after the step 1 had their taxonomy updated in the data sources using the list of unique synonymies, and a new matching operation allowed the extraction and flagging of additional data whenever possible. At the end of this procedure, all species had their scientific names restored to the taxonomy originally informed.
3. ***Direct match with Tetrapod Traits synonymies:*** some data sources may follow more recent taxonomies than those inherited from the fully-sampled phylogenies [20,24–27]. For species without a direct match after the step 2, we updated their taxonomy in the Tetrapod Traits using the list of unique synonymies and repeated the procedures of data extraction and flagging. At the end of this procedure, all species had their scientific names restored to the taxonomy originally informed.
4. ***Manual verification:*** species without a direct match after the step 3 had their scientific names individually searched by hand in specialised taxonomic databases (amphibians [63], reptiles [64], birds [65], and mammals [66]) for potential spelling errors and/or additional synonymies not 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 step-4 were considered as missing data.

Outlier Verification

We implemented two approaches to detect potential inconsistencies in continuous attribute data 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 a suspicious outlier if their value were outside the interval defined between $[q_{0.25} - 1.5 \times \text{IQR}]$ and $[q_{0.75} + 1.5 \times \text{IQR}]$, where $q_{0.25}$ and $q_{0.75}$ are respectively the first and third quartiles, and IQR is the interquartile range $[q_{0.75} - q_{0.25}]$.
2. ***Deviation from allometric relationship:*** 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.

Species flagged by any of the above-mentioned approaches had their body length and/or body mass checked for validity and corrected if necessary, or even purged from the database if not confirmed by a reliable source.

Taxonomic Imputation

The global scope of the present database inevitably comes with gaps that are hard to fill, such as the scarcity of natural history data for species known from a few specimens or only the holotype [67,68]. Previous studies have tackled this challenge by using imputed values at genus-level or close-relatives [42] to reduce data missingness. Although these earlier strategies of 'taxonomic imputation' might reduce variability in attribute values, they are useful to fill gaps in highly conserved attributes, and can ultimately help increase the performance of phylogeny-based imputation methods applied in concert with correlated attribute data [16,17].

We used taxonomic imputations for two particular cases of missingness in microhabitat data: chiropterans with missing data were considered as 'aerial' (113 species), and dolphins and whales were considered as '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), and macrohabitat (17 binary variables informing the IUCN Habitat Classification scheme). If a type of activity time, microhabitat, or macrohabitat appeared in at least 70% of species in the genus, we then assumed such ecological attribute as also present among species with missing data in the respective genus. We did not use taxonomic imputation for continuous attributes. Our goal was to reduce missingness in activity time, microhabitat, and macrohabitat for groups with a well-known ecology (observed data available for at least 70% of species) before running phylogeny-based imputation methods (Table 1).

Phylogenetic Imputation

To minimise missing values in our database we used two imputation techniques proven as robust in recent methods comparisons [12,13], namely *Rphylopars* [14,15] and *missForest* [13]. The *Rphylopars* method uses the phylogenetic tree directly to impute missing values based on the phylogenetic covariances and correlated evolution between numeric attributes, whereas *missForest* is based on a random forest algorithm and allow mixed-type data.

Because of the large dimensionality of data in our analysis, we only performed imputations for body length, body mass, microhabitat, and activity time. All spatially-derived attributes showed more than 99% of data completeness (Table 1). We did not perform phylogeny-based imputations for species lacking range maps and, consequently, spatially-derived attributes. We $\log_{10}$-transformed the continuous variables (body length and body mass) to reduce skewness, and used binary variables to represent each type of microhabitat (fossorial, terrestrial, aquatic, arboreal, aerial) and activity time (diurnal and nocturnal). Note that microhabitat and activity time types are non-mutually exclusive. To account for uncertainty in fully-sampled phylogenies, we used 100 trees of each tetrapod group [20,24–27] to compute imputations. We ran *Rphylopars* using Brownian motion (BM) model of trait evolution and extracted the median value across the 100 trees for each imputed attribute per species. Because *Rphylopars* only allow continuous attributes [15], the imputed values for binary variables could assume values outside the range between 0–1. Thus, for each tetrapod group and binary attribute, we binarised imputed types of microhabitat and activity time using the 0.5 threshold.

The *missForest* algorithm does not include phylogenetic tree directly in computations [13]. To account for phylogenetic information, we selected the first 10 eigenvectors from the phylogenetic covariance matrix of each fully-sampled tree and used them in concert with the observed attribute data in the imputation routine. For each tetrapod group and across the subset of 100 trees, the selected phylogenetic eigenvectors explained on average 96.8% of the phylogenetic variation across the 100 trees of each tetrapod group (97.8% for amphibians, 99.4% for chelonians and crocodilians, 97.1% for squamates, 92.4% for birds, and 97.6% for mammals). For continuous attributes (body length and body mass), we extracted the median imputed value per species across the 100 trees. Imputed binary attributes (types of microhabitat and activity time) had their frequency computed across the 100 trees, with frequencies later made binary using the 0.5 threshold.

For birds only, we complemented the observed attribute data with 10 morphometric traits ($\log_{10}$-transformed) made recently available through the AVONET database [69], and then repeated the imputation routine using the subset of 100 fully-sampled bird trees. Given the high dimensionality of these computations, they became computationally intractable under the *Rphylopars* approach and were only performed through *missForest*. The model parameters used in *missForest* analysis for all tetrapod groups included: 500 trees to grow each decision forest (argument *ntree*), the square-root of total number of predictors as the number of

variables randomly sampled at each split (default of the argument *mtry*), and a maximum of 10 iterations for *missForest* reach the stopping criterion (default of the argument *maxiter*).

We selected the imputed values returned by the imputation approach (*Rphylopars* or *missForest*) identified as most suitable (see Supplementary Information, S1 Text) for each combination of tetrapod group (amphibians, chelonians and crocodilians, squamates, birds, and mammals) and attribute data (body length, body mass, microhabitat, and activity time). Additional fields clearly labelled all imputations included in the Tetrapod Traits database. Computations were performed in R v. 4.1.0 using the packages *Rphylopars* [15], *ape* [70], *gmodels* [71], and *missForest* [13].

