SPECIAL PAPER

A framework for delineating biogeographical regions based on species distributions

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ABSTRACT

Aim Biogeographical regionalizations, such as zoogeographical regions, floristic kingdoms or ecoregions, represent categorizations central to many basic and applied questions in biogeography, ecology, evolution and conservation. Traditionally established by experts based on qualitative evidence, the lack of transparency and quantitative support has set constraints on their utility. The recent availability of global species range maps, novel multivariate techniques and enhanced computational power now enable a quantitative scrutiny and extension of biogeographical regionalizations that will facilitate new and more rigorous uses. In this paper we develop and illustrate a methodological roadmap for species-level biogeographical regionalizations at the global scale and apply it to mammals.

Location Global.

Methods We explore the relative usefulness of ordination and clustering methods and validation techniques. The performance of nine different clustering algorithms is tested at different taxonomic levels. The grain of regionalization (i.e. the number of clusters) will usually be driven by the purpose of the study, but we present several approaches that provide guidance.

Results Non-metric multidimensional scaling offers a valuable first step in identifying and illustrating biogeographical transition zones. For the clustering of regions, the nine different hierarchical clustering methods varied greatly in utility, with UPGMA (unweighted pair-group method using arithmetic averages) agglomerative hierarchical clustering having consistently the best performance. The UPGMA approach allows a tree-like phenetic representation of the relative distances of regions and can be applied at different levels of taxonomic resolution. We find that the new quantitative biogeographical regions exhibit both striking similarities to and differences from the classic primary geographical divisions of the world's biota. Specifically, our results provide evidence that the Sahara, northern Africa, the Arabian Peninsula and parts of the Middle East should be regarded as part of the Afrotropics. Further, the position of the New Guinean continental shelf, Lydekker's Line, is supported as an appropriate border to separate the Oriental and Australian regions.

Main conclusions We propose that this sort of new, quantitative delineation and relationship assessment across taxonomic and geographical grains is likely to offer opportunities for more rigorous inference in historical and ecological biogeography and conservation.

Keywords

Biogeography, cluster analysis, conservation biogeography, faunistic resemblance, mammals, multivariate methods, ordination, regionalization, zoogeographical realms.

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INTRODUCTION

Akin to taxonomy seeking to group species into higher taxa, a central aim in biogeography is to classify the world's biota into meaningful geographical units for analysis (Hengeveld, 1990; Lomolino *et al.*, 2006; Mackey *et al.*, 2008; Escalante, 2009). These so-called biogeographical regionalizations represent fundamental abstractions of the geographical organization of life on Earth in response to past or current physical and biological forces. Biogeographical regionalizations thus provide spatially explicit frameworks for many basic and applied questions in historical and ecological biogeography, evolutionary biology, systematics and conservation (Morrone, 2009). While the delineation of biogeographical regions and centres of endemism as well as the analysis of their historical relationships have been traditionally regarded as a matter of historical or evolutionary biogeography, biogeographical regionalizations also fulfil pragmatic purposes in many other disciplines. For instance, they may determine the extent of local to regional-scale ecological, evolutionary, taxonomic or comparative studies. In the historical biogeography and evolutionary literature, biogeographical regions or areas of endemism are used as geographical templates to test hypotheses regarding the historical relationships among areas, e.g. using cladistic approaches in the form of area cladograms (Nelson & Platnick, 1981; Rosen, 1988; Morrone & Crisci, 1995; Humphries & Parenti, 1999). Often such historical biogeographical analyses are performed with simple acceptance of a geographical delineation of the data that is predetermined by the source (e.g. ecoregions, district-level information). But sometimes areas of endemism (i.e. areas characterized by the congruent distribution of at least two species) or unique regions are also geographically delineated, for example using parsimony analysis of endemicity (PAE) or related approaches (Rosen, 1978, 1988; Nelson & Platnick, 1981; Morrone & Crisci, 1995; Linder, 2001; Morrone & Escalante, 2002; Szumik *et al.*, 2002; Szumik & Goloboff, 2004). Recently, biogeographical regions have found increasing use in macroecological investigations of species richness or other macroecological patterns as a way to capture regional idiosyncrasies and historical contingencies above and beyond present-day environmental correlates (Qian & Ricklefs, 2000; Hawkins *et al.*, 2003; Beck *et al.*, 2006a; Buckley & Jetz, 2007; Davies *et al.*, 2007; Kreft & Jetz, 2007; Hortal *et al.*, 2008). Biogeographical regionalizations also represent useful frameworks central to conservation priority-setting, for example to identify unique assemblages (de Klerk *et al.*, 2002). In the absence of quantitative regionalizations, pseudo-biogeographical divisions based on vegetation structure have been used extensively for broad-scale conservation analyses (Olson *et al.*, 2001; Lamoreux *et al.*, 2006).

Early biogeographical regionalizations based on species distributions date back to the very foundations of biogeography, when 19th-century naturalists started to describe global patterns of vegetation zones or relationship between climate, plant and animal life (e.g. Buffon, 1761; von Humboldt, 1806; de Candolle, 1855). The first global biogeographical regionalization based on the similarity of faunal assemblages was proposed by Sclater (1858) for passerine birds. This seminal work inspired Alfred Russel Wallace, who adopted Sclater's scheme with some modifications for the global mammal fauna (Wallace, 1876). Later, Wallace (1894) also provided a basic definition for biogeographical regions: 'Zoological regions are those primary divisions of the earth's surface of approximately continental extent, which are characterised by distinct assemblages of animal types.' Based on the two criteria of endemism and area, Wallace suggested that only endemism above the level of genera is informative for identifying biogeographical regions. More generally, biogeographical delimitations should maximize the homogeneity in taxonomic composition within regions while maximizing the differences between regions (Stoddart, 1992). Wallace was probably also the first to realize that a hierarchical system of biogeographical units would be needed to incorporate natural differences in faunal resemblance below the level of zoogeographical regions. Consequently, Wallace divided each of the six global regions into four distinct subregions. Reflecting the limited knowledge about species distributions and phylogenetic relationships at the time, Sclater's and Wallace's biogeographical regionalizations were based on intuition informed by extensive taxonomic and faunistic expertise. A major drawback of these early works is that the exact criteria for how to recognize and delineate biogeographical units were only loosely defined. Later, the Armenian plant taxonomist and biogeographer Takhtajan (1978, 1986) proposed a hierarchical biogeographical system for plants and, based on levels of endemism, criteria for how to distinguish biogeographical units at different levels in the hierarchy.

