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An Update of Wallace's Zoogeographic Regions of the World

Ben G. Holt *et al.*
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To examine the temporal profile of ChC production and their correlation to laminar deployment, we injected a single pulse of BrdU into pregnant *Nlx2.1^{CreER};Ai9* females at successive days between E15 and P1 to label mitotic progenitors, each paired with a pulse of tamoxifen at E17 to label NKX2.1⁺ cells (Fig. 3A). We first quantified the fraction of L2 ChCs (identified by morphology) in mPFC that were also BrdU⁺. Although there was ChC production by E15, consistent with a previous study that suggested ventral MGE as a possible source at this time (17), the peak of ChC generation was at E16, when MGE has morphologically disappeared and NKX2.1 expression has appeared at VGZ (Fig. 3, B and C). ChC genesis then diminished but persisted until the end of gestation. This result significantly extends the time course of interneuron generation from NKX2.1 progenitors and suggests that ChCs may be the last cohort, generated at a time when PyN neurogenesis has largely completed. More surprisingly, we found that L5 and L6 ChCs were also BrdU⁺ after E17 induction (Fig. 3, D and E), which indicated that they were generated long after L5 and L6 PyNs, and as late as L2 ChCs. Therefore, the laminar deployment of ChCs does not follow the inside-out sequence, further distinguishing them from MGE-derived interneurons.

NKX2.1 expression during late gestation also included the preoptic area and striatum (6). To prove VGZ as the source of ChCs, we labeled NKX2.1⁺ cells at E16, then transplanted the RFP⁺ VGZ progenitors to the somatosensory cortex of P3 wild-type hosts (Fig. 4, A to B). After 3 weeks, these exogenous progenitors not only differentiated into neurons that spread to the medial frontal areas and settled into appropriate laminae (e.g., L2 and L5) but further matured into quintessential ChCs (Fig. 4, C and D). These results indicate that NKX2.1⁺ progenitors in the late embryonic VGZ are the main source of ChCs. They further demonstrate that the identity of a ChC is determined by its spatial and temporal origin (i.e., lineage and birth time) and, once specified, a cell autonomous program can unfold in ectopic locations, even without proper migration, to direct differentiation.

To examine the role of NKX2.1 in ChC specification, we deleted *Nlx2.1* in VGZ progenitors using a conditional strategy (fig. S8) and transplanted NKX2.1-deficient VGZ cells to the somatosensory cortex of wild-type pups (Fig. 4E). These *Nlx2.1^{KO}* progenitors gave rise to neurons that accumulated in L2 and L5 after 3 weeks (Fig. 4G), a laminar pattern that resembled those of endogenous ChCs. However, *Nlx2.1^{KO}* lineage cells did not differentiate into ChCs, as indicated by the lack of L1 dendrites and almost absence of cartridgelike axon terminals (Fig. 4, F and G). Together with previous studies (6, 7), our results suggest that NKX2.1 may regulate the appropriate temporal competence of progenitors, which likely undergo sequential changes with cell division. They further indicate that NKX2.1 expression in VGZ progenitors is necessary to complete the

specification of a distinct, and probably the last, cohort in this lineage—the ChCs.

A recent study demonstrated that progenitors below the ventral wall of the lateral ventricle (i.e., VGZ) of human infants give rise to a medial migratory stream destined to the ventral mPFC (18). Despite species differences in the developmental timing of corticogenesis, this study and our findings raise the possibility that the NKX2.1⁺ progenitors in VGZ and their extended neurogenesis might have evolved, since rodents, to enrich and diversify cortical interneurons, including ChCs.

Studies in numerous systems (19) have demonstrated that the specification of neuronal identities early in development exerts strong influences in their subsequent positioning, connectivity, and function, but, to what extent this principle applies to the assembly of cortical circuits has been unclear. Here, we discovered that young chandelier cells, once specified through their lineage and birth time in the VGZ, migrate with a stereotyped route and achieve distinct laminar patterns before innervating a subdomain of PyN AIS. Therefore, interneurons with a distinct identity are likely endowed with cell-intrinsic programs that contribute to their subsequent integration into their destined cortical networks. Deficiencies in ChCs have been implicated in brain disorders, including schizophrenia (20). Genetic targeting of ChCs establishes an entry point that integrates studies of fate specification, laminar deployment, connectivity, and network dynamics in the context of cortical circuit assembly and function. This may provide a probe to circuit pathogenesis in models of neuropsychiatric disorders.

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Supplementary Materials

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An Update of Wallace's Zoogeographic Regions of the World

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Modern attempts to produce biogeographic maps focus on the distribution of species, and the maps are typically drawn without phylogenetic considerations. Here, we generate a global map of zoogeographic regions by combining data on the distributions and phylogenetic relationships of 21,037 species of amphibians, birds, and mammals. We identify 20 distinct zoogeographic regions, which are grouped into 11 larger realms. We document the lack of support for several regions previously defined based on distributional data and show that spatial turnover in the phylogenetic composition of vertebrate assemblages is higher in the Southern than in the Northern Hemisphere. We further show that the integration of phylogenetic information provides valuable insight on historical relationships among regions, permitting the identification of evolutionarily unique regions of the world.

Biogeographic and bioclimatic regions are the fundamental units of comparison in many broad-scale ecological and evolutionary studies (1, 2) and provide an essential tool

for conservation planning (3, 4). In 1876, Alfred Russel Wallace published the first map of global terrestrial zoogeographic regions (5), which later became the cornerstone of modern biogeography

(3). Using existing knowledge of his time (6), mostly on the distributions and taxonomic relationships of broadly defined vertebrate families, Wallace divided the world into six terrestrial zoogeographic units largely delineated by what we now know as the continental plates. Despite relying on limited information and lacking a statistical basis, Wallace's original map is still in use today.

Wallace's original zoogeographic regionalization scheme considered ancestral relationships among species, but subsequent schemes generally used data only on the contemporary distributions of species without explicitly considering phylogenetic relationships (7–9). Phylogenetic trees contain essential information on the evolutionary relationships of species and have become increasingly available in recent decades, permitting the delineation of biogeographic regions as originally envisioned by Wallace. The

opportunity now exists to use phylogenetic information for grouping assemblages of species into biogeographic units on a global scale. In addition to permitting a sound delimitation of biogeographic regions, phylogenetic information allows quantifying phylogenetic affinities among regions (e.g., 10). Newly developed statistical frameworks facilitate the transparent characterization of large biogeographic data sets while minimizing the need for subjective decisions (11).

Here, we delineated the terrestrial zoogeographic realms and regions of the world (12) by integrating data on the global distributions and phylogenetic relationships of the world's amphibians (6110 species), nonpelagic birds (10,074 species), and nonmarine mammals (4853 species), a total of 21,037 vertebrates species [see (13) for details]. Pairwise phylogenetic beta diversity ($p\beta$) metrics were used to quantify change in phylogenetic composition among species assemblages across the globe. Analyses of combined taxa $p\beta$ values identified a total of 20 zoogeographic regions, nested within 11 larger realms, and quantified phylogenetic relatedness among all pairs of realms and regions (Fig. 1, figs. S1 and S2, and tables S1 and S2). We also used $p\beta$ to quantify the uniqueness of regions, with the Australian (mean $p\beta = 0.68$), Madagascan (mean $p\beta = 0.63$), and South American (mean $p\beta = 0.61$) regions being the most phylogenetically distinct assemblages of vertebrates (Fig. 2). These evolutionarily unique regions harbor radiations of species from several clades that are either restricted to a given region or found in only a few regions.

Our combined taxa map (Fig. 1) contrasts with some previously published global zoogeographic maps derived exclusively from data on the distribution of vertebrate species (8, 9, 11). The key discrepancy between our classification

of zoogeographic regions and these previous classifications is the lack of support for previous Palearctic boundaries, which restricted this biogeographic region to the higher latitudes of the Eastern Hemisphere. The regions of central and eastern Siberia are phylogenetically more similar to the arctic parts of the Nearctic region, as traditionally defined, than to other parts of the Palearctic (fig. S2). As a result, our newly defined Palearctic realm extends across the arctic and into the northern part of the Western Hemisphere (Fig. 1 and fig. S1). These results bear similarities with the zoogeographic map of (11) derived from data on the global distribution of mammal families. In addition, our results suggest that the Saharo-Arabian realm is intermediate between the Afrotropical and Sino-Japanese realms [see the nonmetric multidimensional scaling (NMDS) plot in fig. S2]. Finally, we newly define the Panamanian, Sino-Japanese, and Oceanian realms [but see the Oceanian realm of Udvardy in (14) derived from data on plants].

Our classification of vertebrate assemblages into zoogeographic units exhibits some interesting similarities with Wallace's original classification, as well as some important differences (fig. S3). For example, Wallace classified islands east of Borneo and Bali in his Australian region (fig. S3), which is analogous to our Oceanian and Australian realms combined (Fig. 1 and fig. S1). In contrast, we find that at least some of these islands (e.g., Sulawesi) belong to our Oriental realm, which spans Sundaland, Indochina, and India (Fig. 1 and fig. S1). Moreover, our Oceanian realm is separate from the Australian realm and includes New Guinea together with the Pacific Islands (14), whereas Wallace lumped these two biogeographic units into the Australian region. Wallace further argued that the Makassar

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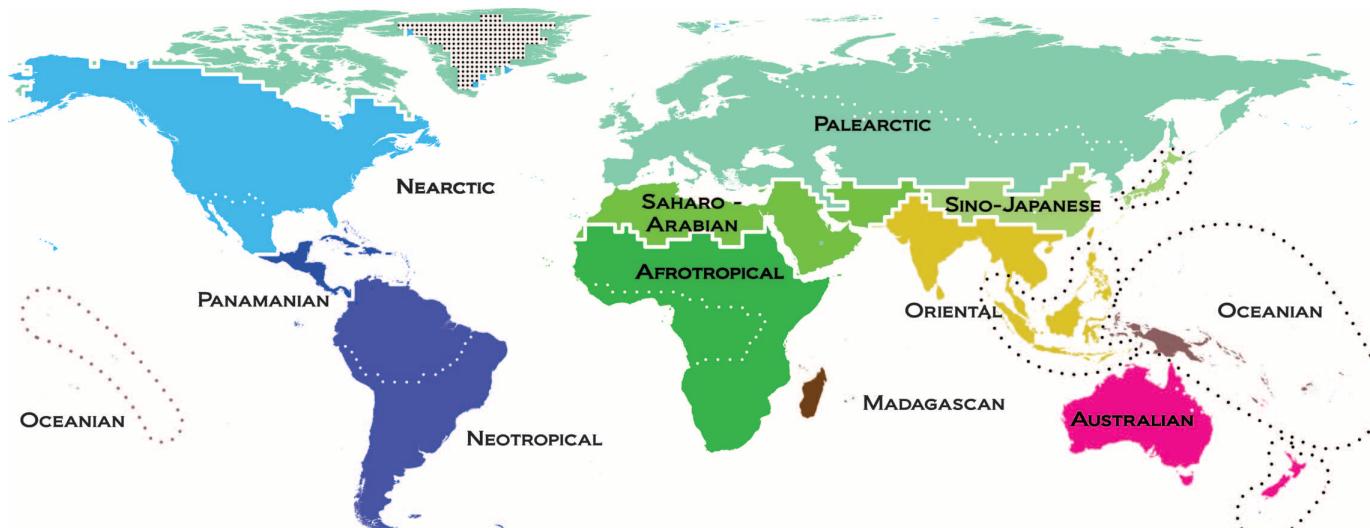


Fig. 1. Map of the terrestrial zoogeographic realms and regions of the world. Zoogeographic realms and regions are the product of analytical clustering of phylogenetic turnover of assemblages of species, including 21,037 species of amphibians, nonpelagic birds, and nonmarine mammals worldwide. Dashed lines delineate the 20 zoogeographic regions identified in this study. Thick

lines group these regions into 11 broad-scale realms, which are named. Color differences depict the amount of phylogenetic turnover among realms. (For more details on relationships among realms, see the dendrogram and NMDS plot in fig. S1.) Dotted regions have no species records, and Antarctica is not included in the analyses.

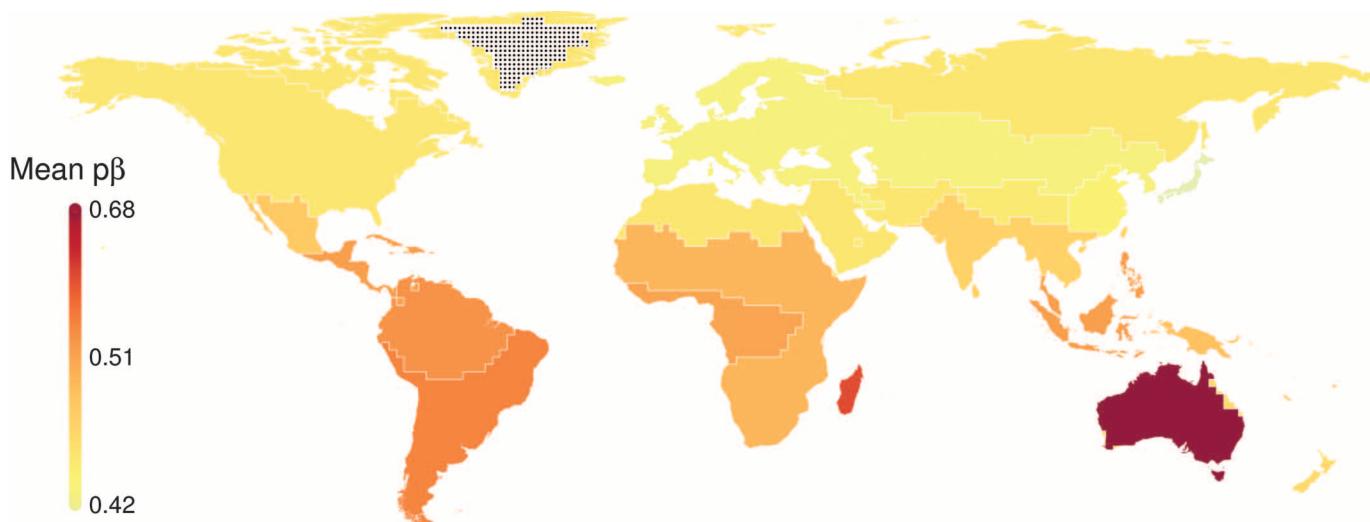


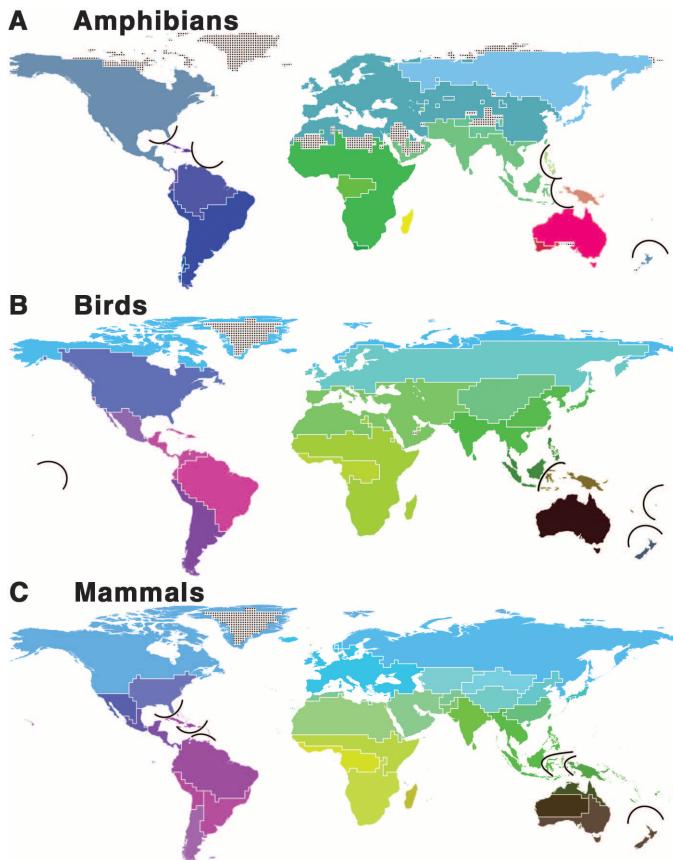
Fig. 2. Map of evolutionary uniqueness for terrestrial zoogeographic regions of the world based on data for 21,037 species of vertebrates. Evolutionary uniqueness is calculated as the mean of pairwise $p\beta$ values between the focal region and all other regions. Colors indicate the degree

to which each region differs from all other regions based on mean pairwise $p\beta$. Regions colored in dark red are the most evolutionarily unique. Dotted regions have no species records, and Antarctica is not included in the analyses.

Strait between Borneo and Sulawesi, now known as “Wallace’s Line” (15), was a major barrier to dispersal that greatly inhibited exchanges between the Australian and Asian land masses. Much debate subsequently arose regarding the precise location of the principal faunal divide between Wallace’s Oriental and Australian realms (15) (see fig. S3 for an illustration of Wallace’s original line). Our combined taxa analyses lend the strongest support to the hypothesis of Weber (16), who positioned this boundary east of Sulawesi, corresponding to the zoogeographic boundary separating our Oriental and Oceanian realms (Fig. 1 and fig. S1). However, our taxon-specific geographic delineation for birds is more consistent with Wallace’s line than Weber’s line (Fig. 3A and figs. S3 and S4A).

The delineation of and relationships among our zoogeographic regions differ among taxa (Fig. 3 and fig. S4), and we find more regions for mammals ($n = 34$ regions) than for amphibians or birds (both $n = 19$ regions). A comparison of $p\beta$ matrices across the three vertebrate taxa reveals that amphibian assemblages located in the northeastern Arctico-Siberian, southern African, and Madagascan regions are more phylogenetically distinct than those of birds or mammals for the same regions (fig. S5). Moreover, the Australian region harbors more phylogenetically distinct assemblages of amphibians and mammals relative to birds (fig. S5). Using a partial Mantel test [see (13) for details on this analysis], which accounts for geographic distances among species assemblages (17), we find that global $p\beta$ values for birds and mammals are more strongly correlated ($r = 0.68$, $P < 0.001$) than for amphibians and birds ($r = 0.39$, $P < 0.001$) or amphibians and mammals ($r = 0.43$, $P < 0.001$). These results might partly reflect a major episode of diversification early in the evolutionary history of amphibians (18). Alternatively, differences in

Fig. 3. Maps of terrestrial zoogeographic regions of the world based on data for (A) amphibians (6110 species), (B) birds (10,074 species), and (C) nonmarine mammals (4853 species). Color differences depict the relative amount of phylogenetic turnover among regions within each taxonomic clade. (For more details on relationships among regions, see the dendrogram and NMDS plots in fig. S4, A to C.) Dotted regions have no species records, and Antarctica is not included in the analyses.



spatial patterns of phylogenetic turnover among vertebrate classes might result from lower dispersal ability (19) and greater sensitivity of amphibians to environmental conditions (20). Interestingly, previous comparative studies documented similar incongruence in the diversity and distribution of amphibians relative to that of birds and mammals (21, 22).