Table 1. Summary of major groups of attributes, species counts, and sources in Tetrapod Traits database. 'Imputed' counts indicate the number of species with taxonomic (Taxon.) or phylogenetic (Phylog.) imputations computed. References used for data acquisition are shown for each attribute and tetrapod group.

Attribute group	Number of species			Number of sources	Major Sources per Tetrapod group				
	Obs. Data	Taxon. Imputed	Phylog. Imputed		Amphibians	Turtles and Crocs	Squamates	Birds	Mammals
Body length	24,472	0	8,809	1559	[72–76]*	[20]*	[77]*	[78–80]*	[22,78]*
Body mass	26,613	0	6,668	460	[72,73,81–84]*	[20]*	[77]*	[42,69,80]*	[22,42,78,85–88]*
Activity time	24,512	588	8,181	347	[72,89–93]*	[94]*	[95–106]*	[42]*	[22,42,82,83,87]*
Microhabitat	31,470	1,125	686	688	[72,89,107]*	[20]*	[95–98,100–112]*	[42,107]*	[22,42,107]*
Macrohabitat	31,621	1,440	0	140	[43,44]*	[43,44]*	[43,44]*	[43,44]*	[43,44]*
Geography	33,125	0	0	7	[18,43,44]	[20,43,44]	[29]	[26,44]	[17,19, 22–26]
Environment	33,125	0	0	3	[49,50]	[49,50]	[49,50]	[49,50]	[49,50]
Human Influence	33,125	0	0	3	[51,52]	[51,52]	[51,52]	[51,52]	[51,52]
Threat Status	32,647	0	0	6	[18,43,113]	[20,43,114]	[43,115]	[43,54]	[43,116]

*For brevity, the references listed include only sources contributing with at least 30 species. All species-specific references are included in the raw files of the Tetrapod Traits database.

Patterns in Data Co-Missingness

We assessed co-occurrence patterns in data missingness across species using the 'checkerboard score' (C-score; [117]), which is less prone to type II errors than other co-occurrence metrics computed under a null model approach [118]. The C-score was based on a binary presence-absence matrix (PAM) of species (columns) by missing attributes (rows), the latter represented by five binary variables informing the missingness of observed values in body length, body mass, activity time, microhabitat, and threat status. Missing data in threat status was represented by DD or non-assessed species. We computed the C-score using individual PAMs for each genus and family with at least 2 species, and each pairwise combination of attribute variable, following recommendations by [119].

To verify whether an observed C-score differed from the value expected by chance, we built a null distribution of C-score values through a randomization algorithm that kept attribute completeness (rows sums) fixed while considering species as equiprobable regarding their chances of showing missing attribute values. 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 C-score and associated p-values and identified the pairwise attribute combinations with aggregated (SES C-score < 0 and $p < 0.05$) or segregated (SES C-score > 0 and $p < 0.05$) co-occurrence pattern of data missingness per taxa. Computations were performed using the *EcoSimR* [120] 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 [16], since imputation errors can increase either with the percentage of missing data or when multiple attributes are imputed simultaneously [12,16,17]. To verify how the inclusion of imputed values affected attribute patterns per taxa, we calculated the per-genus and per-family relative change in attribute property after adding imputed values.

For continuous attributes (body length and mass), the attribute property was represented by the geometric mean attribute value. For binary attributes, we scored types of microhabitat and activity time into continuous metrics of 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). We then extracted the mean verticality and nocturnality per taxon and geographical assemblage. Relative change in attribute values was represented by the ratio of attribute property with imputations (i.e., mean computed using observed + imputed data) to attribute property without imputations (mean computed using observed data only):

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

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 [121] to build a tetrapod super tree by combining the global phylogenies available for amphibians [24], chelonians and crocodilians [20], squamates [25], birds [26], and mammals [27]. The full tetrapod tree topology was only used for visualization 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 assess whether the relative increase or decrease of attribute properties differed with respect to the number of simultaneously imputed attributes through Kruskal-Wallis tests.

Results and Discussion

Data Completeness

We focus our assessment of data gaps on the attributes with considerable missingness, body length, body mass, activity time, microhabitat, and threat status. Across these five focal attributes, we observed complete species-level data for 40.7% of tetrapod species (n = 13,540), 31.5% of genera (n = 1,609), and 19.7% of families (n = 102). Seven tetrapod genera showed no data for these five attributes, all of them were monotypic rodents (*Calassomys*, *Halmaheramys*, *Musseromys*, *Paucidentomys*, and *Waiomys*) or bats (*Dryadonycteris* and *Hsunycteris*). No family showed zero completeness for these five attributes combined. Lowest completeness levels were among attributes related to body length (73.5%), activity time (73.6%), body mass (80%), and microhabitat (94.5%, Table S1-S2). While assessed threat status was available for 98% of tetrapod species, this number decrease to 87.6% if DD species were treated as missing data (Fig. 1).

At the level of geographic assemblages, attribute completeness showed large variation for body length, with Neotropical and Afrotropical assemblages presenting the lowest completeness (Fig. 2A). The low spatial variability in attribute completeness for body mass, activity time, microhabitat, and assessed threat status (Fig. 2B–E) indicated that species with missing data are mostly narrow-ranged [4], which can limit the influence of data missingness in assemblage-level patterns. Of the 6,893 species missing at least two attributes (body length, body mass, activity time, microhabitat, and threat status), 77% occurred in 10 or less 110 × 110 km equal-area grid cells. If we restrict missingness to three or more attributes, then 87% of species filtered occurred in ≤10 grid cells. The completeness of phylogenetic data in the

fully-sampled trees of tetrapods [20,24–27] also showed high variation in spatial coverage (Fig. 2F), with Afrotropical and Indomalayan realms emerging with the highest Darwinian shortfall [28]. Overall, our findings help illustrate that geographical patterns in data coverage can be strongly influenced by data for wide-ranged species.