These seminal works had a great impact on the foundation of biography as a discipline (Nelson, 1978; Lomolino *et al.*, 2006). With growing knowledge about species distributions, updated summary information on species richness, endemism and faunistic resemblance has been assembled and analysed within the classic Wallace scheme (Chapin, 1923; Smith, 1983; Cole *et al.*, 1994; Newton & Dale, 2001). Furthermore, various refinements have been proposed, many of them addressing delineations of subregions, districts etc. within classic Wallace regions (e.g. Chapin, 1923; Hagmeier & Stults, 1964; Hagmeier, 1966; Hershkovitz, 1969; Crowe & Crowe, 1982) or boundaries and transition zones between regions, e.g. between the Oriental and Australian realm (e.g. Mayr, 1944; Simpson, 1977; Vane-Wright, 1991; Beck *et al.*, 2006b). Overall, the largely non-replicable nature of these approaches has also led to considerable confusion and ongoing disagreement (Cox, 2001; Morrone, 2002; Fig. 1), setting constraints on their utility. Recently, Cox (2001) identified conceptual inconsistencies in the traditional approaches (Fig. 1a,c), and similar fundamental questions have repeatedly been raised: How many regions are there? Where should boundaries be drawn? What are the relationships between different biogeographical regions?
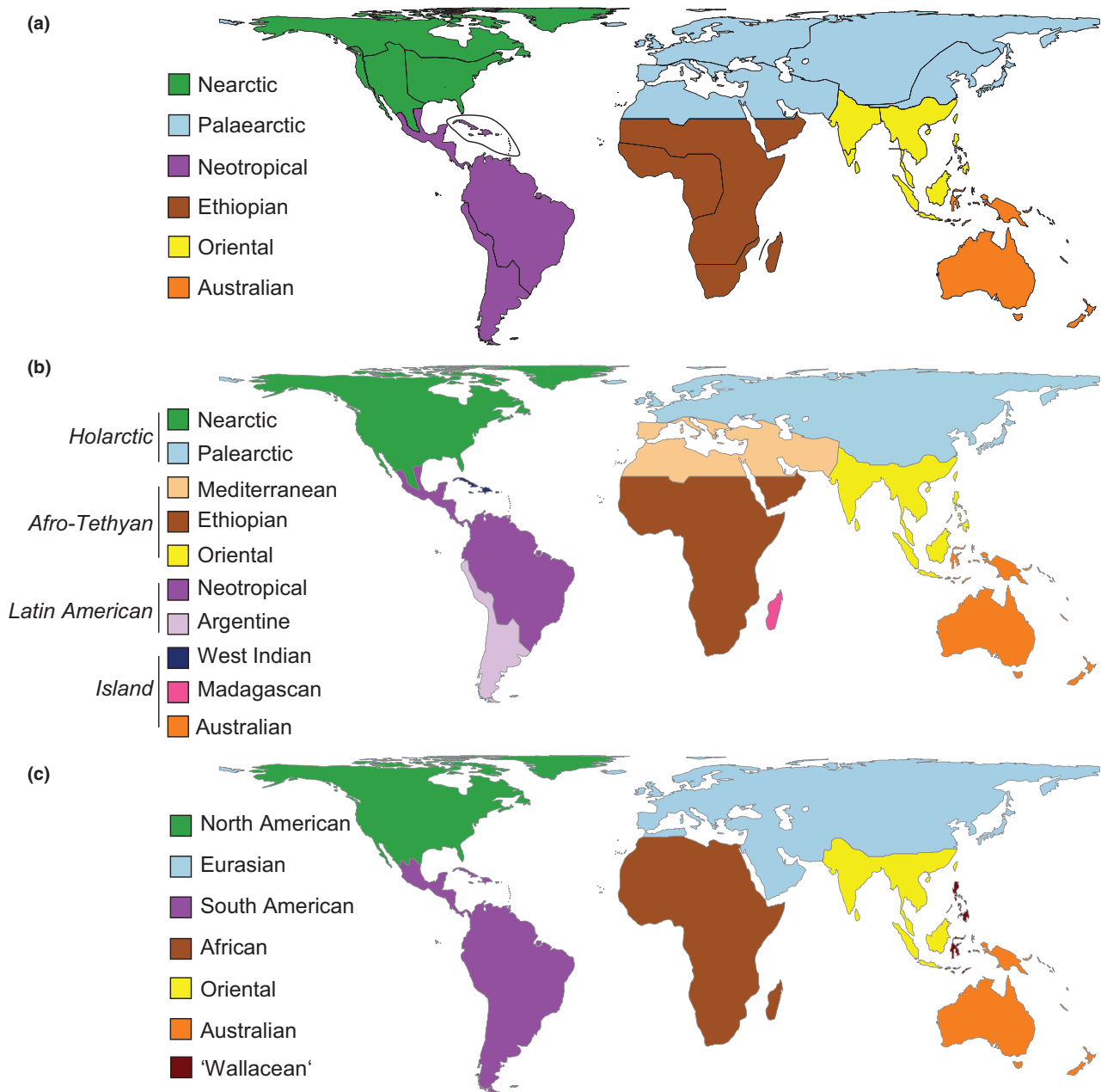
Figure 1 A mélange of zoogeographical classifications. (a) The classical zoogeographical regions as proposed by Wallace (1876). Black boundaries within the six coloured regions demarcate the 24 Wallacean subregions. (b) Smith (1983) used the occurrences of mammal families within these subregions and applied non-metric multidimensional scaling (NMDS) to merge some of them and to investigate phenetic relationships. (c) Cox (2001) identified inconsistencies in the Wallacean classification, shifted borders and proposed simplified names. Maps were redrawn from the original publications and projected using the Behrmann projection. Names follow the original sources.

The lack of sufficiently detailed data at broad geographical scales has long hampered further progress in analysing and refining biogeographical regionalizations and has led to the extensive use of maps of broad vegetation types, biomes or climate classifications as pragmatic shortcuts to define biogeographical provinces and ecoregions. This ecoregional approach is based on the assumption that faunal assemblages show a strong association with vegetation structure (Vestal, 1914; Dasmann, 1972, 1974; Udvardy, 1975; Bailey & Hogg, 1986; Olson *et al.*, 2001), which in turn is primarily determined by

macroclimate (Holdridge, 1947; Woodward, 1987). Similar concepts are still used in global-scale biogeography, as for example, partially, in the WWF ecoregions (Olson *et al.*, 2001).

Different schools and traditions in biogeography – as well as varying extent, grain and quality of data – have left the biogeographical regions of the world ambiguously defined (Cox, 2001; Morrone, 2002). Biogeographical regionalizations can be based on discontinuities of ecologically relevant attributes of the abiotic environment or vegetation structure (e.g. bioclimatic zones, biomes; Hargrove & Hoffman, 2005),

Table 1 Examples of broad-scale biogeographical studies employing different quantitative methods towards some form of biogeographical regionalization.

Reference	Taxon	Taxonomic level	Geographical extent	Geographical grain	Clustering	Ordination	Methods	Dissimilarity measure
Beck et al. (2006b)	Sphingid moths	Species	South East Asia	Islands of varying sizes	x		SL	Preston
Birks (1976)	Ferns (pteridophytes)	Species	Europe	5° lat × 6° long grid cells	x	x	Ward, PCoA	Jaccard
Conran (1995)	Plants (Liliiflorae)	Families, subfamilies, tribes	Global	OGUs of varying sizes	x	x	UPGMA, NMDS, PAE	Kulczynski
de Klerk et al. (2002)	Birds	Species	Sub-Saharan Africa	1 × 1° grid cells	x		UPGMC	Bray–Curtis
Fattorini (2002)	Tenebrionid beetles	Species	Aegean islands	Islands of varying sizes	x	x	PAE, UPGMA, NMDS	Dice, Jaccard, Kulczynski 2, Ochiai
Hagmeier & Stults (1964)	Mammals	Species	North America	OGUs of varying sizes	x		WPGMA	Jaccard
Hagmeier (1966)	Mammals	Species	North America	OGUs of varying sizes	x		WPGMA	Jaccard
Heikinheimo et al. (2007)	Mammals	Species	Europe	50 × 50 km grid cells	x		k-means and probabilistic expectation maximization (EM)	Euclidean
How & Kitchener (1997)	Snakes	Genera, species	Indonesia	Islands of varying sizes	x	x	PCA, UPGMA	Sorensen, Simpson
Linder et al. (2005)	Vascular plants	Species	Sub-Saharan Africa	1 × 1° grid cells	x	x	UPGMA, NMDS	Jaccard
McLaughlin (1989)	Vascular plants	Species	Western United States	OGUs of varying sizes		x	Factor analysis	Otsuka
Morrone & Escalante (2002)	Mammals	Species	Mexico	0.5 × 0.5°, 1 × 1° grid cells, ecoregions and biogeographical OGUs of varying sizes	x		PAE	NA
Nimis & Bolognini (1993)	Plants	Species	Europe	28,900 km²	x		Ward	Euclidean
Patten & Smith-Patten (2008)	Birds	Species	Northern Neotropics	Field site inventories	x		UPGMA	Jaccard / Bray–Curtis
Peterson et al. (2000)	Birds	Species	Philippines	Islands of varying sizes	x		UPGMA	Simpson
Procheş (2005)	Bats	Genera, species	Global	15 × 15° grid cells	x		UPGMA	Bray–Curtis
Procheş (2006)	Bats, conifers	Species	Global	15 × 15° grid cells	x		UPGMA	Bray–Curtis
Rojas-Soto et al. (2003)	Birds	Species	Baja California	7 × 7 km grid cells	x		PAE	NA
Ron (2000)	Anurans, lizards, primates	Species	Neotropics	OGUs of varying sizes	x		PAE	NA
Samyn & Tallon (2005)	Holothuroids	Species	Indian Ocean	1 × 1° grid cells	x		UPGMA, PAE	Dice, Kulczynski, Jaccard
da Silva & Oren (1996)	Primates	Species	Amazonia	OGUs of varying sizes	x		PAE	NA
Smith (1983)	Mammals	Families	Global	24 OGUs of very large and varying size		x	NMDS	Simplified association measure