The contrast between our zoogeographic regions with regions based only on distributional data (Fig. 4) demonstrates the consequences of incorporating phylogenetic information in the delineation of zoogeographic units. Relative to expectations based on turnover of species, spatial turnover in the phylogenetic composition of assemblages of species is generally low in the

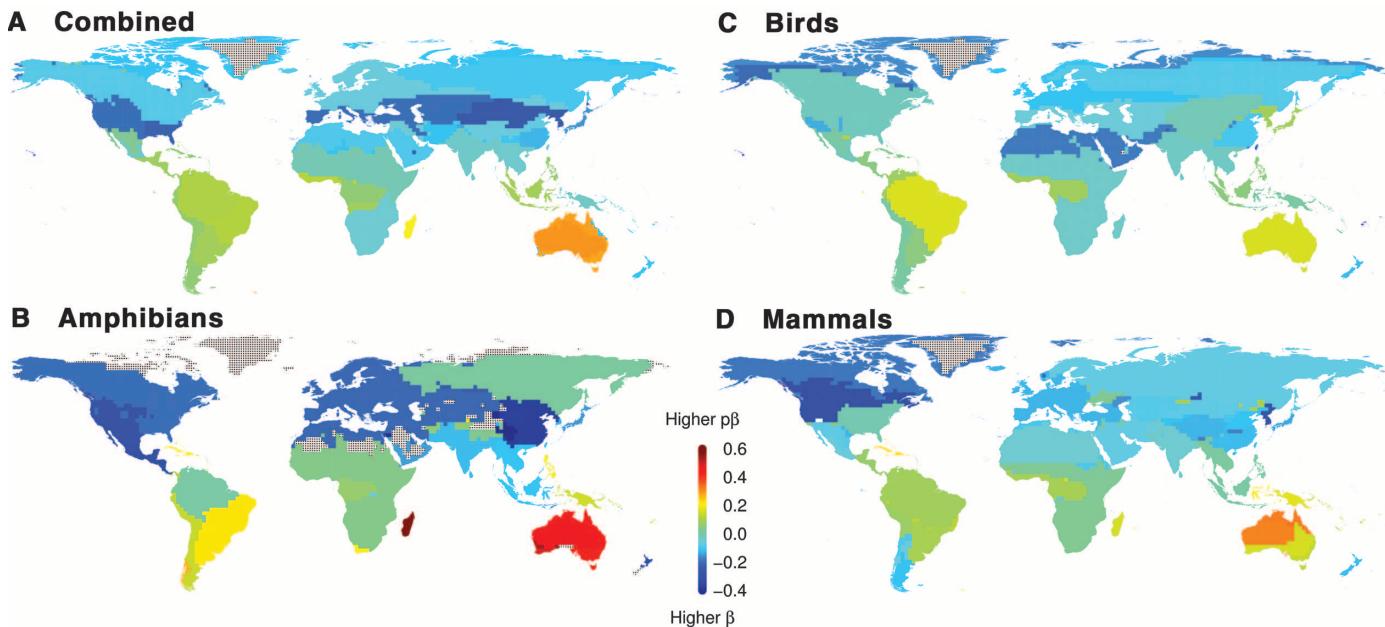


Fig. 4. Combined (**A**) and taxon-specific (**B** to **D**) maps illustrating the degree of phylogenetic turnover relative to the turnover of species observed among zoogeographic regions based on data for species of (**A**) amphibians, (**B**) birds, and (**C**) nonmarine mammals. The color scale depicts the degree to which faunal turnover between the regional assignment of the focal grid cell

and the regional assignment of all other grid cells results from differences in β relative to beta diversity. Red colors indicate regions with a high degree of phylogenetic differentiation relative to compositional differentiation, whereas blue colors indicate the opposite. Dotted regions have no species' records, and Antarctica is not included in the analyses.

Northern Hemisphere, whereas the opposite is true in the Southern Hemisphere (Fig. 4A). In particular, amphibians exhibit low spatial turnover in phylogenetic composition relative to their turnover in the composition of species between the North American and Eurasian regions (Fig. 4B; also compare fig. S4A with fig. S6A). Higher phylogenetic uniqueness in the Southern than in the Northern Hemisphere is consistent with long-term isolation having left a pervasive signature on species assemblages, where oceanic barriers have limited dispersal between continents (23, 24). In the Northern Hemisphere, the newly defined boundaries of the Palearctic realm might reflect the continuous presence of nonglaciated tundra in eastern Siberia and Beringia (25), whereas the subtle differences in the phylogenetic composition of assemblages over the Northern Hemisphere as a whole might be a consequence of a high degree of connectivity and range dynamics. Low rates of extinctions resulting from greater climatic stability in the Southern Hemisphere could also have contributed to this pattern by allowing species that belong to ancient clades to persist through time (26, 27).

Our maps of zoogeographic realms and regions provide a broad overview of the distribution of the world's amphibians, birds, and nonmarine mammals, allowing the identification of geographic areas harboring distinct evolutionary histories [see (28) for links to downloadable maps of zoogeographic realms and regions for projection in GIS (geographic information systems) mapping software and Google Earth]. These maps reflect major advances made in recent dec-

ades regarding our knowledge of the distribution and phylogeny of vertebrates and can be used to elucidate the forces and historical events responsible for the formation of the biogeographic realms and regions we recognize today. Our delineation of the zoogeographic realms and regions of the world, and especially that of the realms, appears robust to the type and quality of distributional and phylogenetic data used [see (13) for details]. Inclusion of additional phylogenetic information on branch length or improved resolution of the phylogenetic trees has the potential to facilitate a finer delineation of regions within our realms. The inclusion of data (when they become available) on reptiles, invertebrates, and/or plants may also affect the boundaries of our realms and regions and the relationships among them. Nevertheless, the maps presented here delineate robust zoogeographic units for vertebrates that can be scaled within specific continents and/or taxonomic clades. Due to these qualities, our analytical approach and zoogeographic maps provide a baseline for a wide variety of comparative ecological, biogeographic, evolutionary, and conservation-based studies (3, 22, 29).

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Figs. S1 to S11
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Supplementary Materials

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Materials and Methods

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Crocodile Head Scales Are Not Developmental Units But Emerge from Physical Cracking

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Various lineages of amniotes display keratinized skin appendages (feathers, hairs, and scales) that differentiate in the embryo from genetically controlled developmental units whose spatial organization is patterned by reaction-diffusion mechanisms (RDMs). We show that, contrary to skin appendages in other amniotes (as well as body scales in crocodiles), face and jaws scales of crocodiles are random polygonal domains of highly keratinized skin, rather than genetically controlled elements, and emerge from a physical self-organizing stochastic process distinct from RDMs: cracking of the developing skin in a stress field. We suggest that the rapid growth of the crocodile embryonic facial and jaw skeleton, combined with the development of a very keratinized skin, generates the mechanical stress that causes cracking.

Ammiates exhibit a keratinized epidermis preventing water loss and skin appendages that play major roles in thermoregulation, photoprotection, camouflage, behavioral display, and defense against predators. Whereas mammals and birds evolved hairs and feathers, respectively, reptiles developed various types of scales. Although their developmental processes

share some signaling pathways, it is unclear whether mammalian hairs, avian feathers and feet scales, and reptilian scales are homologous or if some of them evolved convergently (1). In birds and mammals, a reaction-diffusion mechanism (RDM) (2) generates a spatial pattern of placodes that develop and differentiate into follicular organs with a dermal papilla and cycling

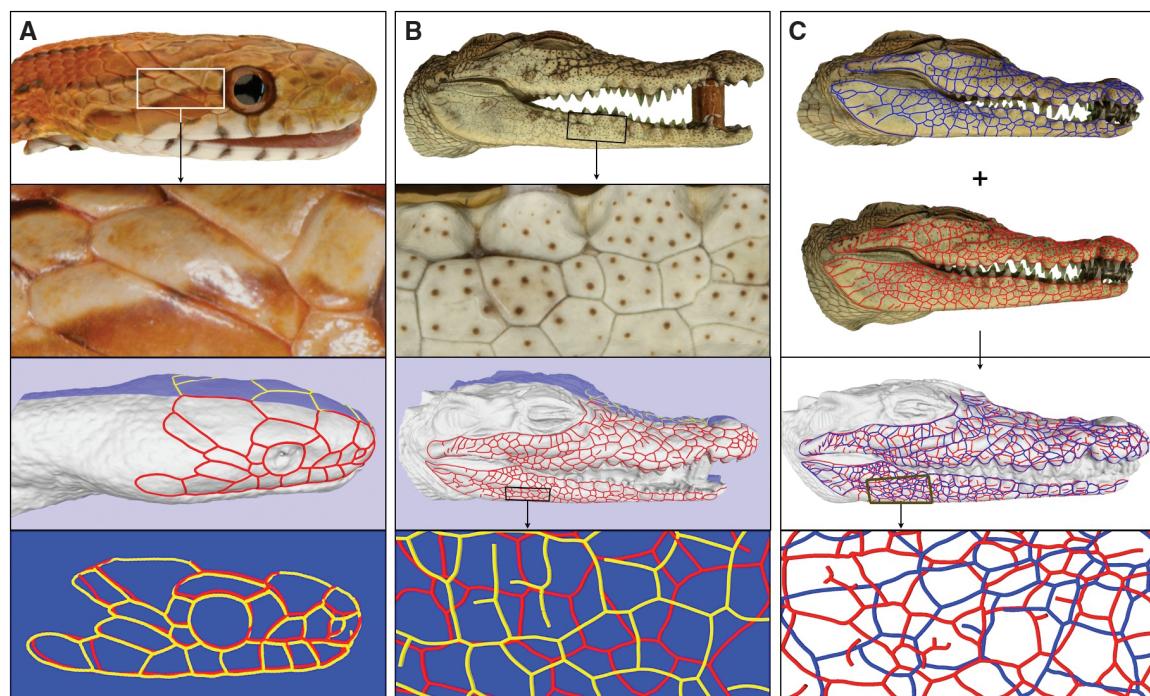
growth of an elongated keratinized epidermal structure (hairs or feathers) (3). However, scales in reptiles do not form true follicles and might not develop from placodes (4). Instead, reptilian scales originate in the embryo from regular dermo-epidermal elevations (1). Whereas the regular spatial organization of scales on the largest portion of the reptilian body is determined by a RDM, additional positional cues are likely involved in the development of the scale plates present on the head of many snakes and lizards. These head scales form a predictable symmetrical pattern (Fig. 1A) and provide mechanical protection.

The face and jaws of crocodilians are covered by polygonal scales (hereafter called "head scales") that are strictly adjoining and nonoverlapping, but these polygons are irregular and their spatial distribution seems largely random (Fig. 1, B and C). Using high-resolution three-dimensional (3D) geometry and texture reconstructions (5–7),

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Fig. 1. Spatial distribution of head scales. (A) Head scales in most snakes (here, a corn snake) are polygons (two upper panels) with stereotyped spatial distribution (two lower panels): left (yellow) and right (red) scale edges overlap when reflected across the sagittal plane (blue). (B) Polygonal head scales in crocodiles have a largely random spatial distribution without symmetrical correspondence between left and right. (C) Head scales from different individuals have different distributions of scales' sizes and localizations (blue and red edges from top and bottom crocodiles, respectively).



Supplementary Materials for

An Update of Wallace's Zoogeographic Regions of the World

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Materials and Methods

Distributional data

The global distributions of all amphibians and terrestrial mammals were based on IUCN Global Assessment distributional data for native ranges, with undescribed or taxonomically ambiguous species excluded (30, 31). Distributional data for species of birds were extracted from a comprehensive global geographic range database for all land and non-pelagic species (32). In this database, the geographic range of each species was mapped at a resolution of $1^\circ \times 1^\circ$ latitude-longitude grid cells following the approach outlined in (33, 34) and in (34-36). Maps represent a conservative extent-of-occurrence of the breeding ranges based on museum specimens, published sight records, and spatial distribution of habitats between documented records, which have subsequently been validated by ornithological experts. Data from more than 1600 references have been used to map distributions of species of birds included in the current article (list of references available in Supplementary Material Appendix S1). The distributions of species were matched to the global taxonomies provided by (37), (38) and (39) following procedures in (40) for mammals and in (21) for amphibians. All distributions were mapped in $2^\circ \times 2^\circ$ latitude-longitude grid cells. Specific occurrences in grid cells were used to produce a presence/absence matrix with names of species as columns and grid cells as rows. Species that did not occur in both the distribution data and the phylogenies were removed. Consequently, 323 species were removed from the amphibian phylogeny, 309 from the mammalian distributional data and 167 from the mammalian phylogeny. All further analyses were based on distributional and phylogenetic data for 6,110 species of amphibians, 10,074 species of birds and 4,853 species of mammals. Note that no records for non-marine vertebrate species occurred in Antarctica, which is consistent with previous similar studies (8). This region is therefore not included in our analyses.

Phylogenetic data

The amphibian phylogeny consisted of a generic-level supertree, with all species added as generic-level polytomies (21), updated according to the latest, species-level amphibian phylogeny (41), which contains only 2,871 species. Species that were not included in (41) were kept in the same lineages as in (21). Topological differences in (41) with bootstrap support less than 50% were not implemented and topology from (21) was retained. The avian phylogeny was similarly constructed as a supertree, but was resolved to the specific level; incorporating hundreds of molecular phylogenies published before summer 2011 (see Supplementary Material Appendix S2 for a full description). Disagreement between source phylogenies was reflected as polytomies, and the final tree was 61% resolved (Fig. S7) The mammal phylogeny consisted of the supertree used in (42), which is an updated version of the tree in (43) and based on taxonomy from (39). Since only the mammal phylogeny included branch length estimates, branch lengths were set to one in all phylogenies for all analyses, in order to maintain consistency across taxa.

Calculating phylogenetic beta diversity

We conducted cluster analyses of assemblages of species for the purpose of delineating zoogeographic regions on pair-wise matrices of phylogenetic beta diversity (hereafter “ $p\beta$ ”). Values for $p\beta$ were calculated using a modified version of the β_{sim} metric originally developed by (44) and later formalized by (45). The β_{sim} metric is preferable to other beta diversity metrics because it is insensitive to differences in species richness among assemblages (45), thus providing unbiased estimation of compositional turnover among grid cells (11):

$$\beta_{sim} = 1 - \frac{a}{\min(b, c) + a}$$

where $a =$ the number of species shared between two grid cells and b and c represent the number of species unique to each grid cell. $p\beta$ measures were produced using the same equation as for β_{sim} with the exception that shared and unique branches of the overall phylogeny were used rather than species. $p\beta_{sim}$ values were calculated for all pair-wise combinations of grid cells to produce the distance matrices for cluster analysis. In order to compare our biogeographic delineation scheme incorporating phylogenetic information with a more traditional scheme based solely on distribution data, we also computed a non-phylogenetically based measure of beta-diversity, i.e. we calculated the β_{sim} metric using only the distributional data. All analyses below were performed on both $p\beta_{sim}$ and β_{sim} matrices, but for simplicity, we used only the term $p\beta_{sim}$ throughout the description of analyses.

Preliminary analyses: choosing a clustering algorithm

Analyses were performed using R statistical software (46) with the packages “ape” (47), “cluster” (48), “phylobase” (49) and “picante” (50). Analyses of $p\beta_{sim}$ matrices were performed with two objectives: (i) defining the zoogeographic regions and (ii) describing relationships among the regions. In order to develop an analytical approach that best fulfills these two objectives, we sought to identify a clustering algorithm that performed well at both tasks. In accordance with the analytical framework of (11) for delineating biogeographic regions, we tested the performance of nine hierarchical clustering algorithms, using $p\beta_{sim}$ matrices for all data sets, as well the non-hierarchical Partitioning Around Mediods (PAM) approach. After testing algorithm performance (see details below) the Unweighted Pair Group Means Algorithm (UPGMA) was selected for the final analysis (51).

Objective one: defining zoogeographic regions

Evaluation criterion: sum of between-cluster $p\beta_{sim}$ / sum of total $p\beta_{sim}$

Our zoogeographic regions were defined by grouping assemblages of species (i.e. grid cells) into regions (clusters). We adopted an approach that focuses on maximizing the explanatory power of the resulting cluster dendrogram. Clustering algorithms were evaluated by estimating which proportion of the sum of global $p\beta_{sim}$ values was represented by between-cluster $p\beta_{sim}$ values, for a given number of clusters. In addition to maximizing between-cluster $p\beta_{sim}$ values, we sought to group species assemblages into as few regions as possible (ideally less than 50 in order to facilitate a workable overview of global patterns). For each of the nine clustering algorithms, we sequentially assessed the proportion (%) of global $p\beta_{sim}$ explained by between-cluster $p\beta_{sim}$, and for all numbers of clusters ranging from two to 100 clusters (results are shown in Fig. S8; Note that only results for two to 40 clusters are shown). The threshold of 99% of global $p\beta_{sim}$ values represented by between-cluster $p\beta_{sim}$ was chosen as the highest possible natural cutoff point without returning an excessive number of clusters (over 50), following comparison of results at the 90%, 95%, 99% and 99.9% levels (Fig. S8). The best performing algorithms for defining these clusters were those which reached the 99% cutoff point with the lowest number of clusters.

Objective two: describing relationships among zoogeographic regions

Evaluation criterion: co-phenetic correlation coefficient

The second objective was to describe the relationships among zoogeographic regions as accurately as possible, via a hierarchical dendrogram. In this case, algorithm performance was assessed using the co-phenetic correlation coefficient (52) as in (11), which reflects how well the original data are represented by the dendrogram. The calculation of a co-phenetic coefficient requires a $p\beta_{sim}$ matrix and co-phenetic matrix derived from a hierarchical dendrogram. In this case, the $p\beta_{sim}$ matrix consisted of the region-by-region matrix, obtained by calculating the mean of all pair-wise grid cell values observed between these clusters. Hierarchical dendograms were then based on the region-by-region matrices using each of the nine clustering algorithms assessed for our first objective.

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From these dendograms, the co-phenetic matrix was obtained by calculating the branch length distances separating each pair of branch tips on the dendogram. The co-phenetic correlation score was then produced for each clustering algorithms as the Pearson product-moment correlation coefficient between the region-by-region $p\beta_{sim}$ matrix (same for all analyses) and co-phenetic distance matrices (unique to each clustering algorithm). The results of these analyses showed that, generally, clustering algorithms that performed well for our first objective (Fig. S8) performed poorly for our second objective (Fig. S9).

In particular, results from these performance tests showed that Ward's algorithm, which outperformed all other algorithms for our first objective (Fig. S8), performed very poorly for our second objective (Fig. S9). In addition to the overall co-phenetic correlation coefficients used here to evaluate cluster algorithm performance, co-phenetic correlation coefficients were also produced for each specific cluster in order to evaluate the validity of the placement of each cluster within the dendrogram (i.e., contrasting $p\beta_{sim}$ between assemblage A and all other assemblages versus the distance on the UPGMA dendrogram). High co-phenetic values indicate strong support for the placement of the cluster whereas low values indicate weak support (see fig. S1, S2, S4 and S6).

Clustering analyses and visual representation of zoogeographic units

In order to choose a single clustering algorithm that performed well for both of our study objectives, we considered the performance of each algorithm across both evaluation criteria. Following examination of the evaluation results (Fig. S8 and S9), the UPGMA method was chosen as the best performing clustering algorithm overall. Global UPGMA dendograms were thus produced to describe relationships among species assemblages. The results of the clustering performance evaluation for objective one were used to cut UPGMA dendograms in order to return the minimum number of clusters required to obtain between-cluster $p\beta_{sim}$ values totaling more than 95% of the sum total of all $p\beta_{sim}$ values. These clusters of grid cells therefore represent the zoogeographic regions for each data set. A few regions produced by the UPGMA algorithm were extremely small (<10 grid cells, i.e. nine for the amphibian data, two for the bird data, one for the mammal data and two for the combined data). These small regions containing only a small number of small assemblages were inconsistent with our goal of identifying broad-scale zoogeographic units and were therefore removed in a manner consistent with (53) treatment of singletons. These grid cells were then merged with the most closely related remaining cluster.

Ordination

To provide a complimentary non-hierarchical description of cluster relationships (Fig. S1, S2, S4 & S6), regions were also plotted in a two-dimensional ordination using a neighbor-joining algorithm (Nonmetric Multidimensional Scaling; hereafter NMDS), following Kruskal's method (54). The NMDS method is acknowledged among community ecologists as being a robust non-parametric method for the depiction of overall turnover values within a matrix in a low-dimensional space (55). NMDS plots were produced for all data sets using the region-by-region $p\beta_{sim}$ matrices for the UPGMA defined regions (produced as described in *Objective two: describing relationships among zoogeographic regions*). The axes of the resulting plots are in arbitrary units, where similar zoogeographic regions occur closer to one another in two-dimensional space and less similar regions occur farther apart.

Illustration of clusters

We illustrated faunal differences among zoogeographic realms and regions using a three-dimensional color scheme wherein color differences relate to faunal differences in multivariate ordination space (11). In order to select colors for plotting the clustering results (i.e. zoogeographic units), three-dimensional NMDS ordination was performed on the cluster $p\beta_{sim}$ matrices. The ordinations were then plotted with each of the NMDS axes representing one of the three primary colors in standard RGB color space, ranging from 0 to 100% for each color. The final color for

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each cluster was determined using primary color levels taken from the NMDS axes, and therefore the similarity of cluster colors reflects the level of $p\beta_{sim}$ among clusters. These colors were used to plot clustering results on global maps, cluster relationship dendograms, and on two-dimensional NMDS ordinations.