Data Co-Missingness

We found non-random co-occurrence patterns in data missingness for 20% of the pairwise attribute combinations at genus-level and 43% at family-level. Almost all non-random co-occurrence patterns showed aggregation of missing values, that is, data missingness was shared among multiple attributes for a same species, particularly among squamates and amphibians (Fig. 3A). In inspecting the co-missingness between threat status and other attributes, we found leaf-litter amphibians (*Craugastor*, *Eleutherodactylus*, and *Pristimantis*, all within the superfamily Brachycephaloidea) standing out among tetrapod genera with highest aggregation in missing values (Fig. 3B). These findings reinforce the view of amphibians and squamates as the least researched tetrapod classes [2,3], besides indicating the uneven sampling coverage of attribute space within certain clades.

Highly aggregated patterns of data missingness were more common among species-rich clades with lower proportion of missing data (Figs 3 and S5). That is, co-missingness was strongest in species-rich and well-sampled taxa, particularly in those holding high proportion of species known only from their type locality or holotype [67,122]. About 86% of the genera and 74% of families within the top 50 taxa in co-missingness (Figs 3 and S5) include 'lost taxa', that is, species that have not been reliably observed in >50 years and yet are not declared extinct [68]. While the rediscovery of such rarely observed species is not uncommon [122], their absence in attribute databases will not be easily filled through field observations [123], which could impair biogeographical research and conservation practice.

Biases uncovered by imputation-based gap filling

We found that the gap filling provided by the imputations resulted in substantial changes in aggregate attribute properties and the insights they would support. These changes occurred in both directions and were strongest in continuous attributes (body length and body mass). About 65% of tetrapod genera and 78% of tetrapod families include at least one species with phylogeny-based imputations. After the inclusion of imputed values, the average attribute value per genus decreased in 5.9% of attribute-genus combinations, and increased in 5%. At the family-level, 14% of attribute-family combinations showed increased in the average attributes after the inclusion of imputed attributes whereas 20% decreased (Fig. 4).

Changes in attribute properties at the level of geographic assemblages revealed substantial changes in the average body size in tropical regions (Fig. 5A-F). In contrast, such differences are largely absent in the temperate regions, reflecting the dedicated mobilization and resulting large availability of biodiversity data in developed countries [2,4,124], particularly throughout North America, Europe, and Asia. Average nocturnality of tetrapod assemblages tended to strongly increase after inclusion of imputed values, highlighting a global knowledge bias from lack of observed attribute data (Fig. 5H-I), particularly for squamates and to a lesser extent, amphibians (Figs S6-S11). We attribute this to both the low detectability of nocturnal species [125,126] and the general lack of data for tropical regions where nocturnal species predominate in the tropics [127]. Changes in average verticality were less pronounced across tetrapod assemblages (Fig. 5K-L), which is somewhat expected given the high completeness of microhabitat data. Even so, fossorial or arboreal species were responsible for 53% of imputed microhabitat whereas they represented about 44% of non-imputed microhabitat categories.

Although imputation biases can increase in the absence of additional correlated attributes [16], we found no relationships between the number of imputed attributes and changes in average attributes after imputation-based gap-filing (Fig. S12). That is, changes in average attributes

were not higher in genera and families including species with multiple missing attributes. Moreover, changes in average attributes were either mostly unrelated with co-missingness (Fig. S13) or occurred in opposite directions, with low co-missingness 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 S14-S16). Those taxa and assemblages with minor completeness and with least species saw the strongest changes in average attribute value. Lower attribute completeness creates more opportunities for variation in attribute space after imputation-based gap-filing, whereas a high species richness can dilute the importance of imputed values in the sample.

Tetrapod Traits – a comprehensive, imputation informed attributes database

We make the full phylogenetically coherent database, Tetrapod Traits, publicly available to support a range of research applications in ecology, evolution, and conservation and to help minimize the impacts of biased data in this system. Briefly, the Tetrapod Traits database includes 75 fields registering observed and imputed species-level attributes followed by respective sources across 33,281 tetrapod species. Attributes in this database show at least 98% of completeness after including imputed values and are organized in 9 major groups (Table 1, see Table S1 for the complete description of each attribute):

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. **Tree –** includes 2 attributes that indicate which fully-sampled phylogeny contains the species, besides informing if the species phylogenetic relationship 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 inform period of activity (e.g., diurnal, fossorial) as dummy variables, data sources, details on the imputation of species activity time, and a diurnality score. Field names: Diu, Noc, ImputedActTime, SourceActTime, Nocturnality.

5. **Microhabitat –** includes 8 attributes inform habitat use (e.g., fossorial, terrestrial, aquatic, arboreal, aerial) as dummy 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 inform 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.

7. **Geography –** includes 12 attributes that inform species range size, average latitude and longitude, and the proportion of species range within each biogeographical realm. Field names: RangeSize, Longitude, Latitude, Afrotropic, Australasia, IndoMalay, Neartic, Neotropic, Oceania, Paleartic, Antartic.

8. **Environment –** includes 5 attributes that inform the average environmental condition within the species geographic range. Field names: AnnuMeanTemp, AnnuPrecip, TempSeasonality, PrecipSeasonality, Elevation.

9. **Human Influence –** includes 10 attributes that inform the within-range average or proportion of human-related activities, assessed statuses and sources. Field names: ETA50K, HumanDensity, PropAnthroHyde, PropUrbanArea, PropCroplandArea, PropPastureArea, PropRangelandArea, PropGrazingArea, AssessedStatus, SourceStatus.