Table 1 Continued

Reference	Taxon	Taxonomic level	Geographical extent	Geographical grain	Clustering	Ordination	Methods	Dissimilarity measure
Smith & Bermingham (2005)	Fish	Species	Mesoamerica	Drainage basins	x		UPGMA	Euclidean, Jaccard
Sneath (1967)	Conifers	Genus	Global	c. 20 × 20° grid cells		x	Ordination (factor analysis)	NA
Unmack (2001)	Fish	Species	Australia	OGUs of varying sizes	x	x	Hierarchical clustering and NMDS	Dice, Ochiai, Kulczynski, Jaccard
Williams (1996)	Bumble bees	Species	Global	Equal-area grid cells: 611,000 km²	x		Divisive polythetic clustering (TWINSPAN)	NA
Williams et al. (1999)	Birds	Species	Africa	1 × 1° grid cells	x	x	Divisive polythetic clustering (TWINSPAN), Decorana ordination	NA
Xie et al. (2004)	Mammals, plants	Species	China	OGUs of varying sizes	x		Ward	Sørensen

OGU, operational geographical unit; PAE, parsimony analysis of endemicity; PCoA, principal coordinates analysis; NA, not applicable; NMDS, non-metric multi-dimensional scaling; SL, single linkage; UPGMA, unweighted pair-group method using arithmetic averages; UPGMC, unweighted pair-group method using centroids; WARD, Ward's method; WPGMA, weighted pair-group method using arithmetic averages.

discontinuities in the taxonomic composition of assemblages (e.g. zoogeographical realms or floristic kingdoms) or a combination and integration of both (e.g. ecoregions; Belbin, 1993; Mackey *et al.*, 2008). In the use of assemblage distinctiveness for identifying biogeographical realms and regions, the question of the scale (grain) of analysis is critical, yet it has been somewhat neglected in definitions to date (but see Morrone & Escalante, 2002): 'Should the delineation of regions maximize the distinctiveness of the whole regional assemblage, or of the set of local or sub-regional assemblages within the region compared to those outside?'. Given the relatively greater contribution of wide-ranging (high-occupancy) species to sub-regional assemblages and their geographically uneven distribution (Jetz & Rahbek, 2002), the resulting regions and their similarity may not be the same (Morrone & Escalante, 2002). The preferred assemblage grain may depend on the purpose of analysis, with an evolutionary biologist seeking to establish area dendrograms potentially preferring the regional-assemblage approach and ecologists instead using finer-grain assemblage data.

Given the widespread importance of global biogeographical regionalizations for heuristic and pragmatic purposes, comparatively few studies have so far tried to test the validity of global biogeographical boundaries using replicable, quantitative methods (Table 1). While these studies had already suggested the promise of multivariate methods for revealing informative biogeographical patterns, they usually remained restricted to coarse taxonomic or spatial resolution. Multivariate methods at the species level and higher spatial resolution have found greater use at regional to continental extents (e.g. Hagmeier & Stults, 1964; Nimis & Crovello, 1991; Williams *et al.*, 1999; Unmack, 2001; de Klerk *et al.*, 2002; Linder *et al.*, 2005; Heikinheimo *et al.*, 2007). Multivariate methods aim to reduce the inherent complexity of biogeographical data, and their great strength is that they give replicable results (Kent, 2006). The increasing availability of high-resolution data on species-level distributions, phylogeny and ecological attributes now opens new avenues for research at this interface between historical, ecological and applied biogeography.

In this study we present a general methodological framework to help scientists to seize on these new opportunities and evaluate the potential of ordination and clustering methods applied to gridded assemblages to illustrate, analyse and interpret complex biogeographical patterns at a global scale. We showcase these approaches and the new light they can shed on long-established biogeographical patterns using data on the global mammal fauna.

MATERIALS AND METHODS

Framework

The application of multivariate techniques to quantitatively delineate biogeographical regions involves multiple steps of analysis (Fig. 2).

1. The goals and uses of the targeted regionalization need to be defined in order to select an appropriate multivariate approach.
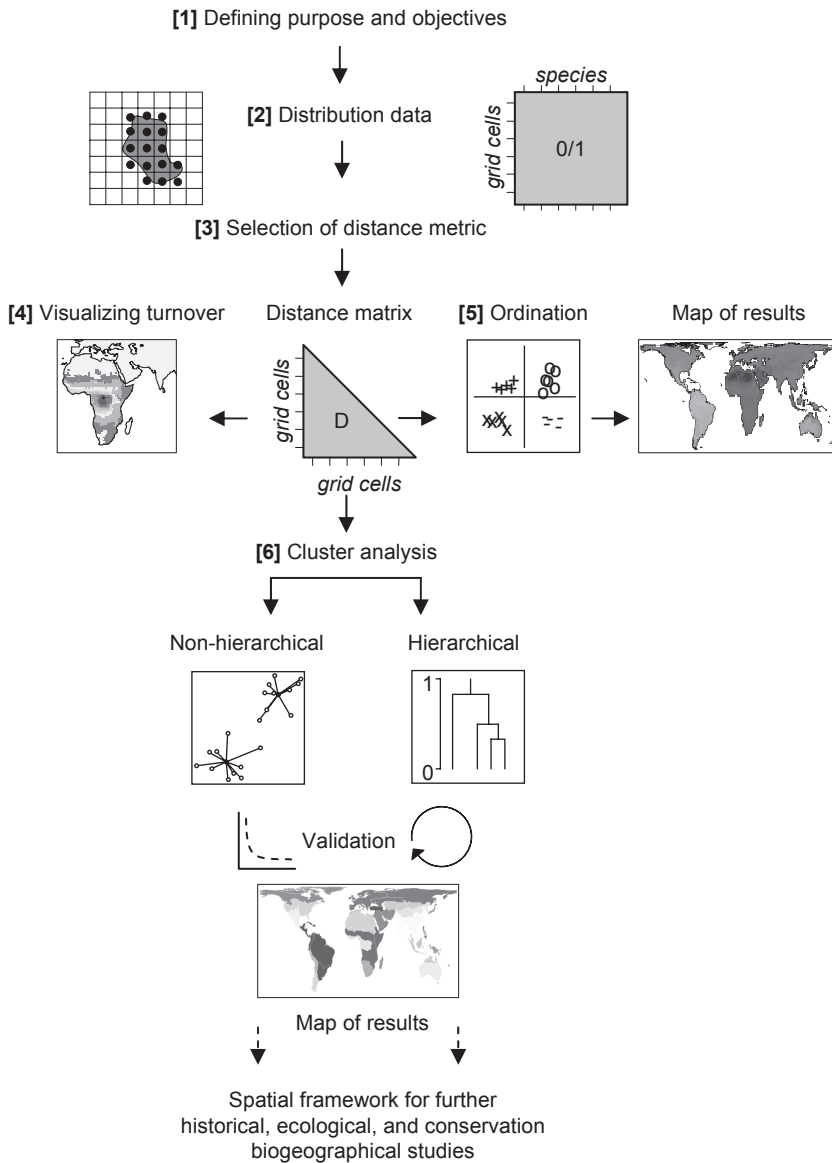
Figure 2 Conceptual diagram of analysis steps and data flow in multivariate biogeographical analyses. Numbers in brackets correspond to the analysis steps described in the text.