Cross-taxon analysis

In order to produce a combined map of our zoogeographic regions for vertebrates (Fig. 1 and Fig. S1), data for the three taxonomic groups (amphibians, birds and mammals) were combined by taking the mean $p\beta_{sim}$ values across the groups and all grid cell comparisons, to produce a mean $p\beta_{sim}$ matrix. A few pair-wise grid cell comparisons did not exist within the combined $p\beta_{sim}$ matrix (< 0.003% of the total number of pair-wise comparisons) — e.g., in cases where two of the three taxa occurred in one grid cell and the remaining taxon occurred only in the other grid cell. These cases were given a value of 1, representing complete turnover. The combined matrix was subsequently analyzed in precisely the same manner described above for the taxon-specific analyses.

Defining zoogeographic realms

For the cross-taxon analysis only, zoogeographical realms were produced in order to visualize larger scale patterns of biological organization in the distributions of clades and species. We defined zoogeographic realms by cutting the cross-taxon UPGMA dendrogram in order to return the minimum number of clusters required to obtain between-cluster $p\beta_{sim}$ values totaling at least 90% of the global sum of $p\beta_{sim}$ values.

Cross-taxon comparison of $p\beta_{sim}$ matrices

We used Mantel's correlation test (17) to assess the strength of the relationship in the geographic distribution of $p\beta_{sim}$ values between each pair of taxa. In addition, we corrected for spatial autocorrelation by including Euclidean distances as a covariate in a Partial Mantel's test. We then examined partial r values to estimate the correlation between $p\beta_{sim}$ matrices after accounting for geographic distances among species assemblages. Table S3 contrasts results from the correlation and partial correlation analyses. These results show that correlation coefficients are weaker, but still significant, after accounting for spatial autocorrelation. More importantly, when compared among taxa, correlation coefficients are proportional to partial correlation coefficients, such that the conclusions we outlined in the text remain valid.

Comparison of phylo-distributional and distributional regionalization schemes

We compared zoogeographic regions obtained using our phylogenetically-based scheme with those obtained using solely distributional data by comparing the $p\beta_{sim}$ and β_{sim} clustering results for the taxon-specific, as well as the combined matrices (Fig. 4).

To compare $p\beta_{sim}$ and β_{sim} schemes, the “distinctiveness” of a grid cell for each scheme was calculated as the mean pairwise $p\beta_{sim}/\beta_{sim}$ distance between that grid cell and all other grid cells according to the region-by-region matrices (see *Inferring relationships among regions*). Therefore comparisons of grid cells belonging to the same region returned a distance of 0, whereas comparisons of grid cells in different regions returned the mean distance between those two regions. We obtained standardized values of distinctiveness by dividing the observed value with the mean values of all grid cells for that clustering scheme.

Difference values representing the difference between $p\beta_{sim}$ and β_{sim} clustering results were then calculated by subtracting β_{sim} -based distinctiveness values from the $p\beta_{sim}$ -based distinctiveness values. The resulting difference values are standardized to have a mean of zero with high values indicating that a grid cell is more distinctive in the phylo-distributional scheme ($p\beta_{sim}$ -based), and

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low values indicating that a grid cell is more distinctive in the distribution-based scheme (β_{sim} -based).

Robustness of results to the choice of analytical approach

We assessed the robustness of our results to the choice of analytical approach by repeating our cross-taxon analysis using two alternative clustering processes and redefining the global realms produced in the main analysis. In order to aid comparison of the different results the number of realms for all analyses was fixed to 11, the same number as in our original analysis. The two additional clustering algorithms chosen for comparison were the Ward's minimum variance criterion (subsequently referred to as "Ward's") and Partitioning Around Medoids (PAM). Table S4 details the key characteristics of these two clustering algorithms plus the UPGMA method used in the main analysis.

Ward's minimum variance criterion

Ward's algorithm clearly outperformed other methods regarding our first evaluation criterion (*sum of between cluster $p\beta_{\text{sim}}$ / sum of total $p\beta_{\text{sim}}$* , Fig. S8). For example, Ward's created 34 regions for the cross-taxon data, the next best algorithm required 83 regions to reach the same cutoff point of 99% of $p\beta_{\text{sim}}$ occurring between regions. However, for our second evaluation criterion (*co-phenetic correlation coefficient*, Fig. S9), Ward's algorithm performed very poorly, and, for this reason, this algorithm was not considered for further analysis. In addition, the tendency of the Ward's method to create roughly equal size clusters can be seen as a significant disadvantage at the scale of realms, forcing smaller but highly distinct areas (such as Madagascar) to be clustered with relatively unrelated regions. Figure S10A shows global cross-taxon realms produced using the Ward's analytical method.

Partitioning Around Medoids

In an attempt to address the problems discussed above for the Ward's method, whilst retaining the benefits of its performance according to our first evaluation criterion, we first defined our regions according to Ward's method and subsequently clustered these regions into realms using the PAM method. Since the PAM method is non-hierarchical, it is not constrained to the assumption that regions are related in a hierarchical manner. Furthermore, the PAM method clusters regions based on their distance values (i.e. $p\beta_{\text{sim}}$), rather than within cluster variance in the case of Ward's method. It is therefore more capable of detecting small, highly distinct clusters. Figure S10B shows global combined taxon realms produced by clustering regions using the PAM method.

Sensitivity analyses

In order to assess the sensitivity of our results to the type of distributional and phylogenetic (or taxonomic) data used for our clustering analyses, we conducted a comparative study using the mammal data as a case study. Mammals were chosen as a test case because more of the relevant data (i.e. phylogenetic tree including branch length, taxonomy, distributional data in equal area grid cells) were available for this taxonomic group than for the other two. Three alternative input data types were tested:

- i) $p\beta_{\text{sim}}$ values calculated using phylogenetic branch length information
- ii) $\text{taxo}\beta_{\text{sim}}$ values calculated using taxonomic information
- iii) $p\beta_{\text{sim}}$ values based on assemblages within equal area global grid cells

These input data were produced as follows:

Using phylogenetic branch length information

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The phylogeny used in our mammalian analysis (43) is fully dated with branch lengths measured in millions of years. These branch lengths were equalized in our main analysis to ensure consistency with the amphibian and bird phylogenies. For this test analysis, branch length data were included by weighting the value of each branch in accordance with its length on the phylogenetic tree. Therefore a unique branch with a length of ten million years would have a value of ten in any $p\beta_{sim}$ calculation (see *Calculating phylogenetic beta diversity*). All pairwise $p\beta_{sim}$ values between mammalian species assemblages were recalculated following this approach. Clustering analyses was then performed on the resulting pairwise $p\beta_{sim}$ matrix following our UPGMA-based protocol described above, with the exception that the number of clusters was fixed at 34 in order to facilitate visual comparison with the original 34 regions defined for the mammal data.

Visual examination and comparison of the maps produced with and without branch lengths show only minor differences in the definition of regions as well as relationships among them (Fig. S11A and S11B). These differences include the separation of Australia into two regions rather than one, and the inclusion of the Philippines in the Oceanian region. It therefore appears that our results are considerably more sensitive to tree topology than to branch length. Nevertheless, the inclusion of phylogenetic information derived from trees with high resolution certainly has the potential to help refine our maps in particular regions.

Using taxonomic information

Phylogenetic data can be expected to be a more accurate reflection of inter-species evolutionary relationship than taxonomies (56). However, the extent to which taxonomy can be used as a surrogate data source (if phylogenetic data are absent or incomplete) is of interest for future studies. For this test analysis, $taxo\beta_{sim}$ values were calculated, whereby all major taxonomic levels within an assemblage (species, genera, subfamilies, families, superfamilies, classes, infraorders, suborders and orders) were used instead of solely species (β_{sim}), or branch lengths ($p\beta_{sim}$). Each taxonomic level was given equal weighting and therefore assemblages were assigned a score of one for every unique and shared taxonomic group they contained. The total of these values was then used within the β_{sim} formula (see *Calculating phylogenetic beta diversity*), with a equal to total shared taxonomic groups and b & c equal to the unique taxonomic groups for each assemblage. All pairwise $taxo\beta_{sim}$ were recalculated following this approach. Clustering analyses was then performed on the resulting pairwise, $taxo\beta_{sim}$ matrix following our UPGMA-based protocol described above, with the exception that the number of clusters was fixed at 34 in order to facilitate visual comparison with the original 34 regions defined for the mammal data.

Visual examination and comparison of the maps produced with a phylogenetic tree and versus a taxonomy show, once again, only minor differences in the definition of regions as well as relationships among them. Noticeable differences mostly relate to relative distances among regions rather than differences in the delineation of zoogeographic regions (Fig. S11A and S11C). In particular, assemblages in the Australian region appear less distinct from those in New Guinea when using $taxo\beta_{sim}$ than with $p\beta_{sim}$. In contrast, assemblages in the Antillean region appear more distinct from those in Central and South America when using $taxo\beta_{sim}$ than with $p\beta_{sim}$. These results are again not fundamentally different from our existing analysis, suggesting that taxonomy may indeed serve as a surrogate to phylogenetic tree in some instances. However, this interpretation must be made with care since taxonomies are constantly updated in the light of new phylogenetic studies and therefore the results for relatively well studied taxa such as mammals may not apply more generally.

Mapping species ranges and range boundaries: defining species assemblages based on equal area grid cells or latitudinal-longitudinal cells

Empirical knowledge of species occurrence exists in the form of locality records. They form the evidence basis for maps of species global distributions, which comes in three general categories:

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1. Generalized maps of species global ranges that are compiled from reference works using small range map pictures published in commercial field guides and handbooks as primary sources. Such data are at least twice or trice removed from the raw data, and “*methods, assumptions, and caveats expressed by the original authors, as well as an accounting of measurement and transcription error, are rarely presented in the secondary data source*- 2. Generalized maps of geographic ranges that are often compiled as above, but using some higher quality regional field guides and books and characterized by the fact that regional experts have quality-proofed these maps in greater details. Such range maps are major improvements relative to the maps in category 1, but still pose problems when defining range boundaries, and contain commission errors. The global range maps of the world’s mammals and amphibians used in our analyses are from this category and the best map of the kind currently available for these groups.
- 3. Maps of extent of occurrence of species that are generated from primary sources (using verified locality information from specimens collected in museums worldwide, published sight records and information from primarily-level scientific monographs) combined with spatial distribution of habitats between documented records. The derived maps are subsequently validated by taxonomic experts for each larger clade (33-36). Compared to the generalized range-maps in category 1 and 2, these extent-of-occurrence maps are less prone to transcription error. In addition, they often provide a higher accuracy in defining species distribution boundaries and reduce the risk of commission errors. The global maps on the world’s species of birds used in our analyses are of this category and based on >1600 references (see Supplementary Material Appendix S1 for a complete list), hundreds of museum’s collections and verified by world ornithological experts and for each individual taxonomic family.

Species assemblages can be described using latitudinal-longitudinal grid cells, where cell area progressively increases somewhat from the equator to the poles. It has been shown that the effect of geographic variation in grid cell area on patterns of species richness is negligible (58, 59). The smaller grid cell area at high latitude, however, results in a slight increase in the number of grid cells with increasing latitude when using latitudinal-longitudinal grid cells. Equal-area gridded maps circumvent any potential issues that geographic differences in the number of grid cells may cause. The projection used to generate such maps, however, differs significantly from the non-equal area maps typically containing or describing the original distribution data. The transfer of such data to equal-area grids is highly problematic, particularly if the data originate from small range maps published in commercial field guides and other secondary literature sources. They are especially prevalent in topographically complex regions and geographic areas with dense aggregations of geographic range boundaries (33). Although range maps of category 1 and 2 are often drawn as polygons, and hence at least technically possible to sample into an equal-area grid, this transfer will likely introduce substantial error associated with commission errors and precision errors of range boundaries. Thus, although it has become more commonplace to use equal-area distributional data for analyses, it is not clear in such studies how the transfer of data from unequal area projections

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was accomplished, how issues of commission and precision errors were tackled or how original locality data related to the subsequent description of species occurrences on equal-area maps.

Despite these issues, we explored the consequences of converting the distributional data from unequal to equal area for mammals. We assessed the effect of using unequal area projection distributional data by projecting the mammalian distributional data to equal area grid cells. The resulting matrix contained 4,416 global Behrmann equal area projection grid cells (60). All pairwise $p\beta_{sim}$ values between mammalian Behrmann equal area projection grid cells were recalculated following this approach. Clustering analyses was then performed on the resulting pairwise $p\beta_{sim}$ matrix following our UPGMA-based protocol described above, with the exception that the number of clusters was fixed at 34 in order to facilitate visual comparison with the original 34 regions defined for the mammal data. We found no noticeable differences between results generated with the equal area data for mammals and the original results (Fig. S11A and S11D).

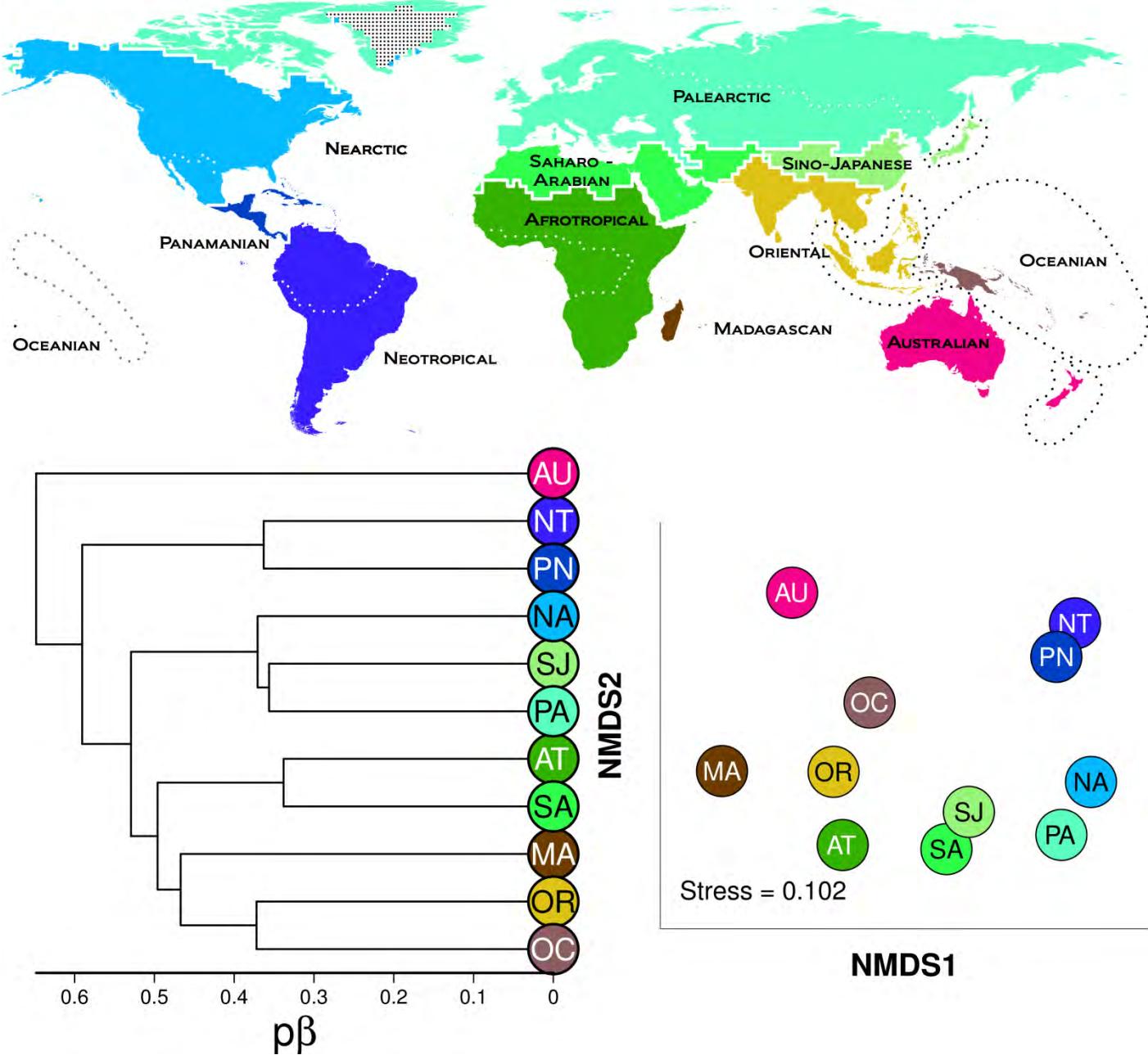


Fig. S1. Map, dendrogram and NMDS of cross-taxon zoogeographic realms based on phylo-distributional data for amphibian, bird and non-marine mammal species of the world. The map represents results of UPGMA clustering of global phylo beta diversity ($p\beta_{sim}$) values for species assemblages in $2^\circ \times 2^\circ$ grid cells. Grid cells are clustered into 11 realms, the minimum number required to result in the sum of between region $p\beta_{sim}$ values accounting for over 90% of the sum total $p\beta_{sim}$. The dendrogram depicts relationships among realms and the $p\beta_{sim}$ axis shows the degree of phylogenetic turnover between branches descending from a node. Note that the dendrogram depicts phylogenetic similarity among regions, which may not reflect shared evolutionary history or common ancestry. Realms colors produced by plotting results within three-dimensional standard RGB color space via a three dimensional NMDS ordination. Therefore the similarity of realms colors reflects the $p\beta_{sim}$ of the clusters themselves. The human eye does not perceive RGB color differences with a high degree of accuracy and therefore inter-cluster relationships are also displayed using UPGMA dendrogram and a two-dimensional NMDS ordination. Stress values reflect the amount of error in the correlation between pairwise distances in the original $p\beta_{sim}$ data matrix and a data matrix calculated from the NMDS plot with 0 representing no error and 1 indicating a complete lack of correlation.