Conclusion

The growth in mobilized attribute data over the last decade has enabled significant progress and increased geographic and taxonomic generality in comparative biology [82,128,129], macroevolution [130], macroecology [131], and conservation biology [132–134]. But research outcomes and their interpretation often remained constrained by non-randomly missing data [6,8,17], and lack of standardisation across data dimensions – trait, phylogenetic, spatial – and data sources [135]. In concert with taxonomic updates [136,137], these issues have imposed additional limits on multi-taxon investigations and global biodiversity synthesis [138–140]. Here, after documenting remaining global data gaps for central traits, we were able to use imputation to fill the gaps and illustrate the knowledge biases these missing attribute data had imposed. By using phylogeny-based imputation methods in concert with inter-related ecological attributes, we were able reveal the hitherto invisible part of the attributes space. Our findings confirmed the predominance of attributes co-missingness, and provide a comprehensive assessment of data gaps and biases across tetrapod groups.

The attributes predictions for species missing data brought to light the key correlates and identified the significant consequences these gaps can have for inference. For instance, larger body size has been related to both high species detectability [34,38,125] and discovery probability [141–143], larger research effort and public interest [40,41,144,145], increased availability of assessed status [146,147], and better data sampling. Despite the research difficulties that a large size may impose – e.g., high species sensitivity to disturbances [148,149], lower abundance [150,151], uneasy collection or transport – the presence of multiple data biases towards small-sized species confirm the struggle of biodiversity scientists to know well the smallest beings in nature. In summary, different knowledge shortfalls [139] can share the similar determinants.

Biodiversity knowledge shortfalls were also clearly related to activity time and microhabitat. Nocturnal species often show lower detectability [125], are typically less researched [40] and underassessed with respect to threat status [146], which helps explain why diurnal species are more likely to have activity time data. In addition, the high detectability of terrestrial than arboreal or fossorial species with standard sampling methods [38,152] can lead to less biased occurrence data [153] and more research effort [30,40]. Although the species foraging stratum may constrain certain aspects of our biodiversity knowledge, we find only a limited influence of verticality on microhabitat data availability.

Attribute imputations can be limited and themselves be biased [16,17]. For tetrapods and this study, these concerns were minimized by an already substantial initial data coverage and a gap-oriented mobilization of additional data. In only 276 tetrapod species (0.8%) all four focal attributes (body length, body mass, activity time, and microhabitat) had to be imputed. No family had the four focal attributes missing in all species, and only eight genera (0.15% of total genera) were missing the four focal attributes. Two important diagnostics offered strong support for the robustness of the attribute predictions. First, there was no association between the number of imputed attributes and changes in average attributes after imputation-based gap-filling (Fig. S12). Second, there was no positive association between co-missingness in

attribute data and changes in average attribute values (Fig. S13). We encourage researchers to carefully consider how assumptions and uncertainty of any imputed data might affect downstream use and interpretation, and the information we developed here is no exception. For many tetrapod research cases, however, we expect the inclusion of species with imputed data to be preferrable to the wholesale exclusion of the data-limited species.

We demonstrate that even for tetrapod species, 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 uncover that these gaps have brought about attribute distributions that have strong geographical and taxonomic biases. We expect the approach and likely the same general insights regarding biodiversity knowledge shortfalls to transcend taxa and systems. The illustrated consequence of biased data can percolate through trait-based metrics and comparative analyses, and ultimately have the potential to mislead research on functional diversity [8,19,154], extinction risk [6,21,155], and ecogeography [156–158]. Here we have provided a new phylogeny-based attribute databased that can help minimise the impact of biased data and support new research avenues in tetrapod conservation, ecology and evolution.

Data Availability

The Tetrapod Traits database and the 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

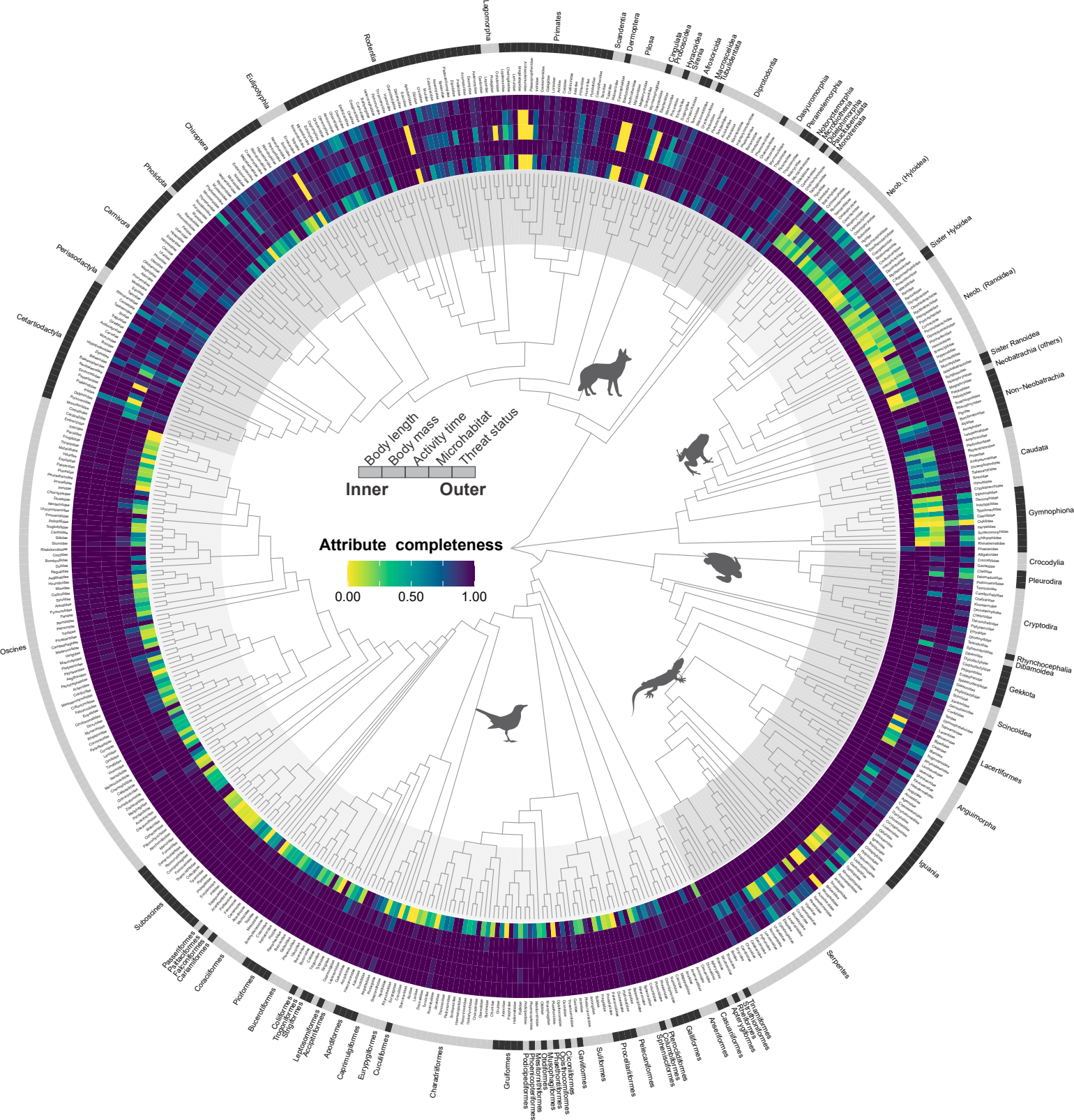
Figure 1. Attribute data coverage (completeness) of tetrapod species by family. Colour rings show the proportion of species with observed attributes in each tetrapod family for the five attributes with lowest completeness. Phylogenetic relationships shown are simple the family-level topology of tetrapod families.