2. Broad-scale species distribution data (e.g. expert-opinion range maps) are selected. An analysis grain is chosen that appropriately reflects the spatial accuracy of the distribution data and that is in line with the study goals (e.g. a 100×100 km or 200×200 km equal-area grid). Species distribution data are converted into a species per site (e.g. grid cell) incidence matrix.

3. A biogeographically relevant distance metric is selected that quantifies pairwise dissimilarities of grid cell assemblages as required for multivariate methods such as ordination or clustering.

4. Dissimilarity values of the resultant distance matrix can be readily visualized by mapping the geographical pattern of turnover of focal grid cells.

5. Reducing the dimensionality of the distance matrix, for example by using non-metric multidimensional scaling, allows simultaneous visualization and mapping of the information contained in the distance matrix.

6. Cluster analyses can be applied to the distance matrix in order to form groups of similar grid cells assemblages. An optimum number of regions can be determined by information extracted from the structure of the dendrogram or from external criteria such as, for example, levels of endemism. Relationships can be visualized by combinations of colours and varying boundary widths, reflecting the topology of the dendrogram.

In the following we discuss each step in detail and in the results section showcase the implementation using global mammal data.

(1) Defining the purpose and the objectives of the study

The biogeographical objectives of a study directly affect all steps of the analysis. For instance, if a biogeographical regionalization is to be compared with an existing

classification of, for example, climate or vegetation (e.g. Heikinheimo *et al.*, 2007), a non-hierarchical clustering algorithm may be a good choice. On the other hand, if the focus is on investigating relationships among regions or if discrete groups are desired that can be named and classified, a hierarchical clustering algorithm is more appropriate. In the case of the global mammal fauna, we may be interested in deriving a meaningful hierarchical global biogeographical regionalization and in comparing these results with previous qualitative studies. The resulting classification should produce biogeographical regions with a maximum internal similarity but with maximum differences from other regions. Furthermore, speciation and biotic dispersion are thought to produce hierarchically structured assemblages (McLaughlin, 1992; Cracraft, 1994). We therefore focus on algorithms that produce discrete hierarchical groupings of clusters, acknowledging that fuzzy clustering algorithms (Jain & Dubes, 1988; Jain *et al.*, 1999) might also offer potential in biogeographical analysis.

(2) Species distribution data

Biogeographical inferences in general and quantitative regionalizations in particular are affected by incomplete taxonomic and distributional knowledge (the so-called Linnean and Wallacean shortfalls; Brown & Lomolino, 1998; Lomolino, 2004; Whittaker *et al.*, 2005). For the last 200 years, information on distribution of species has mostly been scattered in natural history collections, scientific publications or monographs, but it has now become increasingly available in digital formats, even at broad geographical scales (e.g. Jetz & Rahbek, 2002; Stuart *et al.*, 2004; Grenyer *et al.*, 2006; Jetz *et al.*, 2007; Schipper *et al.*, 2008).

Basically, two main types of distribution data can be used for biogeographical analyses (see Table 1). First, extent-of-occurrence maps are usually designed to depict the maximum geographical extent of a species and are usually drawn by experts based on knowledge of museum specimens, field observations or the ecological requirements of species. Extent-of-occurrence range maps thus represent a scale-dependent abstraction of a species' range (Gaston, 2003; Hurlbert & Jetz, 2007), and they are usually portrayed in the form of polygons. Second, in principle at least, point information such as museum specimen or survey data could be used, for example, together with distribution modelling techniques, to infer species geographical ranges. Due to the very limited data availability for many parts of the world and larger errors of omission (Graham & Hijmans, 2006; McPherson & Jetz, 2007), particularly in the tropics, this type of information is currently usable only for few taxa and regions. Extent-of-occurrence range maps, on the other hand, can be compromised by false presences if analysed at excessively fine grains (Hurlbert & White, 2005; Hurlbert & Jetz, 2007; Jetz *et al.*, 2008). A reasonable balance between accuracy and detail is typically obtained at around 1° or 2° latitude/longitude (*c.* 110–220 km near the equator) for the type of range maps used here (Hurlbert & Jetz, 2007). But even at this relatively fine grain size some of the fine-scale faunistic variation (e.g. between mountain ranges and nearby lowlands) might not be reflected in the distribution data and resulting classifications.

For analysis, range maps are extracted across a grid, ideally across grid cells of equal area, to avoid sampling errors associated with varying area sizes. The resulting grid cell assemblages can then easily be transformed into an incidence or presence–absence ('1'–'0') matrix where rows represent grid cells and columns represent species.

We here used the global mammal fauna as a model group to explore the effectiveness of different ordination and clustering techniques for deriving biogeographical regionalizations. Mammals have been a main focus since the early days of zoogeography (Wallace, 1876) and, together with birds, arguably represent the best-known large clade at a global scale. Recently, expert range map data for all mammal species have been assembled and distributed by the IUCN with the input of more than 1700 experts (IUCN, 2008; Schipper *et al.*, 2008). Range maps were downloaded in ESRI polygon shapefile format from the IUCN website (http://www.iucnred list.org/initiatives/mammals/description/download_gis_data). Range maps were then processed for further analyses using ArcGIS/ArcINFO scripts (ESRI, 2005). Species occurrences were extracted over an equal-area grid based on 1° longitude intervals and a grid cell area of 12,364 km^2, a grain size that should yield satisfactory accuracy (Hurlbert & Jetz, 2007). We excluded small oceanic islands and coastal grid cells with ≤ 50% land area to minimize the influence of unequal sampling area. Finally, we excluded grid cells containing fewer than five species. Such small sample sizes can potentially cause considerable distortions in similarity analyses (Lennon *et al.*, 2001; Koleff *et al.*, 2003). We also excluded marine and other fully aquatic species ($n = 125$) as well as non-native parts of species ranges as indicated in the original source. These exclusion criteria left a total of 10,709 grid cells and 4954 species (*c.* 90% of all mammal species) belonging to 1136 genera and 135 families in the analysis. Analyses were conducted at species, genus and family level, and some analyses were separately performed for volant (Chiroptera; $n = 1017$ species) and non-volant species (all non-chiropteran mammals; $n = 3937$ species) to explore putative disparities that are to be expected because of different dispersal abilities (Procheş, 2005, 2006). Presence–absence matrices (rows representing grid cells and columns representing species) were constructed for all five subsets of data (all species, volant and non-volant species, genera, families) to calculate pairwise faunistic distances among all grid cells.