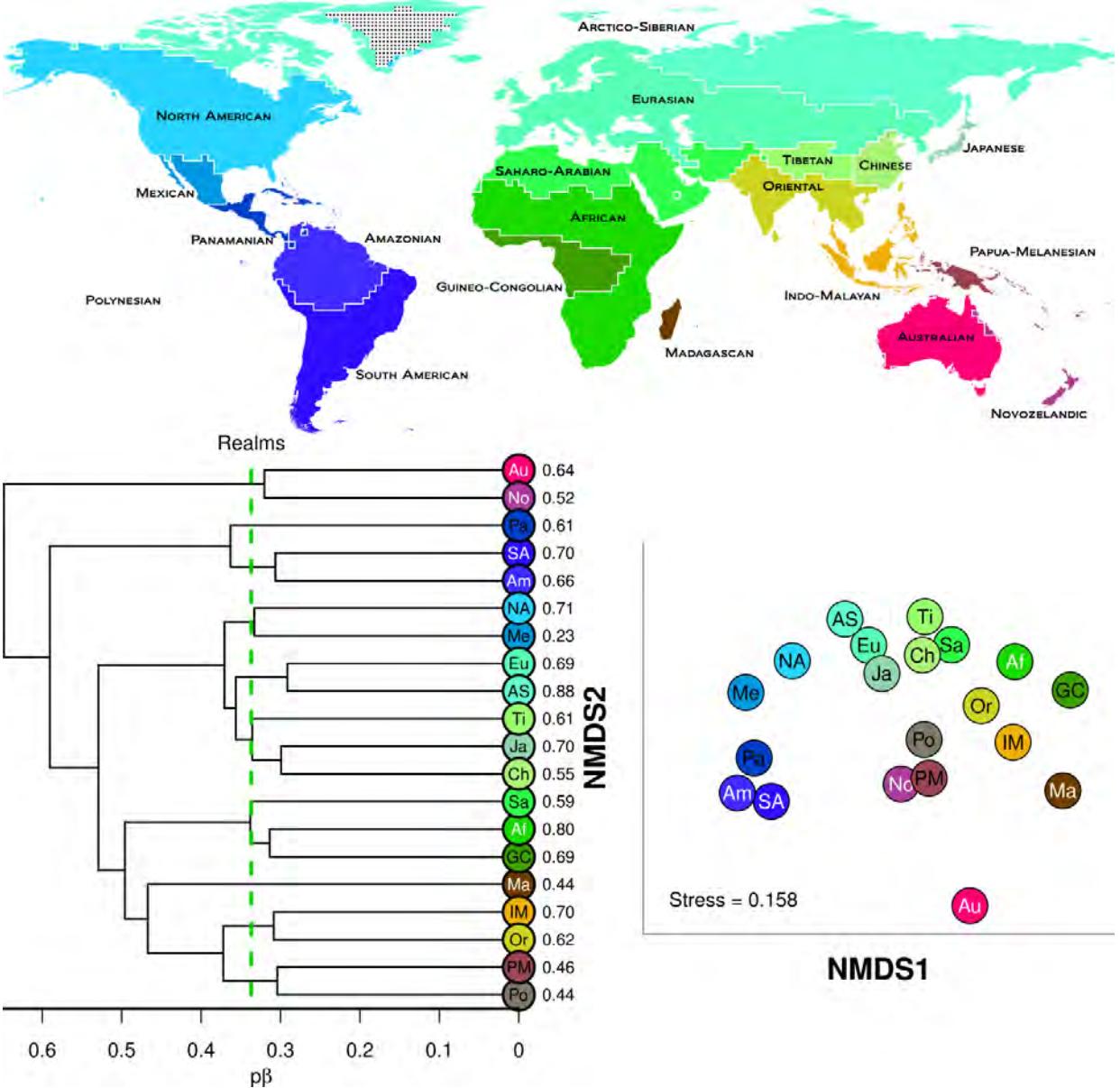


Fig. S2. Global map, dendrogram and NMDS of cross-taxon zoogeographic regions based on phylo-distributional data for (A) amphibian (6,110 spp.), (B) bird (10,074 spp.) and (C) non-marine mammal (4,853 spp.). The map represents results of UPGMA clustering of global phylogenetic beta diversity ($p\beta_{sim}$) values for species assemblages in $2^\circ \times 2^\circ$ grid cells. Grid cells are clustered into 20 regions, the minimum number required to result in the sum of between region $p\beta_{sim}$ values accounting for over 95% of the sum total $p\beta_{sim}$. The dendrogram depicts relationships among regions and the $p\beta_{sim}$ axis shows the degree of phylogenetic turnover between branches descending from a node. Region colors produced by plotting results within three-dimensional standard RGB color space via a three dimensional NMDS ordination. Therefore the similarity of region colors reflects the $p\beta_{sim}$ of the clusters themselves. The human eye does not perceive RGB color differences with a high degree of accuracy and therefore inter-cluster relationships are also displayed using UPGMA dendrogram and a two-dimensional NMDS ordination. Co-phenetic correlation coefficients reflect of how well the data are represented by the UPGMA dendrogram, and are calculated as the strength of the correlation between pairwise distances in the original $p\beta_{sim}$ data matrix and a data matrix calculated from the dendrogram. The overall co-phenetic score (0.58) indicates how well the dendrogram represent relationships between regions generally and values next to the tips of the dendrogram represent region-specific co-phenetic scores. Similarly, stress values reflect the strength of the correlation between pairwise distances in the original $p\beta_{sim}$ data matrix and a data matrix calculated from the NMDS plot. Co-phenetic scores range between 0 and 1, where 0 indicates the lack of a correlation and 1 indicates a perfect correlation between matrices. Stress values reflect the amount of error in the correlation between pairwise distances in the original $p\beta_{sim}$ data matrix and a data matrix calculated from the NMDS plot, with 0 representing no error and 1 indicating a complete lack of correlation.



Fig. S3. Comparison our zoogeographic realms and regions with Wallace's original zoogeographic regions and subregions.

Our zoogeographic realms and regions are based on phylo-distributional data for species of amphibians, birds and terrestrial mammals whereas Wallace's regions and subregions are based on distributional data for families and genera of (mostly) mammals. White lines delineate our zoogeographic realms (full) and regions (dashed) as illustrated in Fig. 1, and red lines delineate Wallace's original regions (full) and subregions (dashed). Black lines delineate non-terrestrial biogeographic boundaries separating our proposed realms. Names in red correspond to Wallace's original regions.

(A) AMPHIBIANS

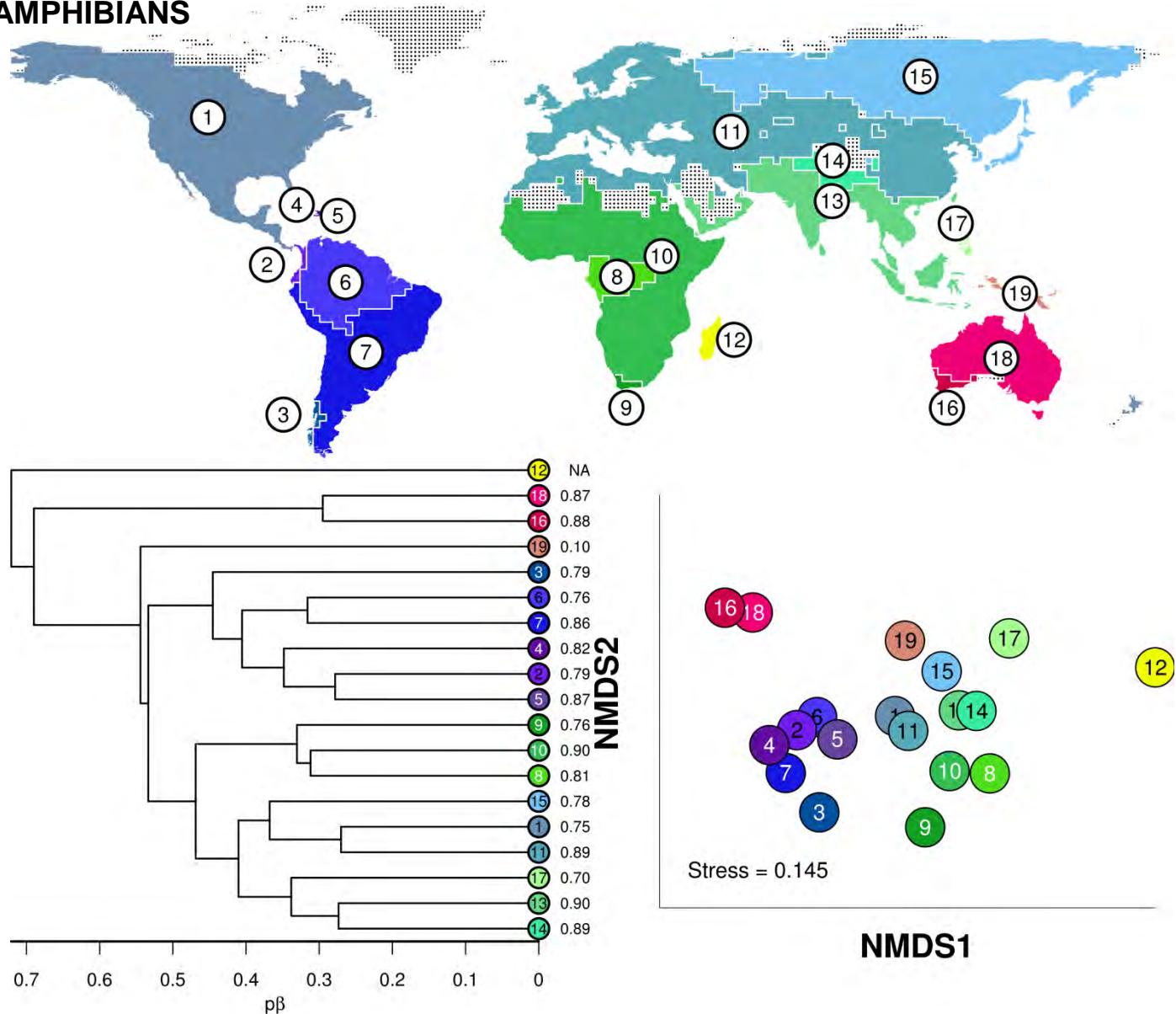


Fig. S4A. Global map, dendrogram and NMDS of taxon-specific zoogeographic regions based on phylo-distributional data for species of amphibians (6,100 spp). The map represents results of UPGMA clustering of global phylo beta diversity ($p\beta sim$) values for species assemblages in $2^\circ \times 2^\circ$ grid cells. Grid cells are clustered into 19 regions, the minimum number required to result in the sum of between region $p\beta sim$ values accounting for over 95% of the sum total $p\beta sim$. The dendrogram depicts relationships among regions and the $p\beta sim$ axis shows the degree of phylogenetic turnover between branches descending from a node. Region colors produced by plotting results within three-dimensional standard RGB color space via a three dimensional NMDS ordination. Therefore the similarity of region colors reflects the $p\beta sim$ of the clusters themselves. The human eye does not perceive RGB color differences with a high degree of accuracy and therefore inter-cluster relationships are also displayed using UPGMA dendrogram and a two-dimensional NMDS ordination. Co-phenetic scores range between 0 and 1, where 0 indicates the lack of a correlation and 1 indicates a perfect correlation between matrices. The overall co-phenetic score (0.80) indicates how well the dendrogram represent relationships between regions generally and values next to the tips of the dendrogram represent region-specific co-phenetic scores. Stress values reflect the amount of error in the correlation between pairwise distances in the original $p\beta sim$ data matrix and a data matrix calculated from the NMDS plot, with 0 representing no error and 1 indicating a complete lack of correlation.

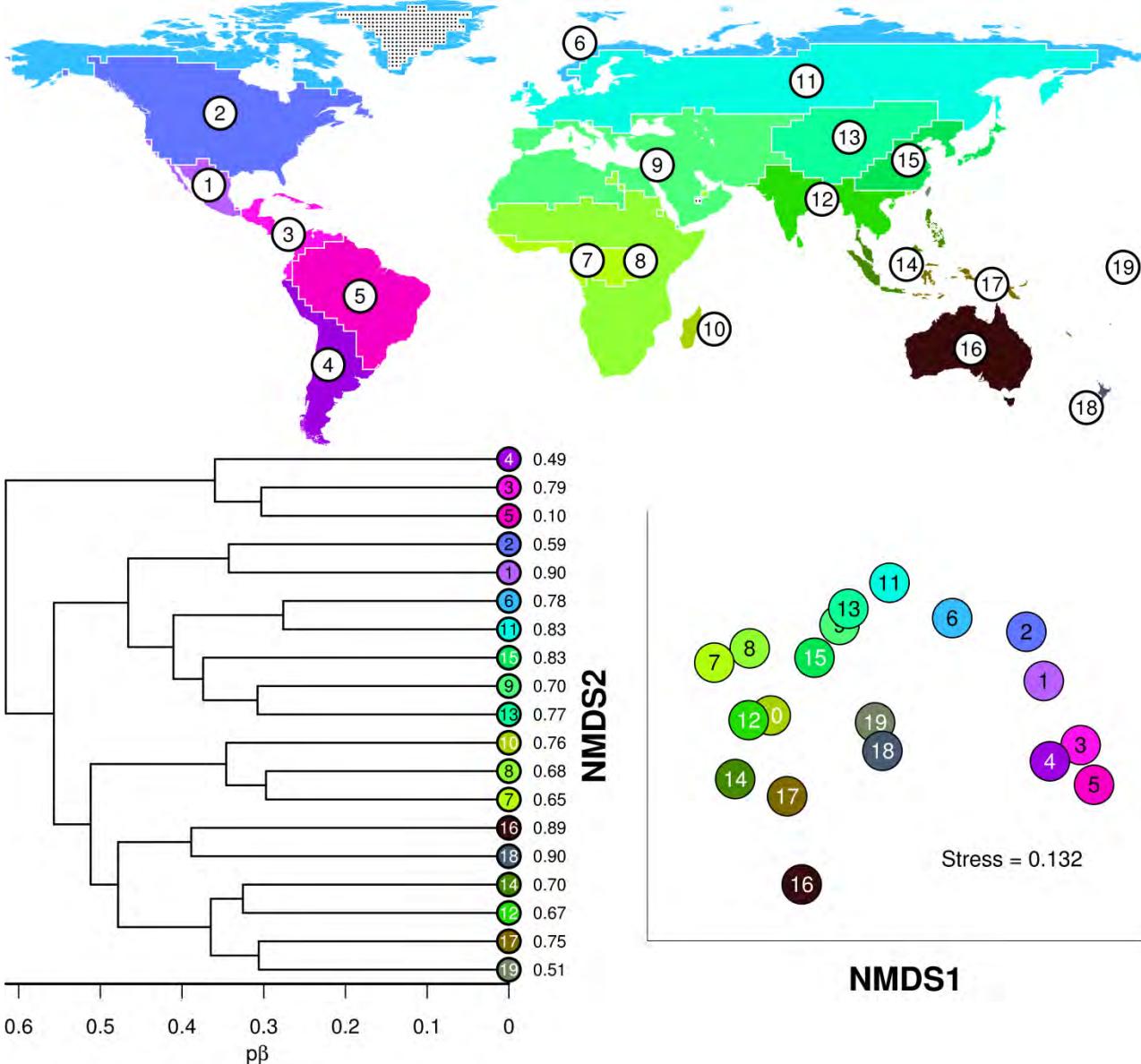


Fig. S4B. Global map, dendrogram and NMDS of taxon-specific zoogeographic regions based on phylo-distributional data for species of birds (10,074 spp.). The map represents results of UPGMA clustering of global phylo beta diversity ($p\beta$ sim) values for species assemblages in $2^\circ \times 2^\circ$ grid cells. Grid cells are clustered into 19 regions, the minimum number required to result in the sum of between region $p\beta$ sim values accounting for over 95% of the sum total $p\beta$ sim. The dendrogram depicts relationships among regions and the $p\beta$ sim axis shows the degree of phylogenetic turnover between branches descending from a node. Region colors produced by plotting results within three-dimensional standard RGB color space via a three dimensional NMDS ordination. Therefore the similarity of region colors reflects the $p\beta$ sim of the clusters themselves. The human eye does not perceive RGB color differences with a high degree of accuracy and therefore inter-cluster relationships are also displayed using UPGMA dendrogram and a two-dimensional NMDS ordination. Co-phenetic scores range between 0 and 1, where 0 indicates the lack of a correlation and 1 indicates a perfect correlation between matrices. The overall co-phenetic score (0.68) indicates how well the dendrogram represent relationships between regions generally and values next to the tips of the dendrogram represent region-specific co-phenetic scores. Stress values reflect the amount of error in the correlation between pairwise distances in the original $p\beta$ sim data matrix and a data matrix calculated from the NMDS plot, with 0 representing no error and 1 indicating a complete lack of correlation.

(C) MAMMALS

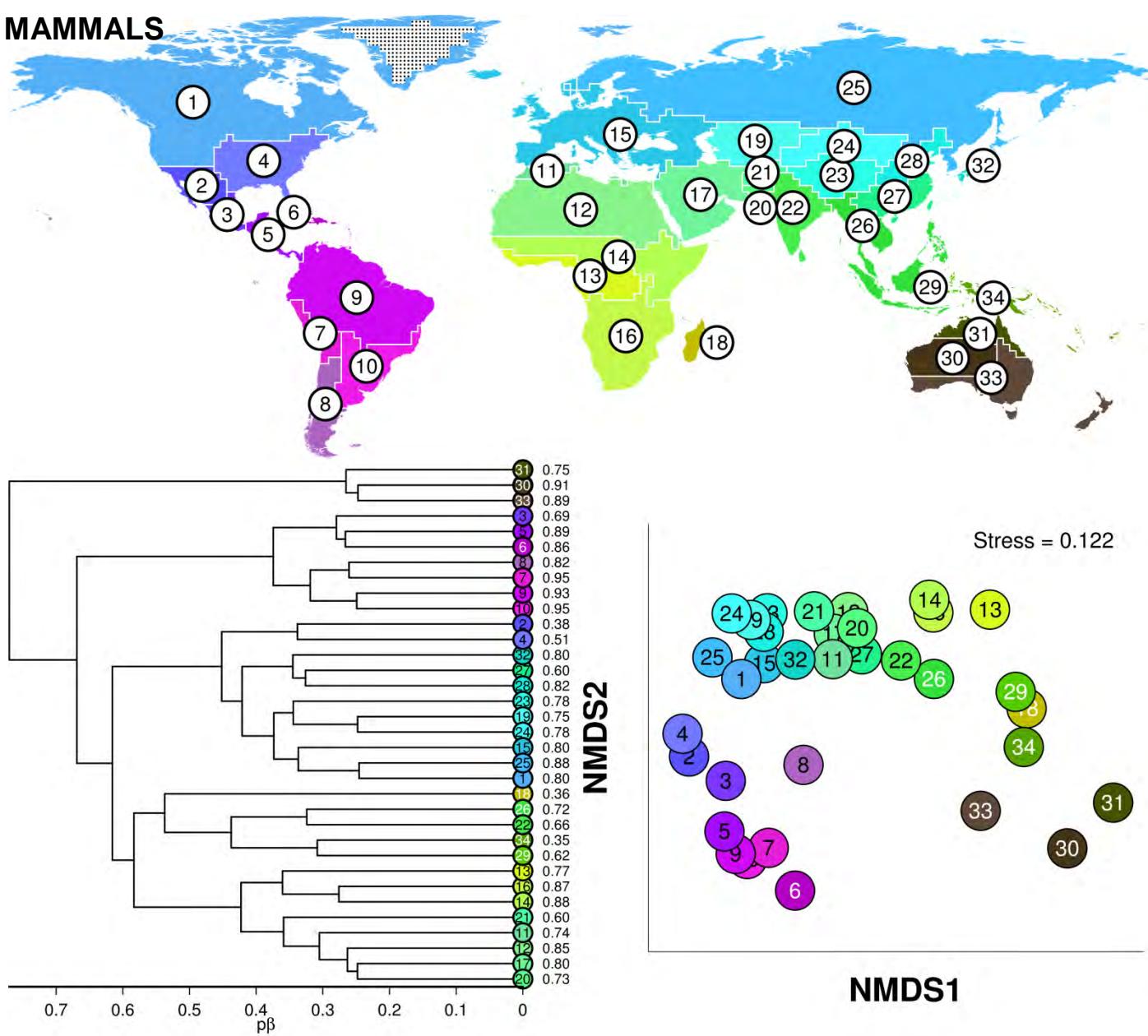
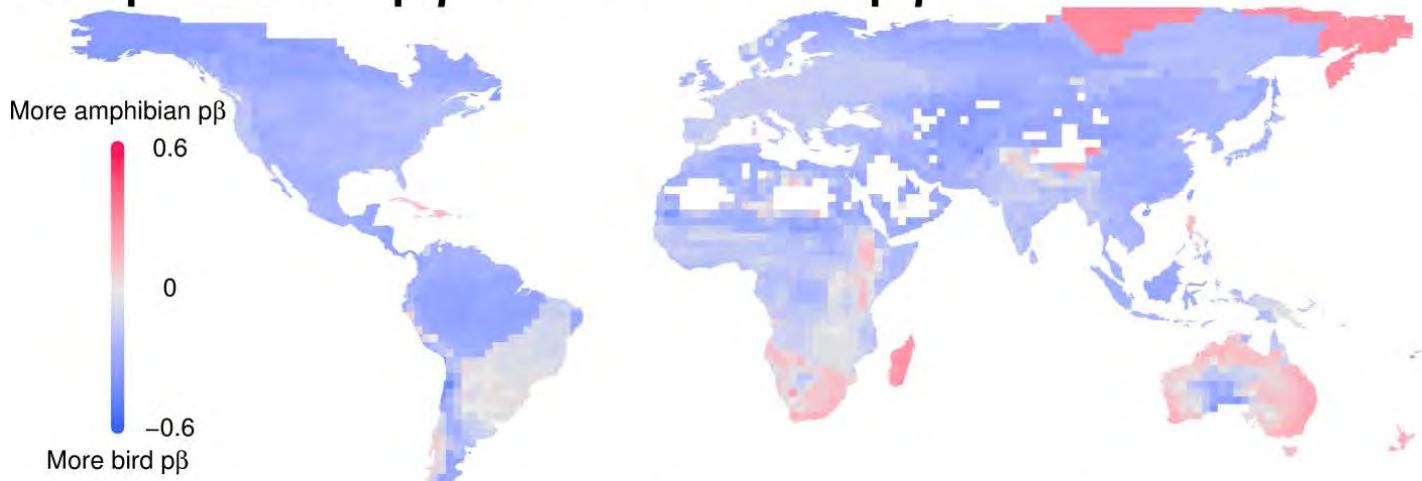
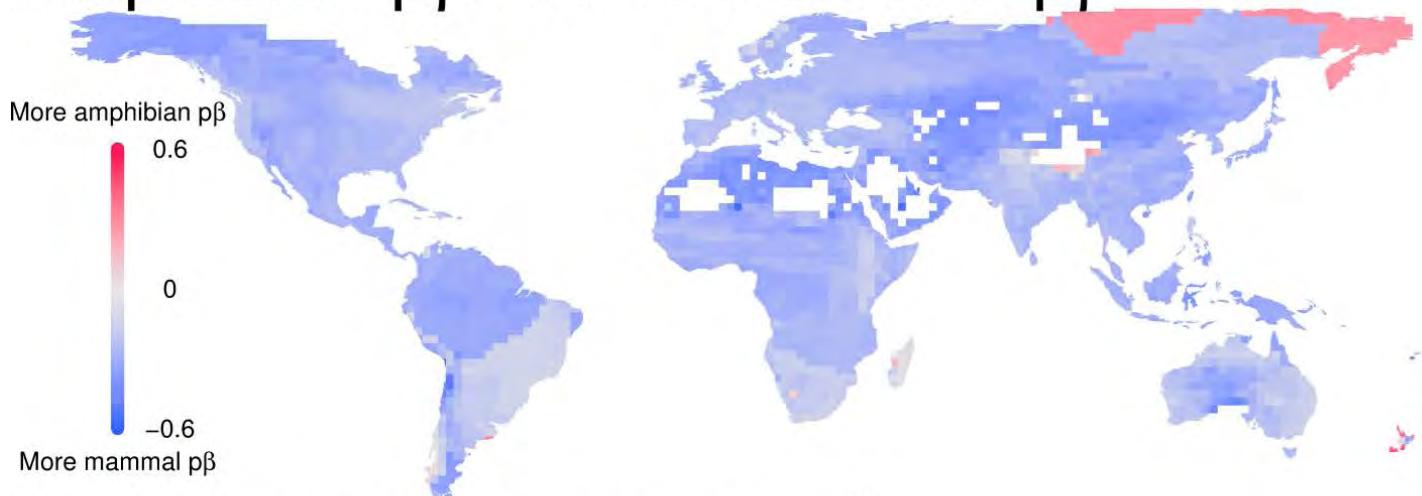