Figure 2. 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, and latitudinal plots C, F, I and L illustrate the average of these cells value across per latitude. See Fig. S4 for spatial patterns of attribute completeness for each tetrapod group. Colour ramps followed Jenks natural breaks classification.

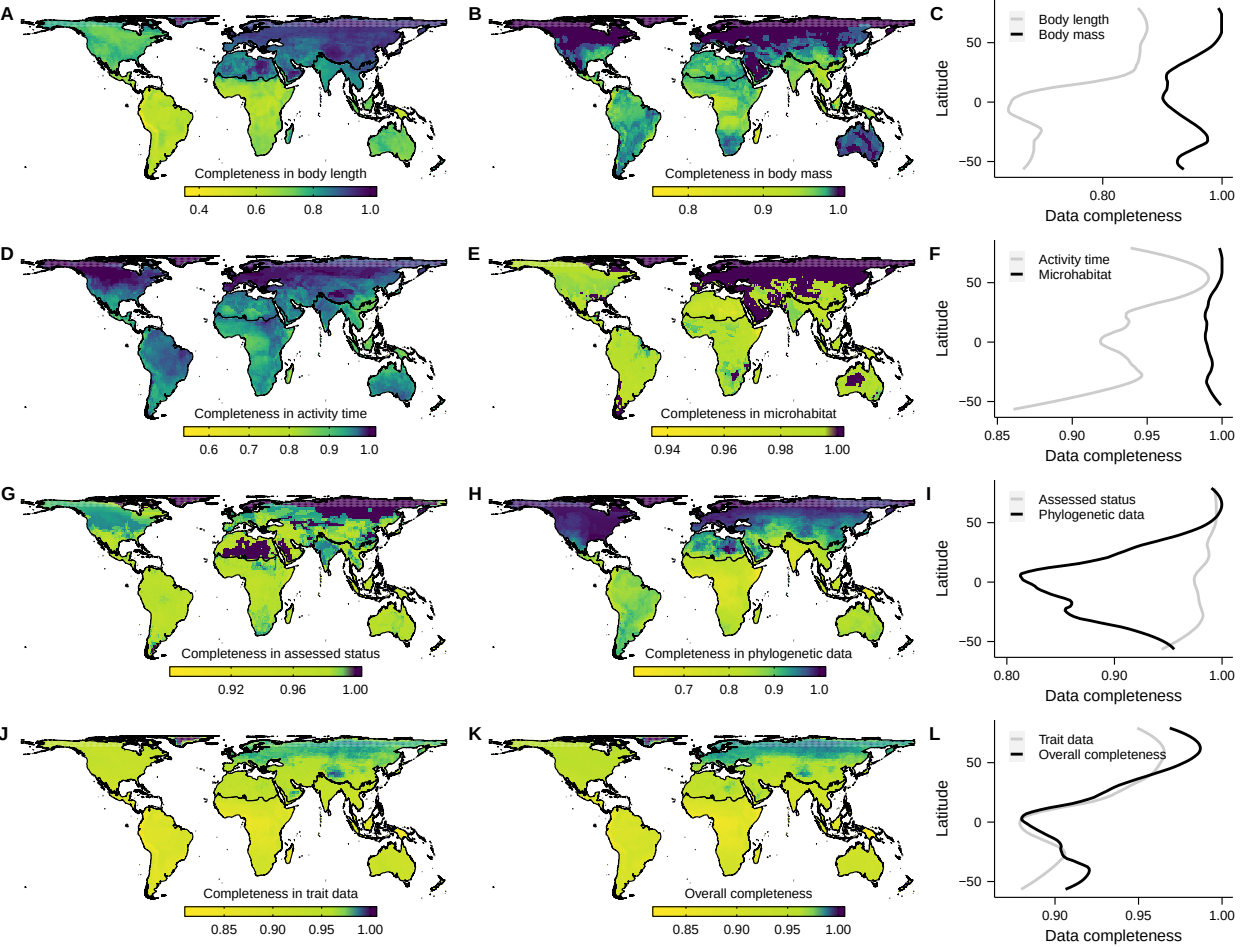
Figure 3. The top 50 tetrapod genera with most pronounced patterns of shared data missingness. For each genus, the aggregation metric equals the median value of the standardised effect-size (SES) of the C-score metric computed across (A) all pairwise attribute combinations; or (B) attribute pairs mandatorily involving threat status. Gray numbers of the left side of each panel indicate the per-genus species richness. See Fig. S5 for aggregation patterns computed at the family-level.