(3) Distance metric

Before applying ordination and clustering methods, an appropriate metric has to be selected that measures pairwise distances between grid cell assemblages. In biogeography and ecology, a number of different beta-diversity or turnover

indices have been proposed (reviewed in Baroni-Urbani & Buser, 1976; Hubalek, 1982; Wilson & Shmida, 1984; Koleff *et al.*, 2003). Beta-diversity indices differ in their statistical properties and in what component of compositional change they measure (Koleff *et al.*, 2003). Among other considerations, choice will depend on the aims of analysis. Three broad categories of indices can be distinguished (Koleff *et al.*, 2003): indices that focus on richness gradients, on differences in species composition or on both. At the spatial scale and extent that are of interest here, two main mechanisms drive beta diversity between pairs of grid cells. First, beta diversity may arise from processes such as filtering when a grid cell assemblage is a subset of a richer regional species pool (Harrison *et al.*, 1992). Second, 'true' species turnover is the replacement of species by others along geographical gradients as a consequence of environmental, historical and spatial differences among sites (Baselga *et al.*, 2007). Previous studies most frequently used metrics as those of Sørensen/Bray–Curtis, Jaccard and Kulczynski (see Table 1), all of which are strongly affected by differences in species richness (Lennon *et al.*, 2001). This means that a change in community composition has a greater relative influence in relatively species-poor than in diverse assemblages, and if there is a large difference in richness between grid cells the obtained values from these indices will also always be large. We argue that for the purpose of biogeographical regionalizations richness-independent turnover is more informative, and therefore suggest the use of metrics that are least affected by the variation in richness.

We thus used the beta-sim index (β_{sim}), which fulfils the above-mentioned richness independence criterion (Lennon *et al.*, 2001; Koleff *et al.*, 2003; Baselga *et al.*, 2007). The β_{sim} index calculates the compositional distance between two grid cells as:

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

where a is the number of shared species (the matching component) and b and c are the number of species unique to each grid cells, respectively. β_{sim} varies between 0 (low dissimilarity, identical taxa lists) and 1 (high dissimilarity, no shared taxa). Application of this index resulted in a global matrix containing 57,335,986 pairwise distance values.

(4) Geographical visualization of turnover

The resulting distance matrix allows some straightforward geographical visualization, for example a map of dissimilarity values of a focal grid cell in relation to all others (Fig. 3). This illustrates patterns of faunistic resemblance and of decay in similarity across geographical and environmental distances and helps to visualize gradients of similar faunistic composition and the location of biogeographical transitions. In a different approach, which considers all grid cells simultaneously, neighbourhood indices of beta diversity are mapped and calculated (Williams, 1996; McKnight *et al.*, 2007; Buckley & Jetz, 2008; Melo *et al.*, 2008). Mapping of these values results

in patterns of regional turnover of species assemblages and helps to identify regions with particularly high rates of compositional change. We selected three well-known biogeographical transition zones to demonstrate this geographical visualization of the distance matrix: Nearctic–Neotropical, Sahara–Congo, Temperate–Tropical East Asia (Fig. 3).

(5) Ordination

Ordination is a widely used technique to produce low-dimensional projections of multivariate data by arranging objects (in our case grid cell assemblages) along reduced axes based on taxonomic composition (Goodall, 1954; ter Braak, 1987; Legendre & Legendre, 1998). Ordination thus represents a useful, heuristic approach for visualizing a global assemblage distance matrix and for studying relationships of geographical regions according to their taxonomic composition. Ordination methods have also found application in broad-scale biogeography (Table 1), for example to establish Gondwanan signatures in the modern distribution of conifer genera (Sneath, 1967), to investigate faunistic relationships across the 24 Wallacean subregions for mammal families (Smith, 1983; Fig. 1b) or to investigate biogeographical transition zones in Afrotropical birds (Williams *et al.*, 1999).

Non-metric multidimensional scaling (NMDS) is regarded as the most robust unconstrained ordination method and has several advantages over other ordination strategies (Minchin, 1987). The basic objective of NMDS is to plot dissimilar objects that are far apart and similar objects close to one another in ordination space (Legendre & Legendre, 1998). In contrast to principal components analysis (PCA) or principal coordinates analysis (PCoA), NMDS makes no underlying assumptions about normality or linearity of the underlying data (Ludwig & Reynolds, 1988), can use any kind of distance matrix and can summarize data more effectively into fewer dimensions (Legendre & Legendre, 1998). NMDS requires the user to specify a number of m dimensions to which the dataset is reduced. The n objects are then placed and ranked in this pre-chosen space and an initial configuration of the objects in m-dimensional ordination space is computed. This configuration is then used for an iterative rearrangement process.

We performed NMDS ordinations at family, genus and species level. Pairwise distances were calculated using β_{sim}. We performed NMDS as recommended by Minchin (1987) and as implemented in the function 'metaMDS' of the vegan library (Oksanen *et al.*, 2006) in the statistical software R (R Development Core Team, 2005). One hundred random starts were used to find a stable solution and to avoid local minima. In order to facilitate interpretation, the function metaMDS a posteriori standardizes the scaling of the ordination results by moving the origin to the average of the axes and by rotating the configuration so that the variance of points is maximized on the first axis (Oksanen *et al.*, 2006). Stress values, i.e. the sum of the squared differences between fitted and original distances, were used to assess how well the configuration of

points in reduced ordination space matches the original distance matrix (Legendre & Legendre, 1998). Values range from 0 to 1, with smaller values indicating better fits (Legendre & Legendre, 1998).

NMDS results were then mapped by assigning a colour to each grid cell according to its position in the two-dimensional ordination space. Therefore, the ordination was rescaled to axes ranging from 0 to 1 and rotated to reach maximal congruence among the three data sets. Rotation, rescaling and transformation is possible with NMDS results as the ordination axes as such have no meaning and only the relative position of points in ordination space matters. The colours blue, green, yellow and red were assigned to the four corners of the two-dimensional ordination plot in clockwise order from the origin. Interjacent colour values were interpolated in 100 steps along each axis resulting in 10,000 colours. NMDS coordinates were assigned to the next colour value that was also used for the mapping of a respective grid cell (Fig. 4).

(6) Cluster analysis

Cluster analyses are part of the larger family of unsupervised learning methods in exploratory data analysis and the central
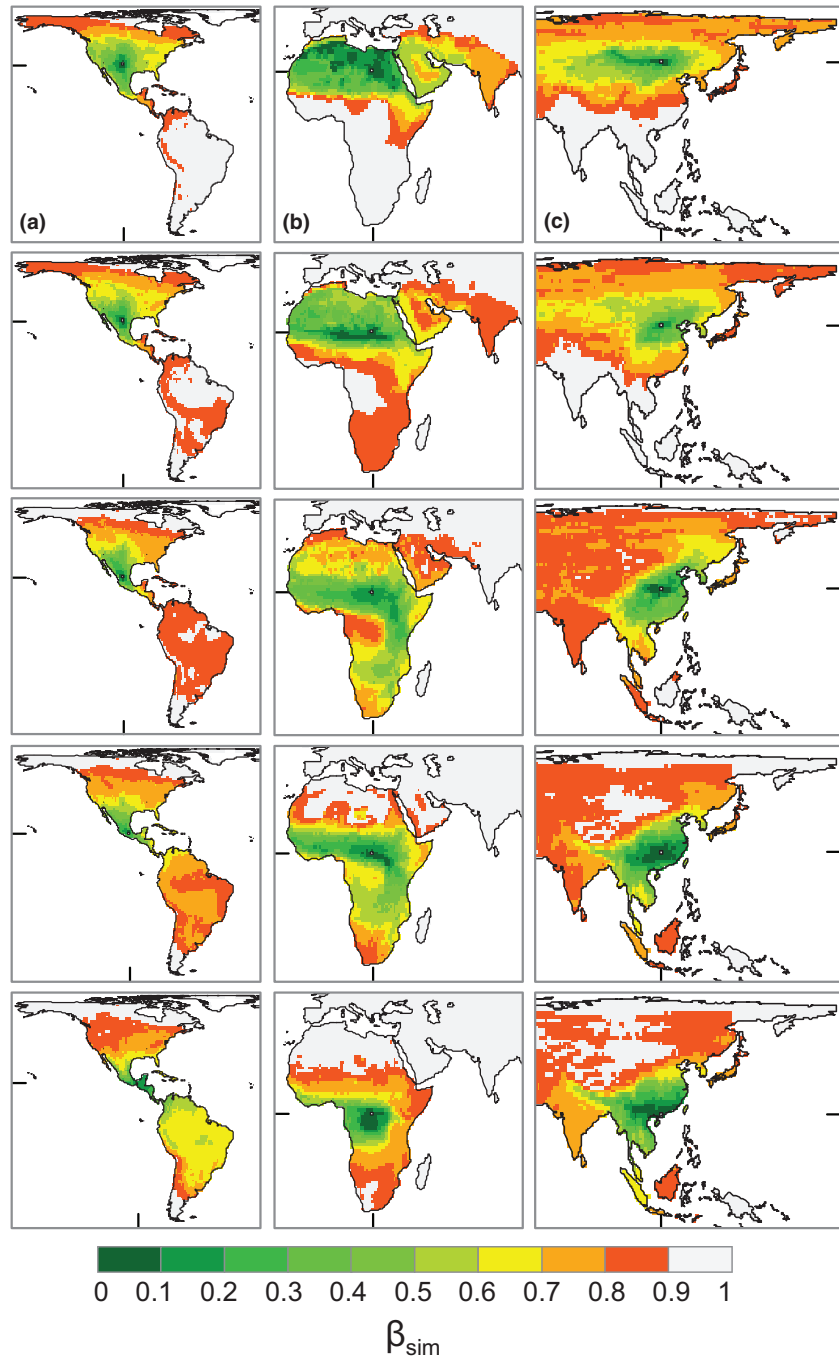