Fig. S4C. Global map, dendrogram and NMDS of taxon-specific zoogeographic regions based on phylo-distributional data for species of non-marine mammals (4,853 spp.). The map represents results of UPGMA clustering of global phylo beta diversity ($p\beta sim$) values for species assemblages in $2^\circ \times 2^\circ$ grid cells. Grid cells are clustered into 34 regions, the minimum number required to result in the sum of between region $p\beta sim$ values accounting for over 95% of the sum total $p\beta sim$. The dendrogram depicts relationships among regions and the $p\beta sim$ axis shows the degree of phylogenetic turnover between branches descending from a node. Region colors produced by plotting results within three-dimensional standard RGB color space via a three dimensional NMDS ordination. Therefore the similarity of region colors reflects the $p\beta sim$ of the clusters themselves. The human eye does not perceive RGB color differences with a high degree of accuracy and therefore inter-cluster relationships are also displayed using UPGMA dendrogram and a two-dimensional NMDS ordination. Co-phenetic scores range between 0 and 1, where 0 indicates the lack of a correlation and 1 indicates a perfect correlation between matrices. The overall co-phenetic score (0.77) indicates how well the dendrogram represent relationships between regions generally and values next to the tips of the dendrogram represent region-specific co-phenetic scores. Stress values reflect the amount of error in the correlation between pairwise distances in the original $p\beta sim$ data matrix and a data matrix calculated from the NMDS plot, with 0 representing no error and 1 indicating a complete lack of correlation.

Amphibian p β minus bird p β



Amphibian p β minus mammal p β



Bird p β minus mammal p β

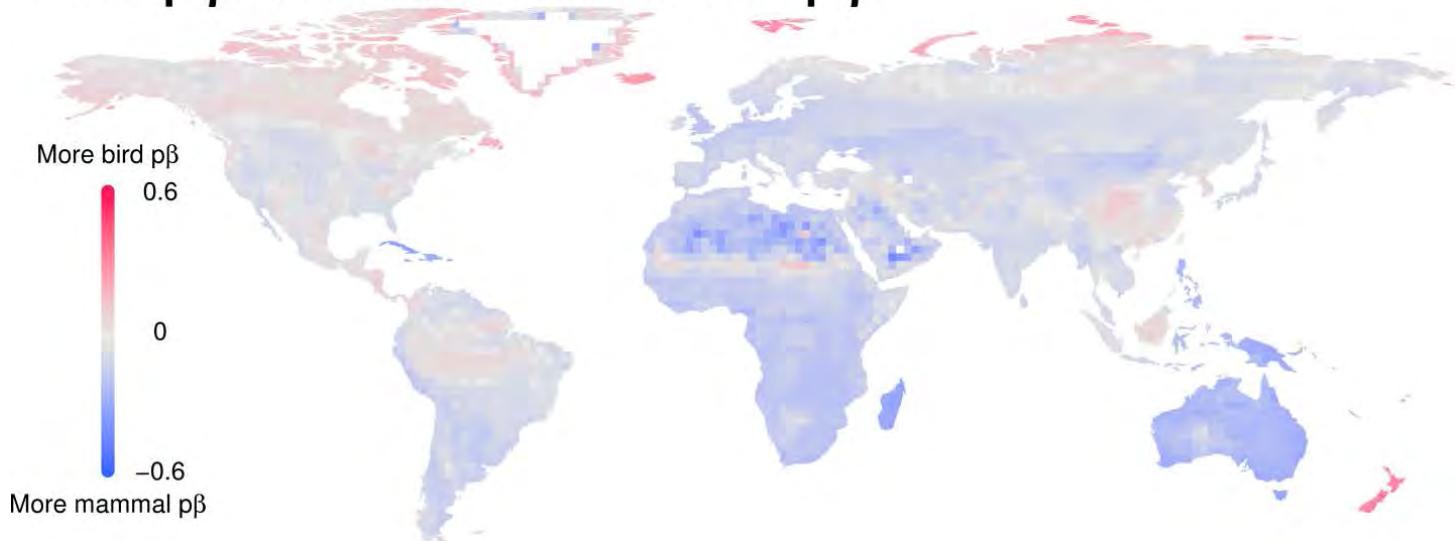


Fig. S5. Cross-taxon comparison of global phylogenetic beta diversity values. Colors indicate for each grid cell the difference in mean phylo beta diversity (p β sim) values between (A) amphibians and birds, (B) amphibians and mammals and (C) birds and mammals.

(A) AMPHIBIANS

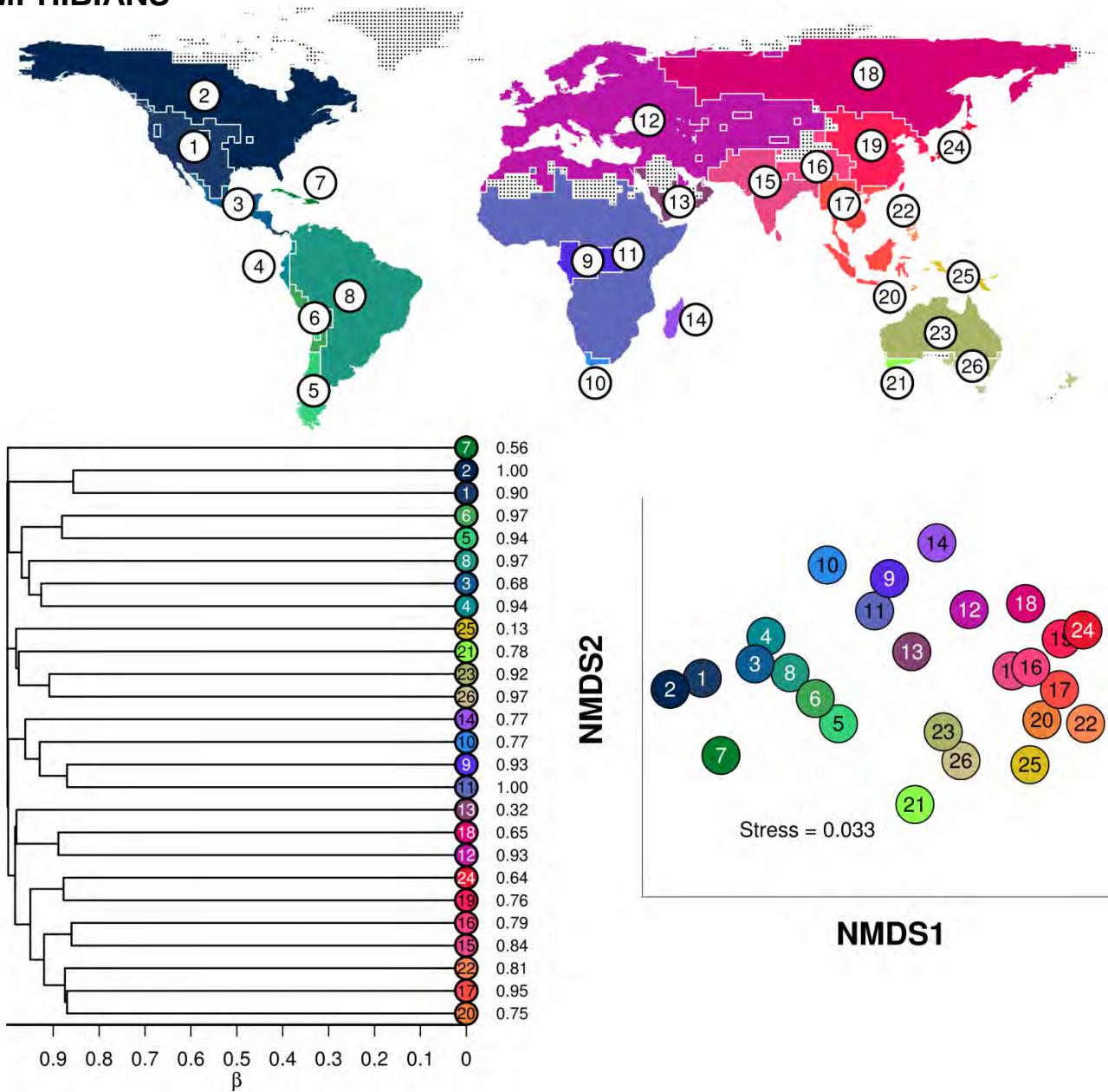


Fig. S6A. Global map, dendrogram and NMDS of taxon-specific zoogeographic regions based on distributional data for species of amphibians (6,110 spp.). The map represents results of UPGMA clustering of global beta diversity (β sim) values for species assemblages in $2^\circ \times 2^\circ$ grid cells. Grid cells are clustered into 26 regions, the minimum number required to result in the sum of between region β sim values accounting for over 95% of the sum total β sim. The dendrogram depicts relationships among regions and the β sim axis shows the degree of compositional turnover between branches descending from a node. Region colors produced by plotting results within three-dimensional standard RGB color space via a three dimensional NMDS ordination. Therefore the similarity of region colors reflects the β sim of the clusters themselves. The human eye does not perceive RGB color differences with a high degree of accuracy and therefore inter-cluster relationships are also displayed using UPGMA dendrogram and a two-dimensional NMDS ordination. Co-phenetic scores range between 0 and 1, where 0 indicates the lack of a correlation and 1 indicates a perfect correlation between matrices. The overall co-phenetic score (0.83) indicates how well the dendrogram represent relationships between regions generally and values next to the tips of the dendrogram represent region-specific co-phenetic scores. Similarly, stress values reflect the strength of the correlation between pairwise distances in the original p β sim data matrix and a data matrix calculated from the NMDS plot. Stress values reflect the amount of error in the correlation between pairwise distances in the original p β sim data matrix and a data matrix calculated from the NMDS plot, with 0 representing no error and 1 indicating a complete lack of correlation.

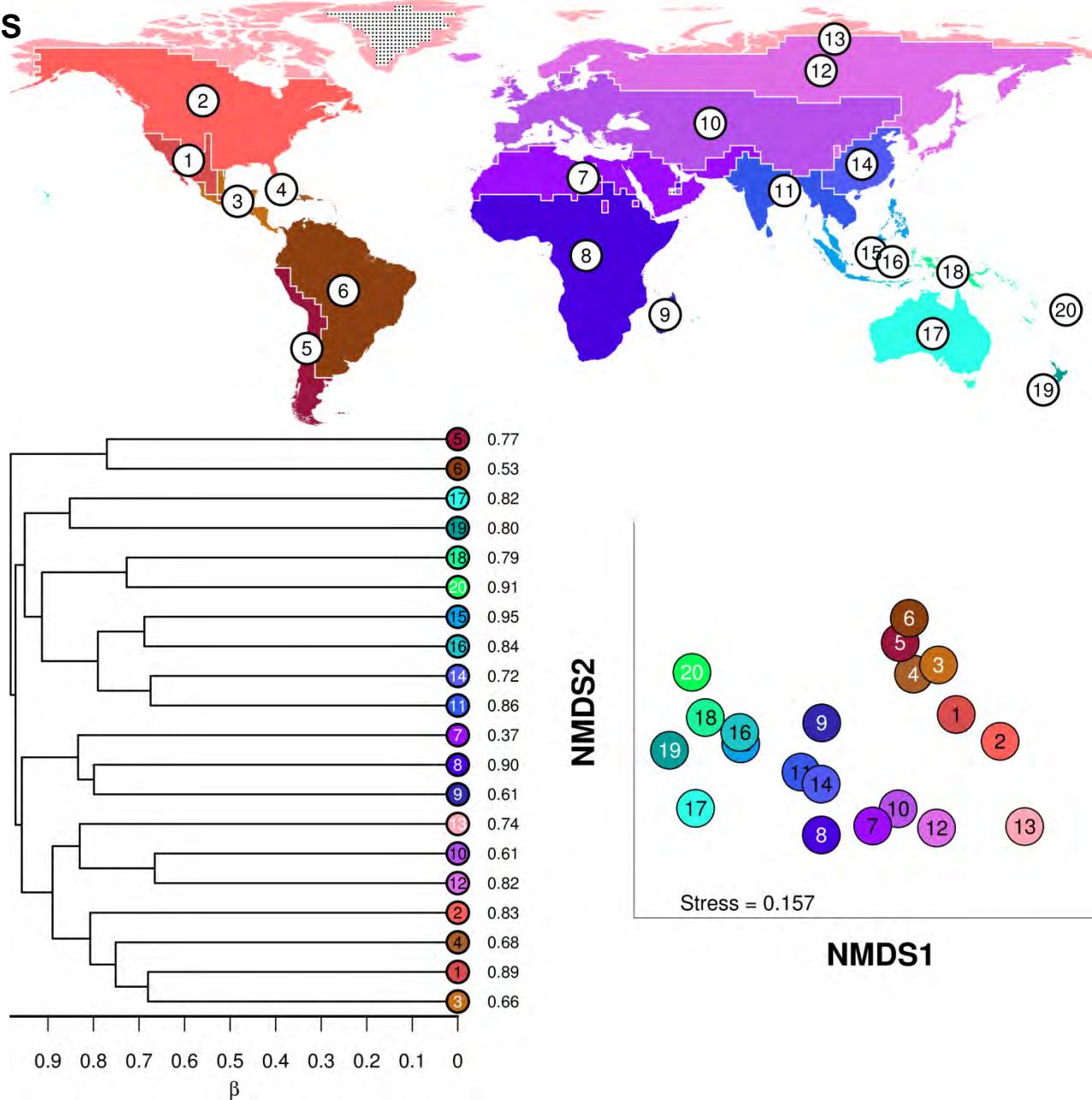
(B) BIRDS

Fig. S6B. Global map, dendrogram and NMDS of taxon-specific zoogeographic regions based on distributional data for species of birds (10,074 spp.). The map represents results of UPGMA clustering of global beta diversity (β sim) values for species assemblages in $2^\circ \times 2^\circ$ grid cells. Grid cells are clustered into 20 regions, the minimum number required to result in the sum of between region β sim values accounting for over 95% of the sum total β sim. The dendrogram depicts relationships among regions and the β sim axis shows the degree of compositional turnover between branches descending from a node. Region colors produced by plotting results within three-dimensional standard RGB color space via a three dimensional NMDS ordination. Therefore the similarity of region colors reflects the β sim of the clusters themselves. The human eye does not perceive RGB color differences with a high degree of accuracy and therefore inter-cluster relationships are also displayed using UPGMA dendrogram and a two-dimensional NMDS ordination. Co-phenetic scores range between 0 and 1, where 0 indicates the lack of a correlation and 1 indicates a perfect correlation between matrices. The overall co-phenetic score (0.76) indicates how well the dendrogram represent relationships between regions generally and values next to the tips of the dendrogram represent region-specific co-phenetic scores. Similarly, stress values reflect the strength of the correlation between pairwise distances in the original p β sim data matrix and a data matrix calculated from the NMDS plot. Stress values reflect the amount of error in the correlation between pairwise distances in the original p β sim data matrix and a data matrix calculated from the NMDS plot, with 0 representing no error and 1 indicating a complete lack of correlation.