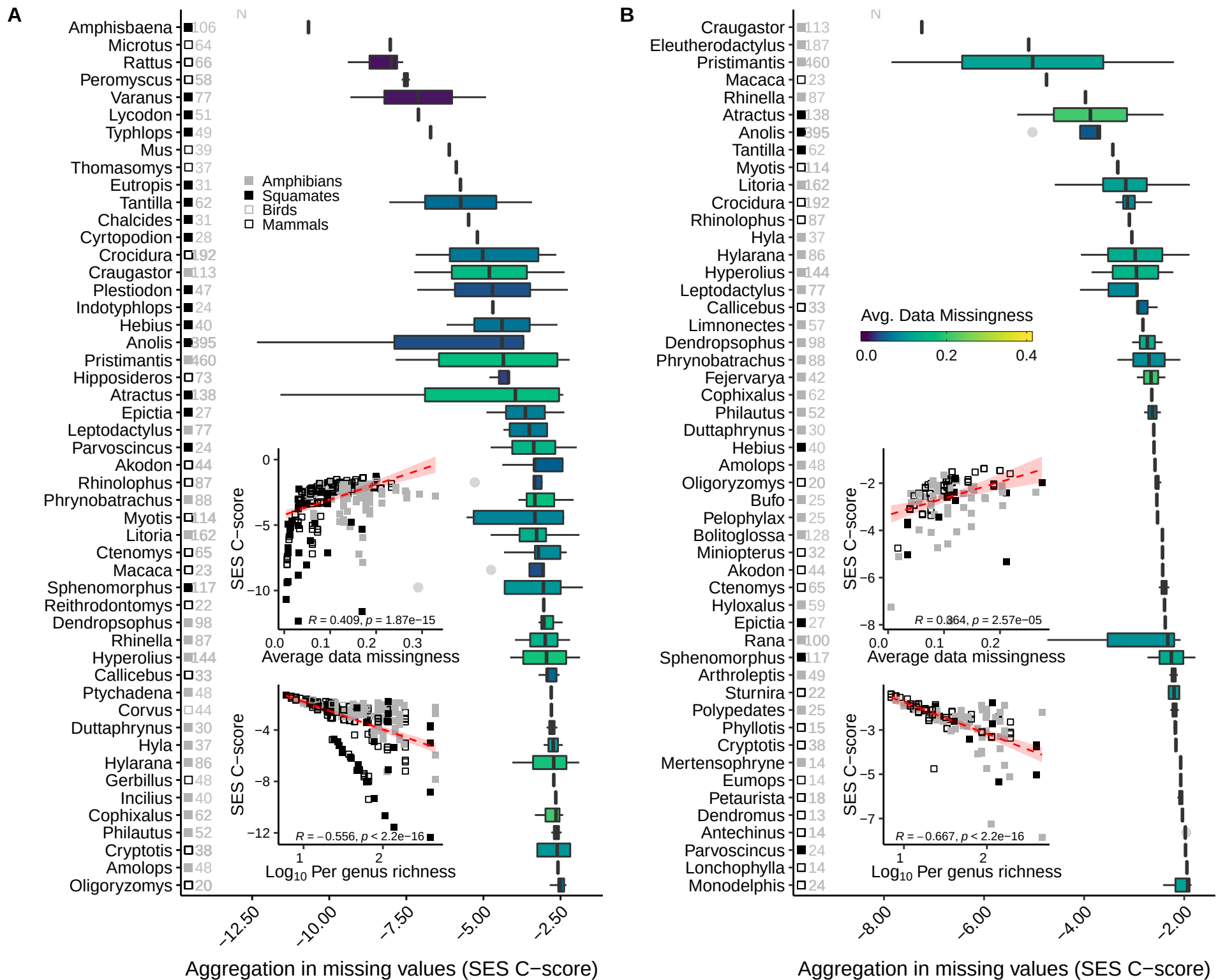
Figure 4. Changes in family-level attributes average after imputation-based gap-filling. For continuous data (BL, body length and BM, body mass), relative change in attribute property quantify the proportional decrease or increase in the geometric mean attribute value per-genus. For binary attributes (types of activity time and microhabitat), relative change in attribute property measured the decrease or increase in mean species nocturnality (Noct) and verticality (Vert) score. The inset donut chart denotes the proportion of genera (inner donut) and families (outer donut) by category of attribute change. See Fig. S11 for individual charts of each tetrapod group.