Figure 3 Maps of mammalian species turnover of focal grid cells in three north–south biogeographical transition zones (columns): (a) Nearctic–Neotropics, (b) Sahara–Congo basin, (c) Eastern Palaearctic–Oriental. β_{sim} values for a focal grid cell (marked in white and position highlighted with tick marks at map margins) were extracted and mapped from the global distance matrix. Green colour shades indicate grid cells that contain similar assemblages compared to the focal cell. Maps are in the Behrmann projection.

aim is to classify similar objects into respective groups. Such a grouping of objects is an essential prerequisite for naming them (Legendre & Legendre, 1998). An important question to ask before applying or performing clustering is whether or not one expects discontinuities to exist in the data (Legendre & Legendre, 1998). In the simplest biogeographical world, all species would be endemic to a region without any blending of faunas into other regions. At the global scale this is obviously not the case (compare Figs 3 & 4). On the other hand, faunal assemblages can also be distinct in composition without necessarily having high proportions of endemics. Due to the long geological and evolutionary isolation of the major landmasses and to dispersal limitation (Briggs, 1989; Cox & Moore, 1993; Cox, 2000), one would a priori expect them to harbour very distinct mammal faunas. Another process leading to discontinuous distribution of species and assemblages is

their strong association with climate and vegetation through space and time (Graham *et al.*, 1996; Fortelius *et al.*, 2002). However, such discontinuities may be diluted in broad-scale ecological transition zones or in regions where biota with long separate histories mix (Marshall *et al.*, 1982; Stehli & Webb, 1985; Vermeij, 1991).

Two main families of clustering approaches can be distinguished.

1. Non-hierarchical or partitioning algorithms divide the data set into an integer number of *k* clusters. Well-known algorithms are *k*-means or partitioning around medoids algorithms (PAMs; Kaufman & Rousseeuw, 1990). A limitation of these algorithms is that they require the user to specify a number of groups and do not yield topological relationships of clusters. We therefore did not consider partitioning algorithms here.
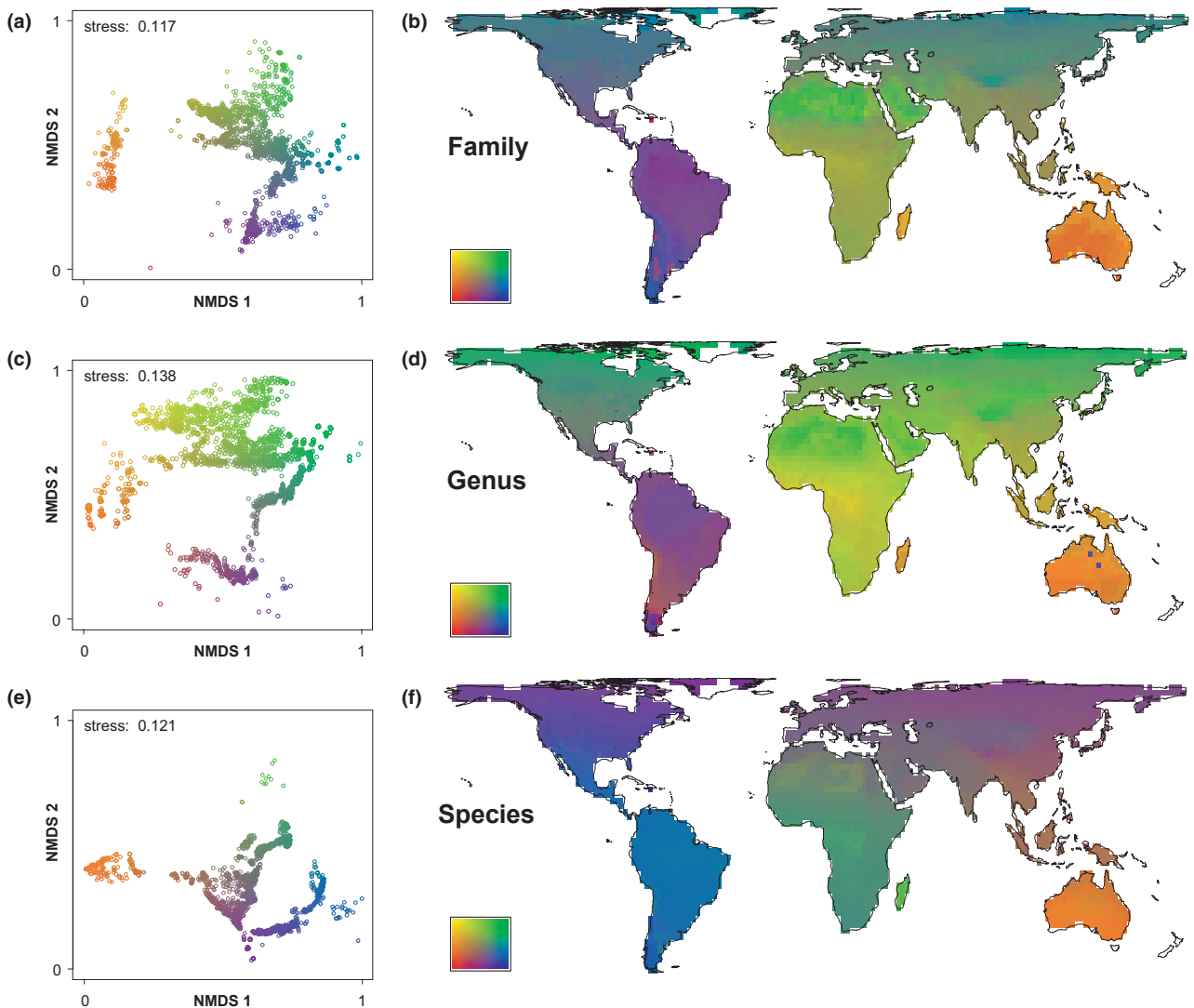

Figure 4 Global biogeographical patterns of mammals inferred from non-metric multidimensional scaling (NMDS) ordination based on β_{sim} distance matrices at (a, b) family, (c, d) genus and (e, f) species level. Each dot in the scatter plots represents a grid cell assemblage. Colours of points in the scatter plots and of grid cells in the maps are identical. Ordination plots were rotated and rescaled to facilitate comparability. Maps are in the Behrmann projection.