(C) MAMMALS

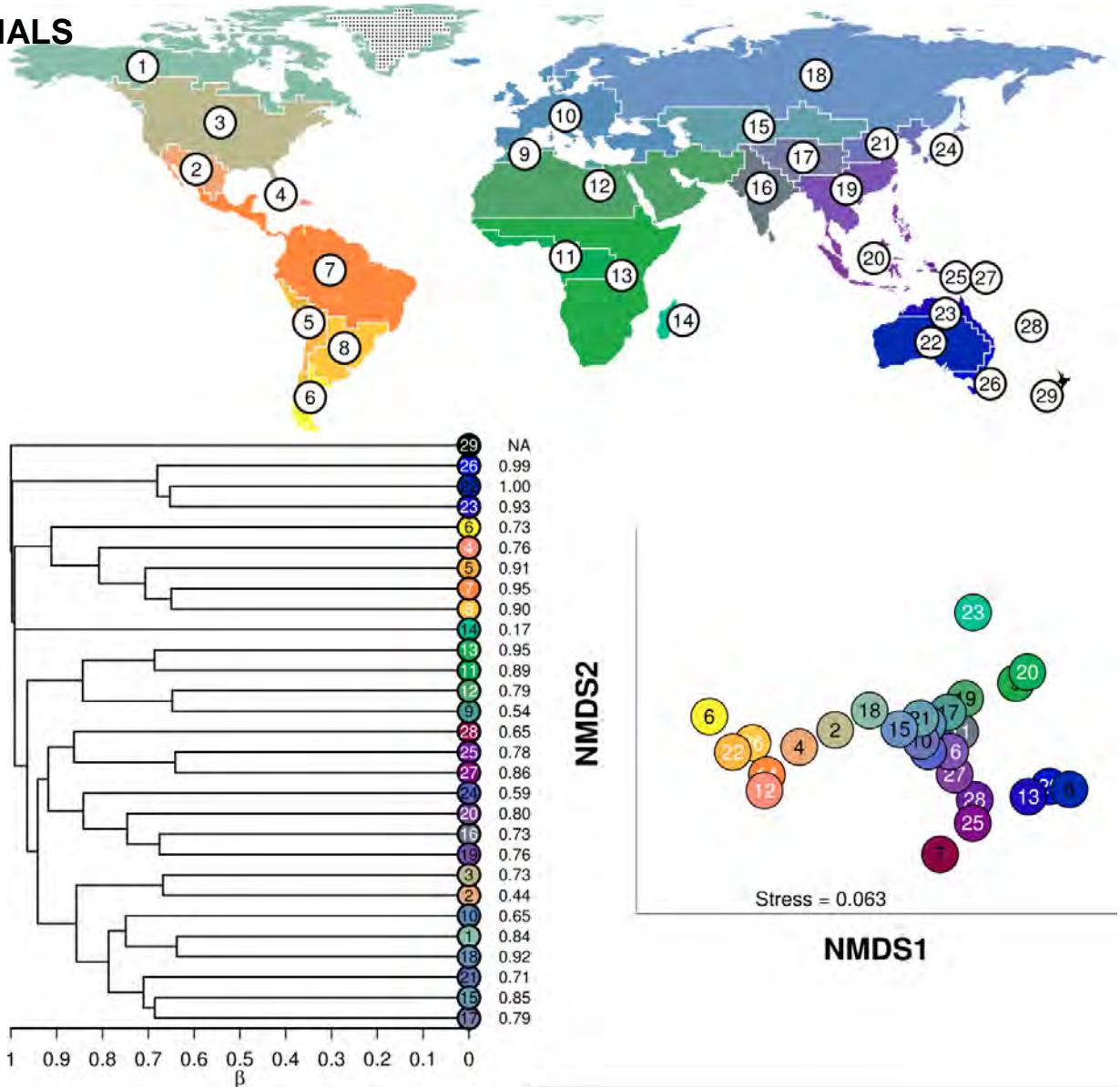


Fig. S6C. Global map, dendrogram and NMDS of taxon-specific zoogeographic regions based on distributional data for species of non-marine mammals (8,564 spp.). The map represents results of UPGMA clustering of global beta diversity (β sim) values for species assemblages in $2^\circ \times 2^\circ$ grid cells. Grid cells are clustered into 29 regions, the minimum number required to result in the sum of between region β sim values accounting for over 95% of the sum total β sim. The dendrogram depicts relationships among regions and the β sim axis shows the degree of compositional turnover between branches descending from a node. Region colors produced by plotting results within three-dimensional standard RGB color space via a three dimensional NMDS ordination. Therefore the similarity of region colors reflects the β sim of the clusters themselves. The human eye does not perceive RGB color differences with a high degree of accuracy and therefore inter-cluster relationships are also displayed using UPGMA dendrogram and a two-dimensional NMDS ordination. N.B. region 29, New Zealand, showed complete turnover (β sim = 1) with all other regions and dominated NMDS plots to the extent that patterns among other could not be determined. Therefore both NMDS plot were calculated after removing this region and region 29 was assigned black coloration. Co-phenetic scores range between 0 and 1, where 0 indicates the lack of a correlation and 1 indicates a perfect correlation between matrices. The overall co-phenetic score (0.81) indicates how well the dendrogram represent relationships between regions generally and values next to the tips of the dendrogram represent region-specific co-phenetic scores. Similarly, stress values reflect the strength of the correlation between pairwise distances in the original β sim data matrix and a data matrix calculated from the NMDS plot. Stress values reflect the amount of error in the correlation between pairwise distances in the original β sim data matrix and a data matrix calculated from the NMDS plot, with 0 representing no error and 1 indicating a complete lack of correlation.

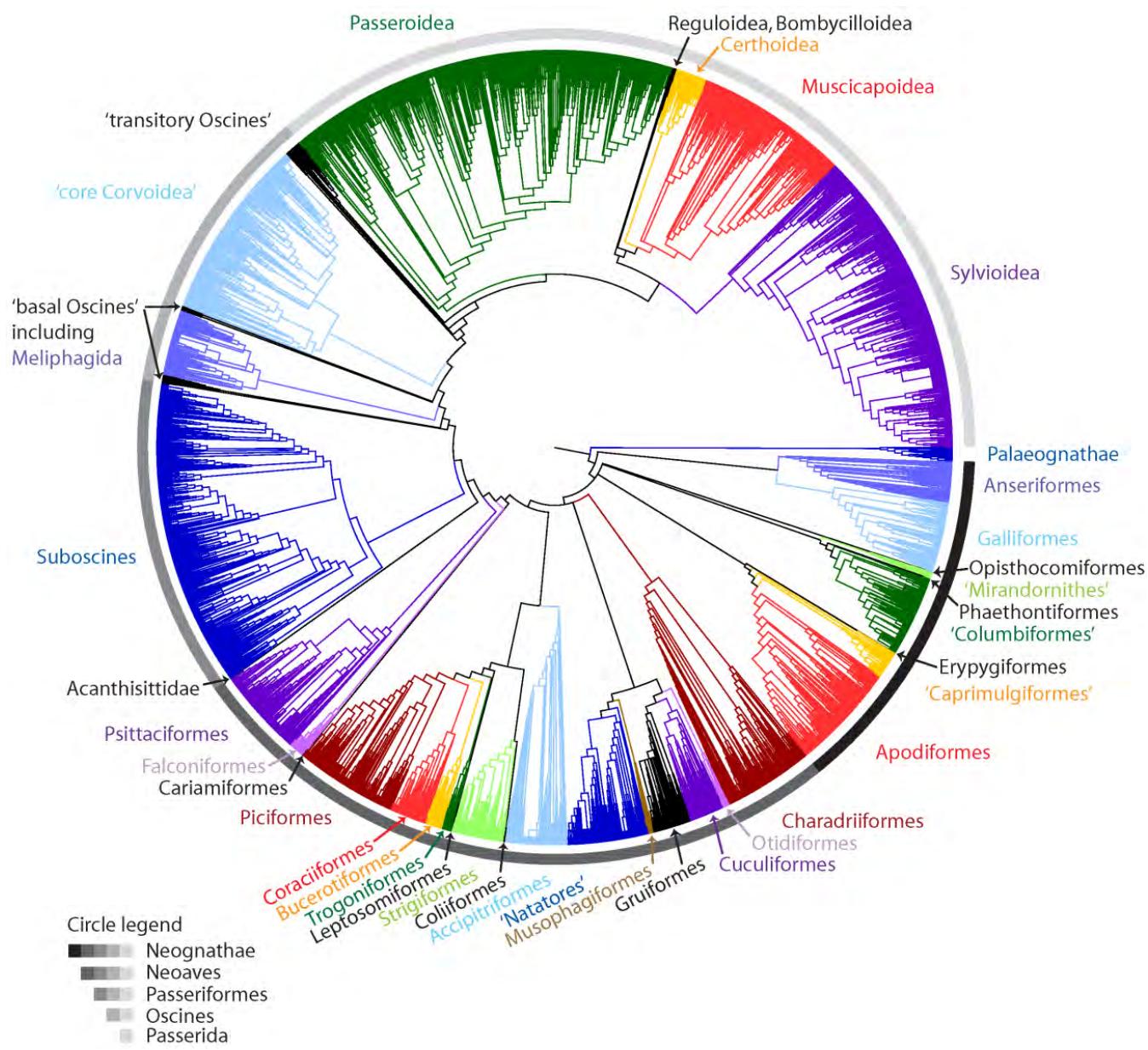


Fig. S7. Global phylogeny for birds. Overview of the global avian phylogeny, showing major clades. Branch lengths are not proportional to time or morphological divergence, but were assigned using the transformation introduced by Grafen (61) for greater clarity (N.B. branch lengths not used in this study, see Materials and Methods). Clade names follow the taxonomy of Gill et al. (38), with these exceptions: Palaeognathae comprise Apterygiformes, Casuariiformes, Rheiformes, Struthioniformes, and Tinamiformes; 'Mirandornithes' include Phoenicopteriformes and Podicipediformes; 'Columbiformes' include Mesornithiformes and Pteroclidiiformes; 'Natatores' include Ciconiiformes, Gaviiformes, Pelecaniformes, Procellariiformes, and Sphenisciformes; 'basal Oscines' include Menurida (Menuridae + Atrichornithidae), Climacterida (Climacteridae, Turnagra and Ptilnorhynchidae), Meliphagida, Pomatostomida (Pomatostomidae + Orthonychidae) and the Cinclosoma-Ptilorrhoa clade; and 'transitory Oscines' comprise Callaeidae, Chaetopidae, Cnemophilidae, Eupetidae, Melanocharitidae, Notiomystidae, Paramythiidae, Petroicidae, and Picathartidae. Note that 'Caprimulgiformes', 'basal Oscines' and 'transitory Oscines' are paraphyletic groupings. For further definitions of major clades within Passeriformes, see Supplementary Material Appendix S2.

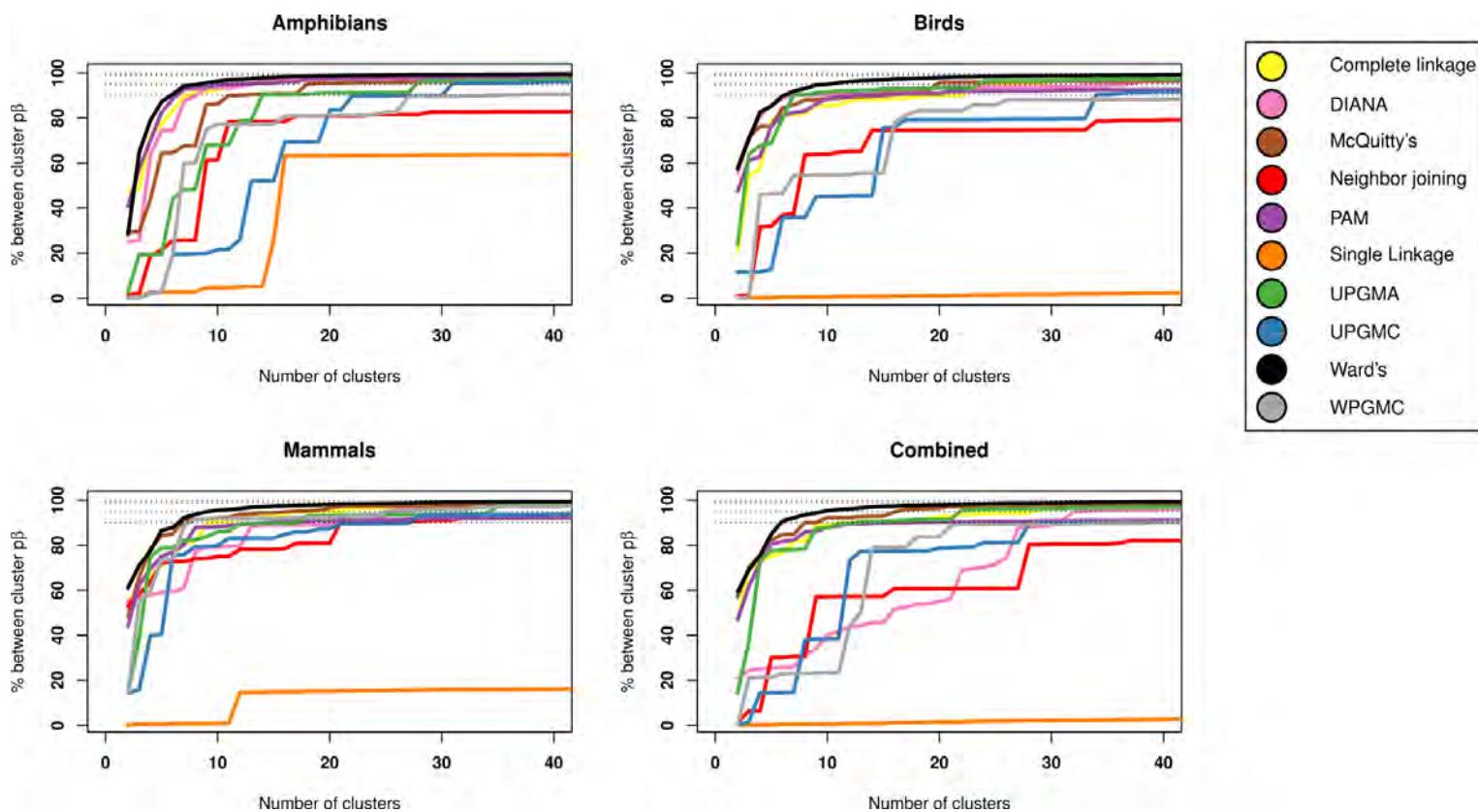


Fig. S8. Cluster algorithm performance analysis — clustering assemblages of vertebrate species into zoogeographic regions based on phylo-distributional data. Plots show performance analysis of ten different clustering algorithms for zoogeographical delimitation of species assemblages within $2^\circ \times 2^\circ$ grid cells for (A) amphibians, (B) birds, (C) mammals and (D) combined taxon analyses. Algorithms are evaluated via their ability to account for the sum total of global phylo beta diversity ($p\beta_{sim}$) values with increasing numbers of clusters (i.e. species assemblages). Algorithms producing clusters that accounted for the highest percentage of total $p\beta_{sim}$, for a given number of regions, were considered superior. Horizontal dotted lines represent different “cutoff” points tested for the final number of regions. These represent the points where 90, 95, 99 and 99.9% of total $p\beta_{sim}$ is found between regions rather than within regions. Higher cut off points represent more informative clustering schemes, but large numbers of cluster hinder interpretation of broad scale patterns. Therefore, the final scheme was chosen as the best performing algorithm at a cutoff point that returned less than 50 clusters.

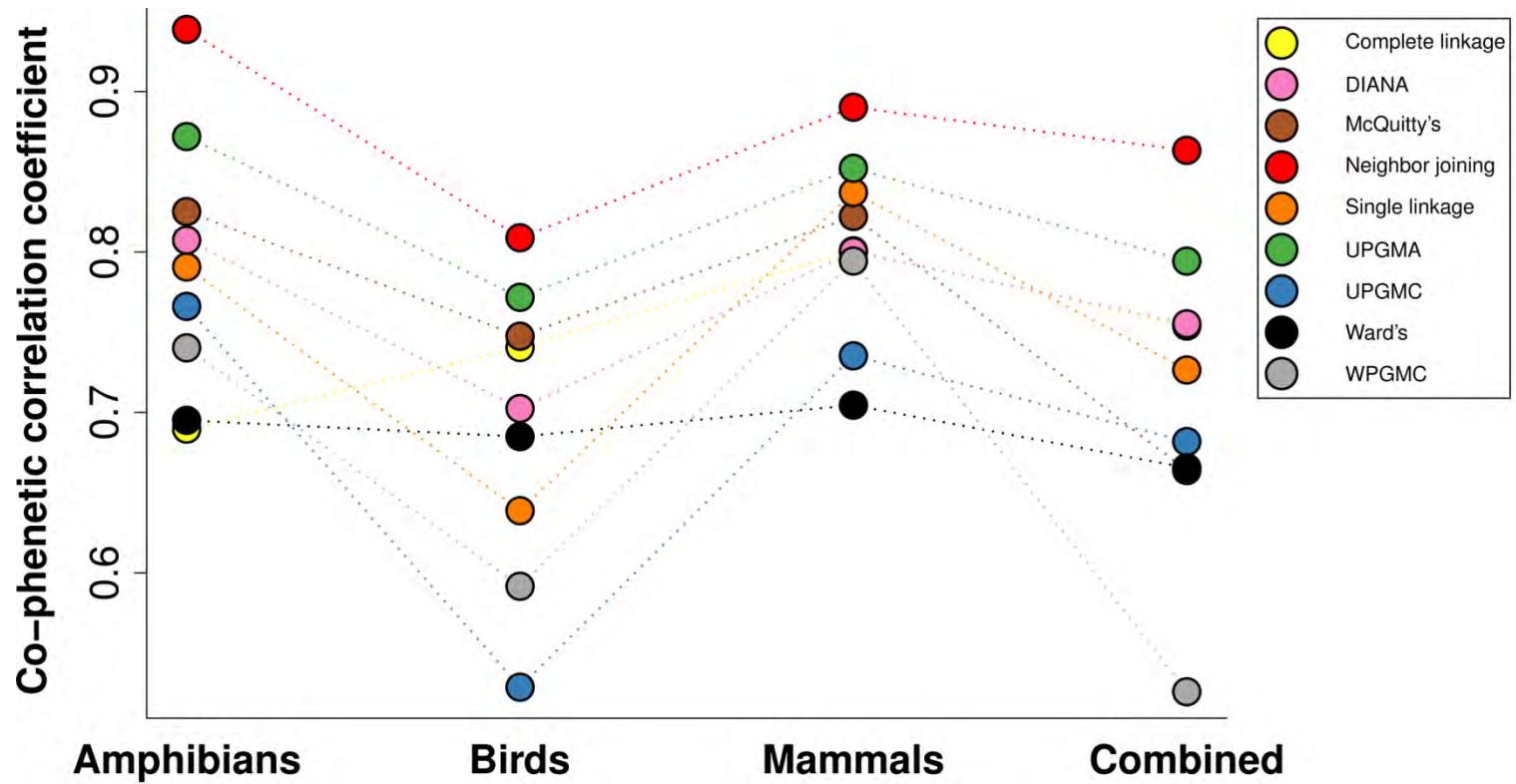


Fig. S9. Cluster algorithm performance analysis — inferring relationships between zoogeographic regions based on phylo-distributional data. Results of evaluation analysis for the performance of nine hierarchical clustering algorithms on zoogeographical regions produced from analysis of amphibians, birds, mammals and combined taxon data. Hierarchical algorithms are compared via their overall co-phenetic coefficients, which reflect of how well the data are represented by the cluster dendrogram. Co-phenetic coefficients are calculated as the strength of the correlation between the original β sim data (see *Material and Methods* for full description) and a data matrix calculated from the dendrogram. Higher values represent superior performance.

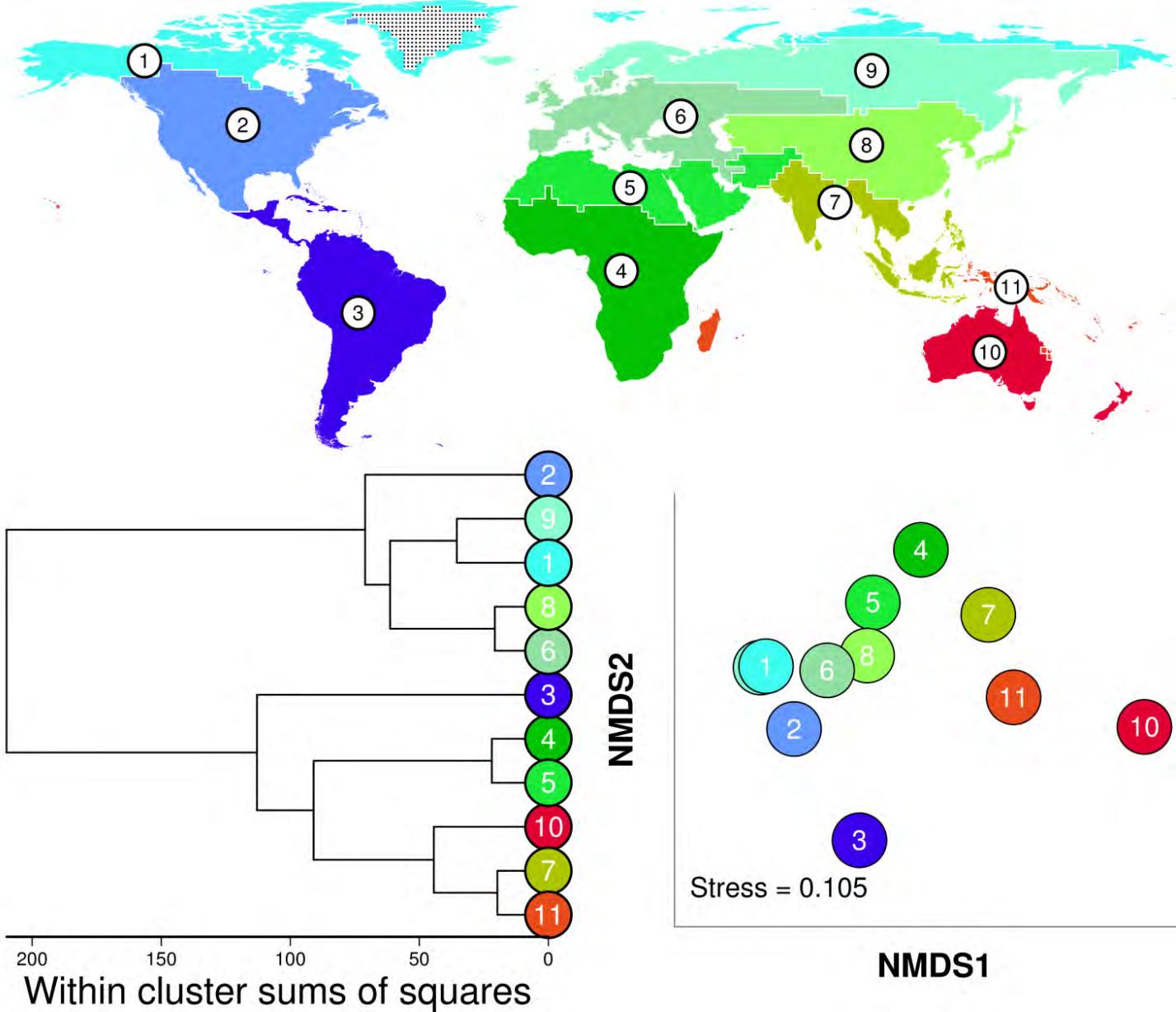


Fig. S10A. Robustness of results to the choice of analytical approach. Partitioning Around Medioids (PAM) clustering of global phylo beta diversity ($p\beta sim$) values for species assemblages in $2^\circ \times 2^\circ$ grid cells within 34 Ward's minimum variances criterion clustered zoogeographic regions. Grid cells are clustered into 11 realms, the number of realms in the main, UPGMA based, analysis. The sum of between realm $p\beta sim$ values accounts for over 93.8% of the sum total $p\beta sim$. Realms colors produced by plotting results within three-dimensional standard RGB color space via a three dimensional NMDS ordination. Therefore the similarity of realm colors reflects the $p\beta sim$ of the clusters themselves (N.B. The Tibetan plateau is clustered within region 9). The human eye does not perceive RGB color differences with a high degree of accuracy and therefore inter-cluster relationships are also displayed a two-dimensional NMDS ordination (N.B. no dendrogram is produced for the non-hierarchical PAM method). Stress values reflect the strength of the correlation between pairwise distances in the original $p\beta sim$ data matrix and a data matrix calculated from the NMDS plot. Stress values range between 0 and 1, where 1 indicate the lack of a correlation and 0 indicates a perfect correlation between matrices.