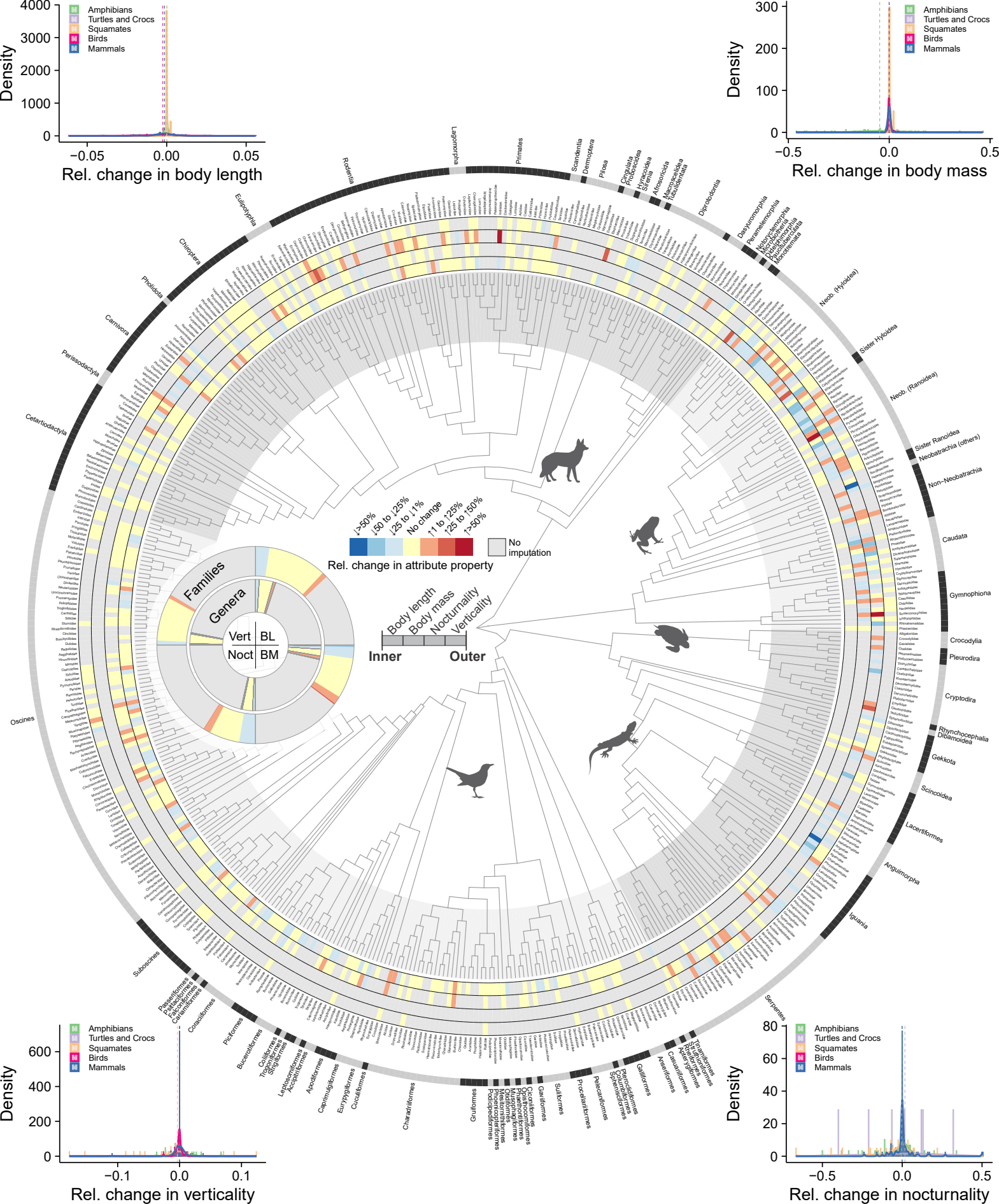
Figure 5. Changes in average attribute per tetrapod assemblage after imputation-based gap-filing. For each grid cell, maps show the average species attribute value and respective relative change in attribute value after inclusion of imputed values for (A─C) body length, (D─F) body mass, (G─I) nocturnality, (J─L) verticality. Body length and body mass were $\log_{10}$ transformed before computations. Gray cells indicate assemblages without species with imputed values. See Figs S6-S10 for patterns of attribute change for each tetrapod group.



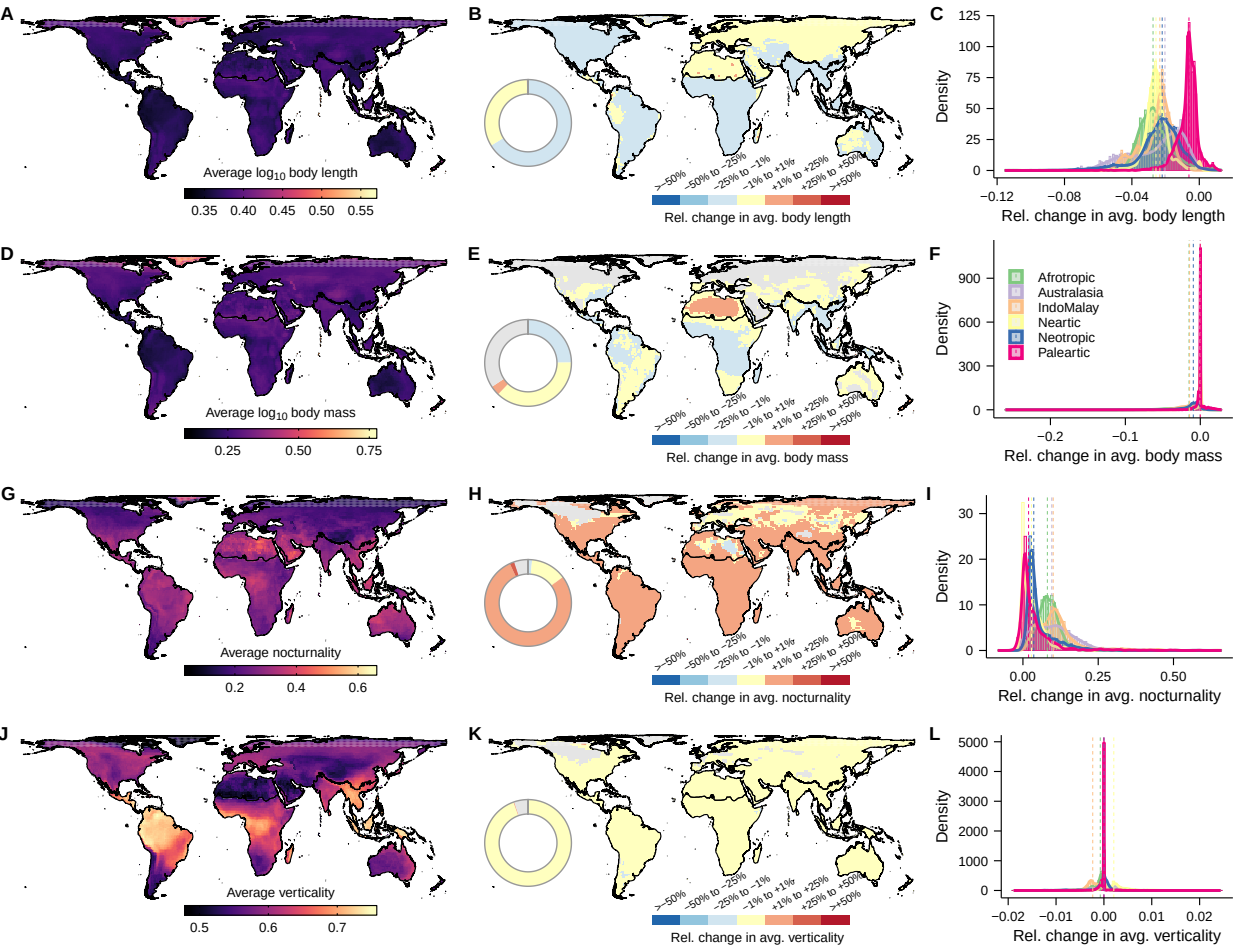
Body length
Body mass
Activity time
Microhabitat
Threat status
Inner
Outer
Attribute completeness
0.00
0.50
1.00
Lagomorpha
Primates
Scandentia
Dermoptera
Pilosa
Cingulata
Proboscidea
Hyracoidea
Sirenia
Afrosoricida
Macroscelidea
Tubulidentata
Diprotodontia
Dasyuromorphia
Peramelemorphia
Notoryctemorphia
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
Apterygiformes
Casuariformes
Anseriformes
Galliformes
Cerrocliformes
Columbiformes
Sphenisciformes
Pelecaniformes
Procellariiformes
Suliformes
Gaviiformes
Ciconiiformes
Phaethontiformes
Otidiformes
Mesitornithiformes
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
1.0
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
0.94
0.96
0.98
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
0.92
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
1.00
K
Overall completeness
0.85
0.90
0.95
1.00
L
Trait data
Overall completeness
Latitude
50
0
−50
0.90
0.95
1.00
Data completeness