2. In contrast, hierarchical methods construct a hierarchy of clusters. This is particularly useful for biogeographical purposes, because biogeographical regions are hierarchically arranged (McLaughlin, 1992; Escalante, 2009) and the relative relationships between regions can be highly informative about underlying biogeographical connections and processes.

Two main categories of hierarchical algorithms exist.

1. Agglomerative clustering algorithms start with each object forming its own cluster groups. The most similar objects are then repeatedly fused according to a linkage function into higher-level clusters until all objects form one group (Kaufman & Rousseeuw, 1990).

2. Divisive algorithms start with all objects in one cluster. Groups are repeatedly separated until each object is in its own cluster (Kaufman & Rousseeuw, 1990).

The resulting dendrogram provides a basis for addressing two important questions related to the interpretation of clustering results (Fielding, 2007): (1) do clusters represent real or useful groups and (2) how many clusters are in the data set? However, it should be noted that the clustering approach establishes only statistical patterns and does not allow direct evolutionary inference on areal relationships and historical patterns of vicariance and dispersal. Instead, through the delineation of regions, clustering provides a starting point for other quantitative, e.g. cladistic, approaches in historical biogeography. The clustering approach is different from the parsimony analysis of endemicity (PAE; Rosen, 1988; Morrone, 1994) in that it is based on whole-assemblage similarities. In contrast, PAE treats the presence and absence of taxa as character states and constructs a maximum parsimony tree which is generally rooted to an outgroup devoid of all species (Morrone & Crisci, 1995; Fattorini, 2002; Morrone & Escalante, 2002). In addition to establishing historical hypotheses about areal relationships, PAE has also been used to delineate areas of endemism by identifying areas in the cladograms that are supported by two or more apomorphic changes (Morrone, 1994). Since the area of endemism concept is different from a spatially inclusive regionalization, we viewed PAE as outside the scope of this study.

The performance of clustering algorithms and linkage functions is largely determined by the characteristics of the input data; outliers, shapes and sizes of groups can affect the performance of various algorithms (Jongman et al., 1987; Jain & Dubes, 1988). In broad-scale biogeographical analyses, hierarchical clustering methods such as the unweighted pair-group method using arithmetic averages (UPGMA) or Ward's method are frequently favoured, and in most studies only a single algorithm is applied (Table 1). But little is known about the performance of various linkage functions for broad-scale distribution data and biogeographical purposes.

Thus, we first tested the performance of seven frequently used linkage functions in agglomerative hierarchical clustering at family, genus and species level and separately for volant and non-volant species: UPGMA, UPGMC (unweighted pair-group method using centroids), WPGMA (weighted pair-group method using arithmetic averages), WPGMC

(weighted pair-group method using centroids), Ward's method, single (SL) and complete linkage (CL) (Table 2, implemented in the cluster package in statistical software R; R Development Core Team, 2005). Additionally, we constructed neighbour-joining trees (Saitou & Nei, 1987). Neighbour joining (NJ) is an iterative algorithm that seeks to identify pairs of operational units in order to minimize the total branch length of a hierarchical tree. NJ analyses were performed in PAUP* version 4.0b10 (Swofford, 2002) using the dissimilarity matrices as an input. Trees were midpoint-rooted using FigTree 1.2.2 (Rambaut, 2006-2009). In addition to these eight agglomerative clustering methods, we evaluated the DIANA-algorithm, a divisive hierarchical method, which constructs a hierarchical clustering starting with one large cluster containing all observations (Kaufman & Rousseeuw, 1990). Cluster groups are repeatedly divided until each cluster contains only a single observation. At each stage, the cluster with the largest diameter in terms of the maximum observed dissimilarity is selected and further divided (Kaufman & Rousseeuw, 1990).

The validity of clustering results was evaluated using the co-phenetic correlation coefficient (Sokal & Rohlf, 1962; Sneath & Sokal, 1973), which correlates pairwise distance from the leaves of a dendrogram to the encompassing node with the distances in the original distance matrix. It thus represents a direct measure of how much of the original information is retained in the dendrogram (Sneath & Sokal, 1973).

The choice of an adequate number of clusters is a long-standing issue in cluster analysis (Milligan & Cooper, 1985). In previous biogeographical applications, arbitrary stopping rules have been employed, e.g. a minimum number of grid cells per cluster (Williams et al., 1999), a certain level of dissimilarity (de Klerk et al., 2002; Proches, 2005) or external criteria such as the number of bioclimatic regions in a study area (Heikinheimo et al., 2007). Alternatively, in situations where the right number of cluster groups is unknown, the inspection of diagnostic graphs – such as an evaluation metric plotted against the number of clusters – offers a more rigorous, data-driven procedure (Salvador & Chan, 2004).

To determine a reasonable number of cluster groups, we inspected evaluation plots (evaluation metric plotted against number of cluster groups) based on three different metrics. The first of these is: (1) height of nodes in the dendrogram. The primary divisions in most datasets occur at rather high levels in the dendrogram with lower nodes being less informative. This is particularly the case here because many grid cells contain very similar assemblages. Alternatively, the endemicity of the biogeographical regions resulting from clustering offers additional useful information, and we assessed the following two metrics: (2) the average proportion of endemic taxa in a biogeographical region for any number of clusters; (3) the total endemism measured as the number of taxa endemic to a single biogeographical region divided by all non-endemic taxa for any number of clusters. The above-mentioned metrics plotted against the number of clusters yield scree-like evaluation plots. We applied the L-method

Table 2 Hierarchical clustering methods compared in this study.

Clustering method (common synonym)	Acronym	Short description
Unweighted pair-group method using arithmetic averages (average linkage)	UPGMA	Distance between two clusters is the average distance between all objects of each cluster
Unweighted pair-group method using centroids (centroid linkage)	UPGMC	Distance between the centroids ('mean point' or centre of gravity) of each cluster
Weighted pair-group method using arithmetic averages (McQuitty's method)	WPGMA	Distance between two clusters is the arithmetic average distance between objects of each cluster weighted by the number of objects in each cluster
Weighted pair-group method using centroids (median linkage)	WPGMC	Distance between two clusters is the Euclidean distance between their weighted centroids
Ward's method (minimum variance)	Ward	Uses an ANOVA approach and minimizes the sum of squares of any two clusters that can be formed at each step
Single linkage (nearest neighbour)	SL	Distance between two clusters is the minimum distance between all objects of each cluster
Complete linkage (furthest neighbour)	CL	Distance between two clusters is the maximum distance between all objects of each cluster
Neighbour joining	NJ	Algorithm starts by identifying the pair of grid cells with the lowest distances and constructs a node. It then calculates the distance of each of the objects in the pair to this new node. It then calculates the distance of all objects outside of this pair to the new node. Finally, the iterative algorithm starts again, considering the pair of joined neighbours as a single group and using the distances calculated in the previous step
Divisive hierarchical method	DIANA	Starting with all observations forming one single large cluster, groups are repeatedly divided until each cluster contains only a single observation. At each stage, the cluster with the largest diameter in terms of the maximum observed dissimilarity is selected (Kaufman & Rousseeuw, 1990)

algorithm proposed by Salvador & Chan (2004) to locate the position of the knee in the evaluation plots, i.e. the point of maximum curvature of the evaluation graph, which is informative to determine a useful number of clusters. Furthermore, an appropriate number of clusters often coincides with sharp drops in the evaluation metric. We hypothesize that the number of cluster groups identified by these metrics will increase with higher taxonomic rank and will be proportional to the average range sizes of taxa. Accordingly, fewer biogeographical regions are to be expected for species than for genera. We acknowledge that more advanced methods, e.g. permutation tests, resampling and dispersion measures (Milligan & Cooper, 1985; Tibshirani *et al.*, 2001), exist. In practice, a drawback of these evaluation functions is that they are computationally very expensive, and we were unable to implement such procedures for the very large matrices in our dataset.