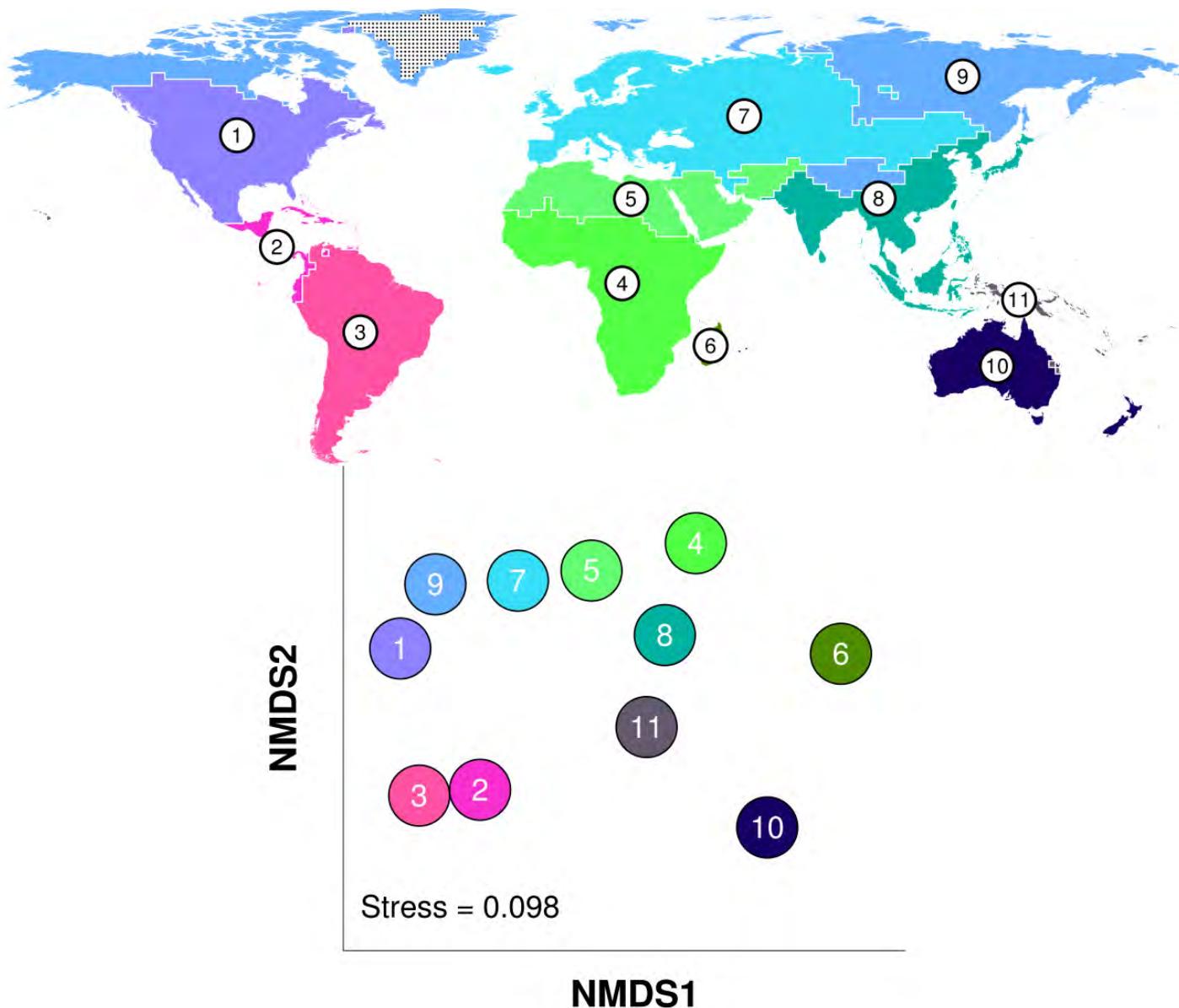
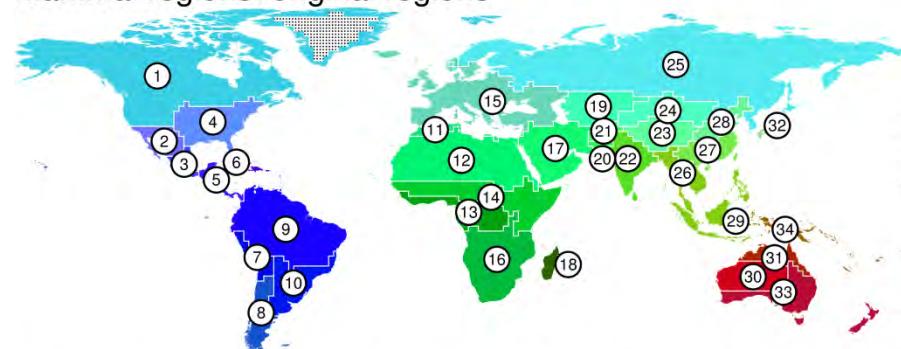


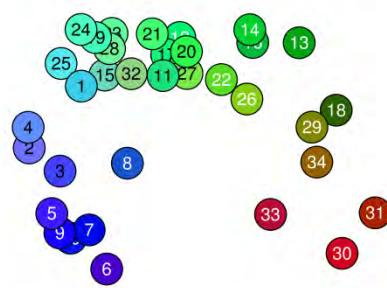
Fig. S10B. Robustness of results to the choice of analytical approach. Partitioning Around Medioids (PAM) clustering of global phylo beta diversity ($p\beta sim$) values for species assemblages in $2^\circ \times 2^\circ$ grid cells within 34 Ward's minimum variances criterion clustered zoogeographic regions. Grid cells are clustered into 11 realms, the number of realms in the main, UPGMA based, analysis. The sum of between realm $p\beta sim$ values accounts for over 93.8% of the sum total $p\beta sim$. Realms colors produced by plotting results within three-dimensional standard RGB color space via a three dimensional NMDS ordination. Therefore the similarity of realm colors reflects the $p\beta sim$ of the clusters themselves. The human eye does not perceive RGB color differences with a high degree of accuracy and therefore inter-cluster relationships are also displayed a two-dimensional NMDS ordination (N.B. no dendrogram is produced for the non-hierarchical PAM method). Stress values reflect the strength of the correlation between pairwise distances in the original $p\beta sim$ data matrix and a data matrix calculated from the NMDS plot. Stress values range between 0 and 1, where 1 indicate the lack of a correlation and 0 indicates a perfect correlation between matrices.

Mammal regions: original regions



Stress = 0.122

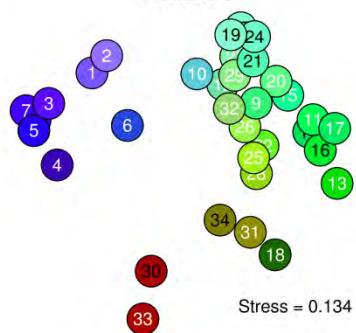
NMDS2



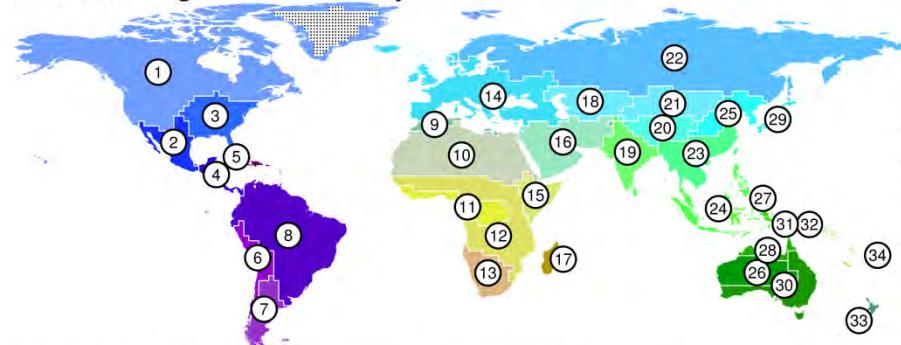
Mammal regions: branch lengths included



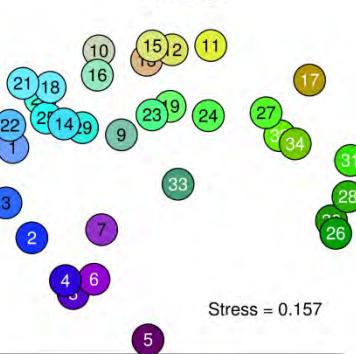
NMDS1



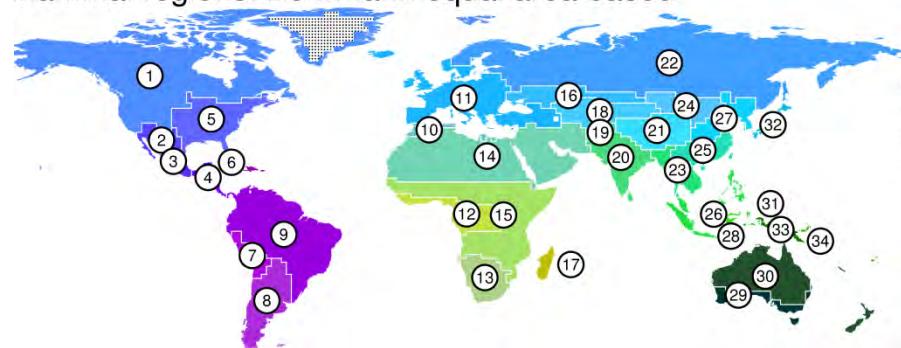
Mammal regions: taxonomy based



NMDS1

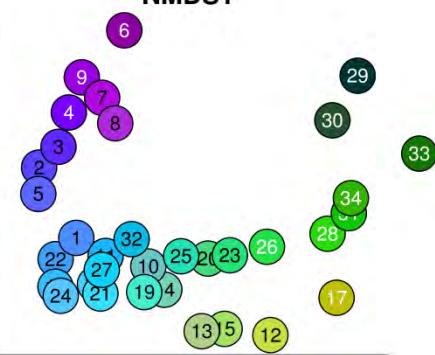


Mammal regions: Behrmann equal area based



NMDS1

NMDS2



NMDS1

Fig. S11. Sensitivity analyses. Comparison of (A) phylogenetically derived map of zoogeographic regions for mammals with maps produced using (B) a phylogenetic tree including branch length, (C) a taxonomy instead of a phylogenetic tree and (D) equal area grid cells instead of 2°× 2° Latitude-Longitude grid cells.

Table S1. Summary information for clustering of zoogeographic regions into realms (Fig. 1 and fig. S1) for cross-taxon analyses on phylogenetic beta diversity values (measured as p β sim). N = number of objects within cluster (i.e. objects = regions). “Within mean” = mean p β sim values for comparisons of objects within a cluster with other objects within that cluster. “Between mean” = mean p β sim values for comparisons of objects within a clusters with objects not within that cluster. “SD” = standard deviations of these values. “Mean silhouette” values (62) reflect both the tightness (similarity of within cluster objects) and separation (similarity of objects outside a cluster to objects within a cluster). Silhouettes values are calculated for each object as: $s(i) := (b(i) - a(i)) / \max(a(i), b(i))$; where $a(i)$ = mean of p β sim values between object i and all other objects of the cluster to which object i belongs, $b(i)$ = the mean of p β sim values with object i's neighbour cluster (i.e. the nearest cluster i does not belong to). Values range from -1 to 1, with positive mean values for a cluster indicating that objects within a cluster are, on average, appropriately placed within that cluster.

Realm	N	Within mean	Within SD	Between mean	Between SD	Within mean/ Between mean	Mean Silhouette
Afrotropical	570	0.24	0.10	0.55	0.15	2.26	0.26
Australian	287	0.25	0.15	0.65	0.18	2.63	0.35
Madagascan	29	0.11	0.08	0.63	0.14	5.51	0.70
Nearctic	723	0.20	0.12	0.47	0.17	2.41	0.41
Neotropical	478	0.26	0.11	0.59	0.15	2.32	0.28
Oriental	344	0.25	0.12	0.54	0.16	2.18	0.21
Palearctic	1994	0.23	0.13	0.50	0.17	2.21	0.25
Panamanian	88	0.22	0.12	0.56	0.16	2.51	0.34
Papuan-Melanesian	269	0.23	0.20	0.52	0.19	2.22	0.28
Saharo-Arabian	297	0.19	0.09	0.47	0.15	2.51	0.41
Sino-Japanese	165	0.26	0.14	0.45	0.16	1.71	0.18

Table S2. Summary information for clustering of species assemblages into zoogeographic regions (Fig. S2) for cross-taxon analyses on phylogenetic beta diversity values (measured as p β sim). N = number of objects within cluster (i.e. objects = species assemblages). “Within mean” = mean p β sim values for comparisons of objects within a cluster with other objects within that cluster. “Between mean” = mean p β sim values for comparisons of objects within a cluster with objects not within that cluster. “SD” = standard deviations of these values. “Mean silhouette” values (62) reflect both the tightness (similarity of within cluster objects) and separation (similarity of objects outside a cluster to objects within a cluster). Silhouettes values are calculated for each object as: $s(i) := (b(i) - a(i)) / \max(a(i), b(i))$; where $a(i)$ = mean of p β sim values between object i and all other objects of the cluster to which object i belongs, $b(i)$ = the mean of p β sim values with object i 's neighbour cluster (i.e. the nearest cluster i does not belong to). Values range from -1 to 1, with positive mean values for a cluster indicating that objects within a cluster are, on average, appropriately placed within that cluster.

Region	ID	N	Within mean	Within SD	Between mean	Between SD	Within mean/ Between mean	Mean Silhouette
African	9	459	0.21	0.09	0.53	0.15	2.53	0.23
Amazonian	5	197	0.17	0.08	0.57	0.15	3.34	0.40
Arctico-Siberian	14	1200	0.15	0.09	0.47	0.19	3.10	0.39
Australian	17	231	0.22	0.11	0.68	0.15	3.16	0.23
Chinese	15	62	0.14	0.08	0.45	0.16	3.24	0.49
Eurasian	11	794	0.21	0.10	0.44	0.17	2.10	0.14
Guineo-Congolian	7	111	0.19	0.08	0.56	0.15	2.97	0.36
Indo-Malayan	16	152	0.19	0.11	0.56	0.16	3.03	0.25
Madagascan	10	29	0.11	0.08	0.63	0.14	5.51	0.60
Mexican	3	59	0.16	0.07	0.51	0.15	3.29	0.49
North American	2	664	0.17	0.10	0.47	0.17	2.71	0.34
Oriental	12	192	0.18	0.10	0.50	0.16	2.75	0.24
Panamanian	4	88	0.22	0.12	0.56	0.16	2.51	0.21
Polynesian	1	12	0.12	0.11	0.43	0.17	3.73	0.52
Saharo-Arabian	8	297	0.19	0.09	0.47	0.15	2.51	0.33
South American	6	281	0.22	0.11	0.58	0.16	2.61	0.23
Tibetan	13	65	0.16	0.09	0.46	0.16	2.87	0.37
Oceanian	61		0.16	0.07	0.51	0.15	3.30	0.41

Japanese	158	0.21	0.11	0.45	0.16	2.08	0.14
Novozelandic	124	0.09	0.10	0.39	0.21	4.17	0.15

Table S3. Results from the Mantel and partial Mantel correlation tests between the β sim matrices of each pair of taxa included in this study. A matrix of pair-wise Euclidean distances was used as a covariate in the partial Mantel test.

Variables	Correlation		Partial correlation	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Mammals vs. Birds	0.81	< 0.001	0.68	< 0.001
Mammals vs. Amphibians	0.61	< 0.001	0.43	< 0.001
Birds vs. Amphibians	0.58	< 0.001	0.39	< 0.001

Table S4. Summary information for alternative statistical approaches considered for clustering species assemblages into zoogeographic realms (main analysis shown in Fig. S1) based on cross-taxon analyses of phylogenetic beta diversity values (measured as $p\beta_{sim}$).

	UPGMA	Ward's	PAM (clustering Ward defined regions)
Basis for consideration for global bioregion analysis	Best all round method; considering both our evaluation criteria	The best performing method with regards to evaluation one: maximizing total $p\beta$ between regions	Unlike all other methods tested, groups regions into realms without <i>a priori</i> assumption regarding the structure of relationships between them
Results figure	S1	S10a	S10b
Description	Agglomerative. Successively clusters most similar pairs of objects.	Agglomerative. Variance based. Successively clusters pairs of objects that minimize the error (i.e. within cluster) sums of squares.	Non-hierarchical. First selects a predefined number of regions then clusters remaining regions to these. Regions based on Ward clustering to >95% of global $p\beta_{sim}$ is between clusters cutoff value.
Assumptions of data structure	Hierarchical	Hierarchical	None
Sensitivity to highly localized patterns (i.e., size of regions/realms created)	High. Very small, distinct clusters can appear close to the root of the clustering dendrogram. N.B. these clusters were removed at the region definition step (see <i>Materials and Methods</i>)	Very low. Tends to produce roughly equal sized clusters	Low. Attempts to optimize clusters across entire dataset
Branch length calculation	Branch lengths of dendrogram based on	Branch lengths of dendrogram based on	NA

	unweighted mean values	sums of squares	
Realm definition details	UPGMA dendrogram cut at 11 clusters. The lowest number where > 90% of global $p\beta_{sim}$ is between clusters (20 clusters required for 95% cutoff).	Ward dendrogram cut at 11 clusters in order to match the number of realms in the UPGMA analysis. For these 11 Ward realms, 96.1% of global $p\beta_{sim}$ is between clusters.	Number of clusters set <i>a priori</i> to 11 in order to match the number of realms in the UPGMA analysis. For these 11 PAM realms, XX% of global $p\beta_{sim}$ is between clusters.

Supplementary Material Appendix S1:

List of references for avian distributional database.

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Supplementary Material Appendix S2:

Construction of the global avian phylogeny.