A
N
Amphisbaena 106
Microtus 64
Rattus 66
Peromyscus 58
Varanus 77
Lycodon 51
Typhlops 49
Mus 39
Thomasomys 37
Eutropis 31
Tantilla 62
Chalcides 31
Cyrtopodion 28
Crocidura 192
Craugastor 113
Plestiodon 47
Indotyphlops 24
Hebius 40
Anolis 395
Pristimantis 460
Hipposideros 73
Atractus 138
Epictia 27
Leptodactylus 77
Parvoscincus 24
Akodon 44
Rhinolophus 87
Phrynobatrachus 88
Myotis 114
Litoria 162
Ctenomys 65
Macaca 23
Sphenomorphus 117
Reithrodontomys 22
Dendropsophus 98
Rhinella 87
Hyperolius 144
Callicebus 33
Ptychadena 48
Corvus 44
Duttaphrynus 30
Hyla 37
Hylarana 86
Gerbillus 48
Incilius 40
Cophixalus 62
Philautus 52
Cryptotis 38
Amolops 48
Oligoryzomys 20
Amphibians
Squamates
Birds
Mammals
SES C−score
R = 0.409, p = 1.87e−15
Average data missingness
R = −0.556, p < 2.2e−16
Log10 Per genus richness
−12.50
−10.00
−7.50
−5.00
−2.50
Aggregation in missing values (SES C−score)
B
N
Craugastor 113
Eleutherodactylus 187
Pristimantis 460
Macaca 23
Rhinella 87
Atractus 138
Anolis 395
Tantilla 62
Myotis 114
Litoria 162
Crocidura 192
Rhinolophus 87
Hyla 37
Hylarana 86
Hyperolius 144
Leptodactylus 77
Callicebus 33
Limnonectes 57
Dendropsophus 98
Phrynobatrachus 88
Fejervarya 42
Cophixalus 62
Philautus 52
Duttaphrynus 30
Hebius 40
Amolops 48
Oligoryzomys 20
Bufo 25
Pelophylax 25
Bolitoglossa 128
Miniopterus 32
Akodon 44
Ctenomys 65
Hyloxalus 59
Epictia 27
Rana 100
Sphenomorphus 117
Arthroleptis 49
Sturnira 22
Polypedates 25
Phyllotis 15
Cryptotis 38
Mertensophryne 14
Eumops 14
Petaurista 18
Dendromus 13
Antechinus 14
Parvoscincus 24
Lonchophylla 14
Monodelphis 24
Avg. Data Missingness
0.0
0.2
0.4
SES C−score
R = 0.364, p = 2.57e−05
Average data missingness
R = −0.667, p < 2.2e−16
Log10 Per genus richness
−8.00
−6.00
−4.00
−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
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
Dactylopsilia
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
Coraciformes
Piciformes
Bucerotiformes
Coliiformes
Trogoniformes
Strigiformes
Leptosomiformes
Accipitriformes
Apodiformes
Caprimulgiformes
Eurypygiformes
Cuculiformes
Charadriiformes
Gruiformes
Podicipediformes
Phoenicopteriformes
Mesitornithiformes
Otidiformes
Musophagiformes
Phaethontiformes
Ciconiiformes
Ciconiiformes
Gaviiformes
Suliformes
Procellariiformes
Pelecaniformes
Pteroclidiformes
Columbiformes
Sphenisciformes
Galliformes
Anseriformes
Casuariiformes
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
125 100 75 50 25 0
−0.12 −0.08 −0.04 0.00
Rel. change in avg. body length
D
Average log10 body mass
0.25 0.50 0.75
E
>−50% −50% to −25% −25% to −1% −1% to +1% +1% to +25% +25% to +50% >+50%
Rel. change in avg. body mass
F
Afrotropic
Australasia
IndoMalay
Neartic
Neotropic
Paleartic
Density
900 600 300 0
−0.2 −0.1 0.0
Rel. change in avg. body mass
G
Average nocturnality
0.2 0.4 0.6
H
>−50% −50% to −25% −25% to −1% −1% to +1% +1% to +25% +25% to +50% >+50%
Rel. change in avg. nocturnality
I
Density
30 20 10 0
0.00 0.25 0.50
Rel. change in avg. nocturnality
J
Average verticality
0.5 0.6 0.7
K
>−50% −50% to −25% −25% to −1% −1% to +1% +1% to +25% +25% to +50% >+50%
Rel. change in avg. verticality
L
Density
5000 4000 3000 2000 1000 0
−0.02 −0.01 0.00 0.01 0.02
Rel. change in avg. verticality