The phylogeny was based on the taxonomy of Gill et al. (38), excluding the hybrid *Pycnonotus nieuwenhuissii*. A comprehensive search has been made to find potential source trees, mainly based on review of key journals, supplemented with searches of the bibliographical databases Zoological Record & Biosis (post 1995). This resulted in 800 references (some of which were redundant and are therefore omitted from the references below). From the source trees, the phylogeny was constructed by hand as a consensus supertree (see fig. S7 for the general topology).

A supertree construction is a controversial way of evaluating and integrating data from different sources (63). Some parsimony matrix representations exist but we preferred to judge the suitability of the various source trees or parts of source tree, starting with a hand-drawn draft (64). Many source trees, especially those produced in the 1990s, are based on single mitochondrial genes and may not provide a reliable representation of the species tree. Some source trees comprise a well-sampled core group of species, but biased sampling of other parts (for instance, with only species from particular geographical areas), or a poorly chosen outgroup. This may give an unreliable branching, even if the support values are high. Other studies are based on several mitochondrial as well as nuclear markers, which provide a basis for determining congruence between the gene trees and a well-supported combined tree. In general, we assume that nuclear markers give the best information about deep branching events, but nuclear exons may give different tree topologies from introns (65, 66), maybe as a consequence of some selective constraints. We therefore preferred combined datasets, or intron data for exons, and notably the deeper nodes that are supported by some rare molecular events such as insertions. Furthermore, we preferred topologies based on comprehensive Bayesian searches. However, densely sampled parts of single gene trees can be useful for providing details about the terminal branching of phylogenies.

Throughout the tree, we adopt a cautious principle of using polytomies where the evidence is conflicting. Although numerous studies have shown that traditionally accepted genera may be para- or polyphyletic, we accept that species placed in the same genus in the taxonomy used can be placed together in one (unresolved) genus. However, genera are split apart where, in absence of molecular support, there are other valid arguments in the literature for regarding a genus as not being a natural unit. Species which are not yet covered in a molecular study, and which cannot confidently be placed in an unresolved genus on other evidence, are “parked” at the base of the relevant larger group. However, only very few species cannot confidently be placed in a family-level category and only two species were excluded due to their placement being highly debatable (*Lophotriorchis kieneri*: Accipitridae, and *Clytolaema rubricauda*: Trochilidae). For branches that are not yet covered by molecular data, we used a morphology-based phylogeny (see below for references) or we relied on the current classification, with unresolved arrangement of the genera, and unresolved arrangement of the species within genera (e.g. in Threskiornithidae). Within unresolved genera, we grouped together species that have been recognized as species groups or superspecies in the traditional taxonomy.

Genera that were *incertae sedis* in the taxonomy used were placed at family level (*Achaetops*, *Cryptillas*, *Eulacestoma*, *Icteria*, *Ifrita*, *Macroosphenus*, *Melampitta*, *Melocichla*, *Sphenoeacus*, *Sylvietta*, *Turnagra*, *Xenoligea*, *Zeledonia*). Exceptions were *Calyptura* and *Piprites* (included in Tyrannidae), *Myzornis* (included in Timaliidae) and *Pachycare* (included in Acanthizidae). If families and genera were polyphyletic according to our molecular source trees, the genera (or species) responsible were elevated to family level (or genus level) and placed; or they were moved into other families (or genera) if there was substantial evidence supporting this move. All these changes are referenced below. A unit of branch length was assigned to lead to each valid taxonomic category (order, family, or genus), and to each well-supported split between or above these (e.g., superorders, subfamilies, subgenera, species groups).

For the deepest branching (ordinal level) we follow Hackett et al. (67), except that we take into account the uncertainty about the monophyly of the Metaves clade, which we leave as a trichotomy, including *Opistocomus* (based on 68). Additionally, we included information from a range of studies for the deep branching between major clades, orders, and some families (65, 68-81). Within each major clade, we give additional references and major taxonomic changes (relative to 38) below (Table S5). “Renaming” of species was performed in order to keep genera monophyletic (details are not listed here, but usually subgenera were elevated to generic level, or a genus name was abolished for another one that took precedence). Although the resulting phylogenetic tree is too large to be depicted in detail here, it is available from S.A.F. upon request (but see fig. S7 for a general overview of the topology).

Table S5: Major taxonomic changes, and sources additional to the ones in the main text, for each major bird clade. Palaeognathae comprise Tinamiformes, Struthioniformes, Rheiformes, Casuariiformes, and Apterygiformes; otherwise, all bird orders in the taxonomy are listed except those without major taxonomic change and without specific references (Phoenicopteriformes, Cariamiformes, Eurypygiformes, Pteroclidiiformes, and Opisthomocomiformes). Note that Passeriformes had to be split into (partly nested) smaller clades.

Clade	Major taxonomic changes relative to (38) and clade-specific references for source trees
Palaeognathae	no major taxonomic change (82-87)
Galliformes	<i>Ptilopachus</i> is outside Phasianidae, as sister group to Odontophoridae; <i>Alectura</i> is nested within <i>Aepyptodius</i> ; complex rearrangements within Phasianidae (88-110)
Anseriformes	<i>Dendrocygna</i> , <i>Bucephala</i> and <i>Nettapus</i> are paraphyletic; many deeper branches remain unresolved (97, 109, 111-116)
Sphenisciformes	no major taxonomic change (117-122)
Gaviiformes	no major taxonomic change (123)
Procellariiformes	Hydrobatidae is deeply paraphyletic, the <i>Oceanodroma-Hydobates</i> clade is sister to all other Procellariiformes; <i>Oceanodroma</i> is paraphyletic with respect to <i>Hydrobates</i> ; <i>Calonectris</i> is nested within <i>Puffinus</i> (124-132)

Podicipediformes	<i>Tachybaptus</i> is deeply paraphyletic (133, 134)
Phaethontiformes	no major taxonomic change (66, 67, 135)
Ciconiiformes	no major taxonomic change (136-139)
Pelecaniformes	no major taxonomic change (66, 67, 87, 135-145)
Accipitriformes	<i>Aquila</i> is polyphyletic; significant rearrangements at generic level; <i>Accipiter</i> left unresolved (146-163)
Falconiformes	no major taxonomic change; <i>Falco</i> left largely unresolved (147, 152, 158, 164, 165)
Otidiformes	<i>Eupodotis</i> and <i>Neotis</i> are paraphyletic (166-168)
Mesornithiformes	no major taxonomic change (66, 169)
Gruiformes	<i>Rallina</i> is outside Rallidae, as sister group to Sarothruridae; <i>Grus</i> , <i>Gallinula</i> , <i>Laterallus</i> , <i>Porzana</i> , and <i>Rallus</i> are paraphyletic (170-177)
Charadriiformes	<i>Pluvialis</i> is outside Charadriidae, as sister group to the Recurvirostridae-Ibidorhynchidae-Haematopodidae clade; <i>Esacus</i> is nested within <i>Burhinus</i> ; <i>Charadrius</i> , <i>Vanellus</i> , and <i>Gallinago</i> are paraphyletic; significant generic rearrangement of Laridae (134, 178-202)
Columbiformes	<i>Gallicolumba</i> and <i>Phaps</i> are polyphyletic; <i>Drepanoptila</i> is nested within <i>Ptilinopus</i> (72, 203-207)
Psittaciformes	no major taxonomic change (208-228)
Musophagiformes	<i>Musophaga</i> is nested within <i>Tauraco</i> (229, 230)
Cuculiformes	no major taxonomic change (231-233)
Strigiformes	<i>Ninox</i> , <i>Glaucidium</i> , <i>Bubo</i> , <i>Strix</i> , and <i>Asio</i> are paraphyletic (234-238)
“Caprimulgiformes”	polyphyletic, as Apodiformes are nested within; <i>Eurostopodus</i> and <i>Caprimulgus</i> are paraphyletic (239-243)
Apodiformes	<i>Cypseloides</i> is nested within <i>Streptoprocne</i> , and <i>Hydrochous</i> within <i>Aerodramus</i> ; <i>Chalcostigma</i> , <i>Heliangelus</i> , <i>Amazilia</i> , and <i>Hylocharis</i> are paraphyletic (244-256)
Coliiformes	no major taxonomic change (66, 257)
Trogoniformes	no major taxonomic change (72, 258-261)
Leptosomiformes	no major taxonomic change (66, 262)
Coraciiformes	no major taxonomic change (72, 262-268)
Bucerotiformes	no major taxonomic change (269-272)
Piciformes	<i>Melichneutes</i> is nested within <i>Indicator</i> , <i>Geocolaptes</i> within <i>Campetheria</i> , and <i>Lybius</i> within <i>Tricholaema</i> ; <i>Melanerpes</i> , <i>Picoides</i> , <i>Dendrocopos</i> , <i>Picus</i> , and <i>Stactolaema</i> are paraphyletic (72, 273-291)
Passeriformes	<i>Oxyruncus</i> is included within Tyrannidae, instead of being in its own family; <i>Acanthisitta</i> is nested within <i>Xenicus</i> . References for deep branching (292-297); for more details, see major passeriform clades (Suboscines and Oscines) listed below
Suboscines	<i>Phibalura</i> is included in the ampelionid group of the Cotingidae, not Pipridae. <i>Sylviorthorhynchus</i> is nested within <i>Leptasthenura</i> , <i>Limnoctites</i>

	<p>within <i>Cranioleuca</i>, <i>Machaeropterus</i> within <i>Pipra</i>, and <i>Tyranneutes</i> within <i>Neopelma</i>; <i>Asthenes</i>, <i>Automolus</i>, <i>Cercomacra</i>, <i>Eurylaimus</i>, <i>Hemitriccus</i>, <i>Myiophobus</i>, <i>Myrmeciza</i>, <i>Myrmotherula</i>, <i>Ochthoeca</i>, <i>Percnostola</i>, <i>Phyllomyias</i>, <i>Schizoeaca</i>, <i>Synallaxis</i>, <i>Upucerthia</i>, <i>Xenopipo</i>, <i>Xiphorhynchus</i>, <i>Xolmis</i> are paraphyletic.</p> <p>References for deep branching and small families (298-318), relationships within Conopophagidae are after pers. comm. of H. Batalha Filho; additional references for Furnariidae including Dendrocolaptinae (319-332), Thamnophilidae (330-339), and Tyrannidae (340-358)</p>
Oscines	<p><i>Cinclosoma</i> and <i>Ptilorrhoa</i> are outside Psophodidae, and form a clade more basal in the Oscines; <i>Mohoua</i> and <i>Finschia</i> are outside Acanthizidae, and form a deep branch in the core Corvoidea. <i>Monachella</i> is nested within <i>Microeca</i>, and <i>Tregellasia</i> within <i>Eopsaltria</i> (Petroicidae).</p> <p>References for deep branching and small families (63, 65, 359-383); for more specific additional references, see major clades listed below (Meliphagida, core Corvoidea, and Passerida; for each of these clades, all families included in it are named for greater clarity)</p>
Meliphagida	<p><i>Origma</i> is nested within <i>Sericornis</i>, and <i>Conopophila</i> and <i>Lichenostomus</i> are paraphyletic.</p> <p>References for Acanthizidae, Dasyornithidae, and Pardalotidae (384-386); Maluridae (387, 388); Meliphagidae (389-392)</p>
Core Corvoidea	<p><i>Rhagologus</i> is outside Pachycephalidae and in a polytomy with Aegithinidae and Pityriasiidae; <i>Alaeadryas</i>, <i>Oreocica</i> and <i>Pitohui cristatus</i> are outside Pachycephalidae, and form a basal clade; <i>Pitohui dichrous</i> and <i>P. kirhocephalus</i> are included in Oriolidae, not Pachycephalidae; <i>Bias</i> and <i>Megabyas</i> are outside Platysteiridae, <i>Philentoma</i> is outside Tephrodornithidae, and these three are in a basal polytomy near Vangidae; <i>Platylophus</i> is outside Corvidae, in a polytomy basal to the Corvidae-Laniidae clade; <i>Lamprolia</i> is outside Monarchidae, <i>Chaetorhynchus</i> outside Dicruridae, and these two form a clade that is sister to Rhipiduridae.</p> <p><i>Lophorina</i> is nested within <i>Ptiloris</i>, and <i>Metabolis</i> within <i>Monarcha</i>; <i>Chlorophoneus</i>, <i>Colluricincla</i>, <i>Coracina</i>, <i>Cyanocorax</i>, <i>Cyanolyca</i>, <i>Symposiarchus</i> and <i>Urocissa</i> are paraphyletic.</p> <p>References for deep branching and Aegithinidae, Artamidae, Corcoracidae, Cracticidae, Machaerirhynchidae, Neosittidae, Pityriasiidae, Platysteiridae, Prionopidae, Psophodidae, and Tephrodornithidae (393-398); Campephagidae (399-401); Corvidae (402-416); Dicruridae (72, 417); Malaconotidae (418-420); Monarchidae (421-425); Laniidae (426-430); Oriolidae and</p>

	Pachycephalidae (401, 431-435); Paradisaeidae (436-439); Rhipiduridae (440, 441); Vangidae (442-445); Vireonidae (446-451)
Passerida	<p>Timaliidae as defined by the taxonomy is polyphyletic, and in our phylogeny therefore includes Sylviidae and Zosteropidae; Promeropidae only contains <i>Promerops</i>, while <i>Modulatrix</i>, <i>Arcanator</i> and <i>Kakamega</i> form the Modulatricidae, both at the base of the Passeroidea; <i>Cephalopyrus</i> is provisionally placed outside Remizidae, in a polytomy with Remizidae and Paridae; <i>Coereba</i> is included within Thraupidae, instead of being in its own family; <i>Hylia</i> and <i>Pholidornis</i> are outside Cettidae, as a clade in a more basal polytomy; <i>Microligea</i> is outside Parulidae, and is sister to <i>Xenoligea</i>; <i>Pnoepyga</i> is outside Timaliidae, and is placed as sister to the Megaluridae-Donacobiidae-Bernieridae clade; <i>Rhabdornis</i> is included within Sturnidae, instead of being in its own family; <i>Salpornis</i> is outside Certhiidae, and is sister to Sittidae; <i>Saltator</i> is outside Cardinalidae as sister to Thraupidae, except for <i>Saltator rufiventris</i> which is included in Thraupidae; <i>Spindalis</i> is outside Thraupidae, and <i>Terestistris</i> is outside Parulidae, and both form a clade that is sister to <i>Icteria-Zeledonia</i>-Parulidae.</p> <p><i>Alethe</i>, <i>Brachypteryx</i>, <i>Heinrichia</i>, <i>Heteroxenicus</i>, <i>Myophonus</i>, and <i>Pseudalethe</i> are included in Muscicapidae, not Turdidae; <i>Amaurospiza</i>, <i>Piranga</i>, <i>Habia</i>, and <i>Chlorothraupis</i> are in Cardinalidae, not Thraupidae; <i>Chlorospingus</i> is in Emberizidae, not Thraupidae; <i>Grandala</i> and <i>Pinarornis</i> are in Turdidae, not Muscicapidae; <i>Graueria</i> is in Acrocephalidae, not Cettidae; <i>Gubernatrix</i>, <i>Porphyrospiza</i>, and <i>Paroaria</i> (Emberizidae), and <i>Pakerthraustes</i> (Cardinalidae) are included in Thraupidae; <i>Histurgops</i>, <i>Philetairus</i>, <i>Plocepasser</i>, and <i>Pseudonigrita</i> are in Ploceidae, not Passeridae; <i>Hypocryptadius</i> is in Passeridae, not Zosteropidae; <i>Malia</i> (Pycnonotidae) and <i>Nesillas</i> (Acrocephalidae) are included in Megaluridae; <i>Robsonius</i> is in Megaluridae, not Timaliidae; <i>Scotocerca</i> is in a basal position in Cettidae, not Cisticolidae.</p> <p>For lists of contained paraphyletic genera, of contained families and of references additional to the ones cited in Passeriformes or Oscines, see the six major clades listed below.</p>
Sylvoidea	<p><i>Chamaea</i> is nested within <i>Paradoxornis</i>, <i>Crosslyeia</i> within <i>Xanthomixis</i>, <i>Haplochelidon</i> within <i>Notiochelidon</i>, <i>Poliolais</i> within <i>Camaroptera</i>, <i>Spizixos</i> within <i>Pycnonotus</i>, and <i>Strophocincla</i> within <i>Trochalopteron</i>.</p> <p><i>Alophoixus</i>, <i>Andropadus</i>, <i>Bradypterus</i>, <i>Cettia</i>, <i>Chlorocichla</i>, <i>Cisticola</i>, <i>Heterophasia</i>, <i>Ixos</i>, <i>Locustella</i>, <i>Lophozosterops</i>, <i>Macrosphenus</i>, <i>Megalurus</i>, <i>Parus</i>, <i>Phylloscopus</i>, <i>Pomatorhinus</i>, <i>Prinia</i>, <i>Seicercus</i>, <i>Speirops</i>, <i>Stachyris</i>, <i>Sylvia</i>, <i>Tesia</i>, <i>Turdoides</i>,</p>

	<i>Yuhina</i> , and <i>Zosterops</i> are paraphyletic. Acrocephalidae (452-458), Aegithalidae (459); Alaudidae (460-463); Bernieridae, Donacobiidae, and Megaluridae (464-468); Cettidae (469-473); Cisticolidae (465, 474-476); Hirundinidae (477-481); Hyliotidae; Nicatoridae; Panuridae; Paridae and Remizidae (482-495); Phylloscopidae (496-507); Pycnonotidae (508-516); Stenostiridae (440, 517); Timaliidae including Sylviinae and Zosteropinae (450, 467, 518-539)
Reguloidea	Regulidae (540-542)
Bombycillidea	Bombycillidae (543); Dulidae; Hylocitreidae; Hypocoliidae; Mohoidae; Ptilogonatidae
Certhoidea	<i>Thryothorus</i> and <i>Troglodytes</i> are paraphyletic. Certhiidae (544); Polioptilidae (545); Sittidae (546, 547); Tichodromidae; Troglodytidae (548-555)
Muscicapoidea	<i>Nesocichla</i> and <i>Psophocichla</i> are nested within <i>Turdus</i> ; <i>Basilornis</i> , <i>Cercomela</i> , <i>Copsychus</i> , <i>Cossypha</i> , <i>Erithacus</i> , <i>Muscicapa</i> , <i>Myadestes</i> , <i>Luscinia</i> , and <i>Oenanthe</i> are paraphyletic. Buphagidae; Cinclidae (556-558); Muscicapidae (440, 559-582); Mimidae and Sturnidae (583-594); Turdidae (348, 595-608)
Passeroidea	<i>Chlorothraupis</i> is nested within <i>Habia</i> , <i>Neospiza</i> within <i>Crithagra</i> , <i>Plectrophenax</i> within <i>Calcarius</i> , and <i>Pyrgilauda</i> within <i>Montifringilla</i> . <i>Aimophila</i> , <i>Amandava</i> , <i>Anthreptes</i> , <i>Arremon</i> , <i>Atlapetes</i> , <i>Cacicus</i> , <i>Carpodacus</i> , <i>Cinnyris</i> , <i>Conirostrum</i> , <i>Cyanocompsa</i> , <i>Cyanomitra</i> , <i>Dendroica</i> , <i>Dicaeum</i> , <i>Geothlypis</i> , <i>Hedydipna</i> , <i>Hemispingus</i> , <i>Loxigilla</i> , <i>Melozone</i> , <i>Nectarinia</i> , <i>Neochmia</i> , <i>Oporornis</i> , <i>Oryzoborus</i> , <i>Parula</i> , <i>Phrygilus</i> , <i>Ploceus</i> , <i>Prionochilus</i> , <i>Saltator</i> , <i>Serinus</i> , <i>Sporophila</i> , <i>Tachyphonus</i> , <i>Tangara</i> , <i>Thraupis</i> , <i>Tiaris</i> , <i>Vermivora</i> , and <i>Wilsonia</i> are paraphyletic. Calciidae (609), Cardinalidae and Thraupidae (610-631); Chloropseidae and Irenidae (632); Dicaeidae (633); Emberizidae (634-649); Estrildidae and Viduidae (650-660); Fringillidae (661-684); Icteridae (685-698); Modulatricidae; Motacillidae (699-709); Nectariniidae (710-713); Parulidae (714-722); Passeridae (723-726); Ploceidae (727-729)

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