Results from clustering were displayed in the form of dendrograms and maps. To indicate cluster memberships and relative relationships, regions were mapped using a combination of colours and varying boundary widths.

RESULTS

Geographical visualization of turnover

Two distinct patterns became apparent. First, patterns of concentric distance decay could be found and occur, for instance, in North America (Fig. 3a, row 1) or in the Congo

Basin (Fig. 3b, row 5) if focal grid cells were situated in or near the centre of a broader homogeneous zone of similar environmental conditions and similar vegetation. Second, latitudinally elongated shapes of regions with low faunistic dissimilarity were found in, for example, the Sahel (Fig. 3b, row 2) or Mongolia (Fig. 3c, row 1), suggesting relatively strong latitudinal changes in faunistic composition. While such maps offer a useful illustration for focal grid cells they do not easily permit the globally informed identification of boundaries and regions. Hence their scope for synthesis and general inference is limited.

Ordination

NMDS ordinations led to satisfactory but not perfect projections of dissimilarity matrices into two-dimensional space indicated by relatively low stress values of 0.117, 0.138 and 0.121 at the family, genus and species level, respectively (Fig. 4a,c,e). NMDS ordinations and the resulting maps showed continuous biogeographical transitions in many parts of the world, but also exhibited some marked discontinuous changes in faunistic composition (Fig. 4b,d,f). Ordination plots and resulting maps also intuitively allowed inference about the faunistic distances between and within biogeographical regions.

At the family level (Fig. 4a,b), a clear separation occurred between Australia–New Guinean grid cell assemblages and those in the adjacent Oriental region. Madagascar was clearly separated from mainland Africa but placed close to New Guinean grid cell assemblages. Sub-Saharan African and

Oriental assemblages formed distinct groups but showed relatively close resemblance to each other. The Saharan and Arabian Peninsula grid cells formed a dispersed cloud with closer affinities to Tropical Africa than to the Palaearctic. Nearctic and Palaearctic grid cells formed an arc-like shape with two sides connected via high-latitude grid cells. The transition from the core Nearctic to the Neotropics appeared to be relatively gradual, but there was a visible discontinuity at about 29° latitude in northern Mexico coinciding with the commonly recognized boundary between both realms. South and Central American grid cells formed an arc-like shape that was differentiated into two groups: the core tropical part and the southern temperate portion which extended northwards in the Andean region to about the Peruvian–Chilean border at *c.* 18° S. There was a distinctive gap between Australia (including New Guinea) and the Oriental realm, supporting the location of Lydekker's Line.

Overall, a broadly similar pattern was obtained at the genus level. Here, some clear artefacts occurred in northern Central Australia where two grid cells were placed closer to South America than to Australia. Although broadly similar to the genus- and family-level results, the species-level NMDS showed some noteworthy differences. For instance, Madagascar was clearly separated from all other regions, but placed most closely to Africa.

In general, NMDS ordination is a useful method for illustrating the broad transition zones between continental biota, such as North America–Eurasia and North America–Central America. Relatively sharp transition zones, indicated by abrupt changes in colours, occurred between sub-Saharan Africa and the Sahara Desert, in the Himalaya–Tibet region, and between (sub-)tropical and temperate South America. At all three taxonomic levels, Palaearctic grid cells formed a cloud linking North America, Africa and Asia. On the whole, Saharan grid cells showed greater affinities to sub-Saharan Africa than to the Palaearctic. Probably the main advantage of NMDS is that it only requires the user to specify the distance metric and the count of dimensions, and no other pre-determinations. Overall, however, the usefulness of NMDS ordination in revealing biogeographical patterns is limited. Due to the transitional, rather than abrupt changes, in most regions, biogeographical groups are often not easy to recognize and no classification occurs. With more than two dimensions, the colour space that is necessary for mapping, as well as potential artefacts, constrain inference.

Cluster analysis

Choice of algorithm

The nine clustering algorithms showed vastly different performances, and co-phenetic correlation coefficients ranged from 0 to 0.89 for different methods across the subsets of the data (Fig. 5, and see Appendices S1 and S2 in Supporting Information). UPGMA was the consistently best performing clustering algorithm across all investigated data sets (mean
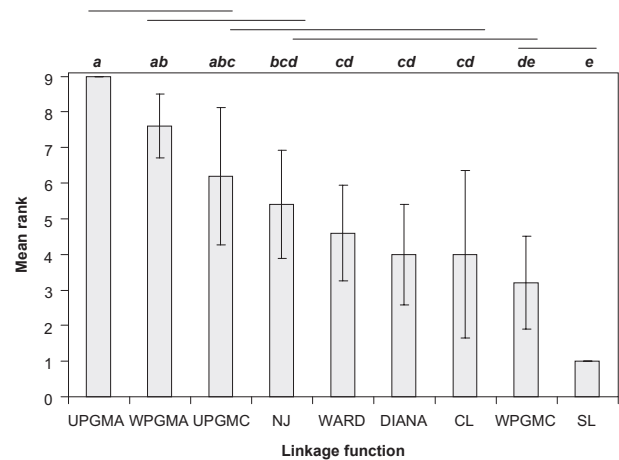

Figure 5 Performance of nine different clustering algorithms compared across five different subsets of the distribution data (families, genera, all species, volant and non-volant species of mammals). Clustering results for each subset were ranked according to the co-phenetic correlation coefficient (see text for details). Highest ranks indicate best performance. Bars indicate mean ranks, error bars give standard deviations. To test for significant differences in the performance of algorithms, an ANOVA with a subsequent Tukey's honestly significant difference (HSD) *post hoc* test was performed. Results are indicated by letter codings and horizontal lines. For acronyms and explanations of the clustering algorithms see text and Table 2.

co-phenetic $r = 0.87$), followed by WPGMA, which always had lower co-phenetic r values but was statistically indistinguishable from UPGMA results (Fig. 5; Appendices S1 and S2). On the other hand, single linkage performed consistently worst (mean co-phenetic $r = 0.3$). Ward's algorithm and neighbour joining, which are often favoured in biogeographical analyses, showed intermediate levels of performance.

Geographical patterns and area dendrogram

Mapping of the first 12 groups of the UPGMA classifications largely yielded spatially coherent and intuitively sensible clusters (Fig. 6). Only at the family level were there some incoherently placed grid cells (Fig. 6a). The UPGMA dendrograms allow interpretations not only of the topology of relationships but also of their depth. In the following, we first assess dendrograms based on both the individual grid cell assemblages. In the family-level grid cell assemblage dendrogram (Fig. 6a), a primary division occurred at a β_{sim}-value of *c.* 0.8 between a group consisting of assemblages in Madagascar and Australia and those in all other regions. At a β_{sim} value of 0.7, the Neotropics split and a distinct Caribbean group further split at a β_{sim} value of *c.* 0.4. Africa, including most parts of the Sahara and northern Africa as well the Arabian Peninsula and parts of Middle East, i.e. 'Saharo-Sindia' (compare Wickens, 1976; Brenan, 1978), forms a group with the Oriental region. Surprisingly, in contrast to Wallace's classic scheme, the Oriental included
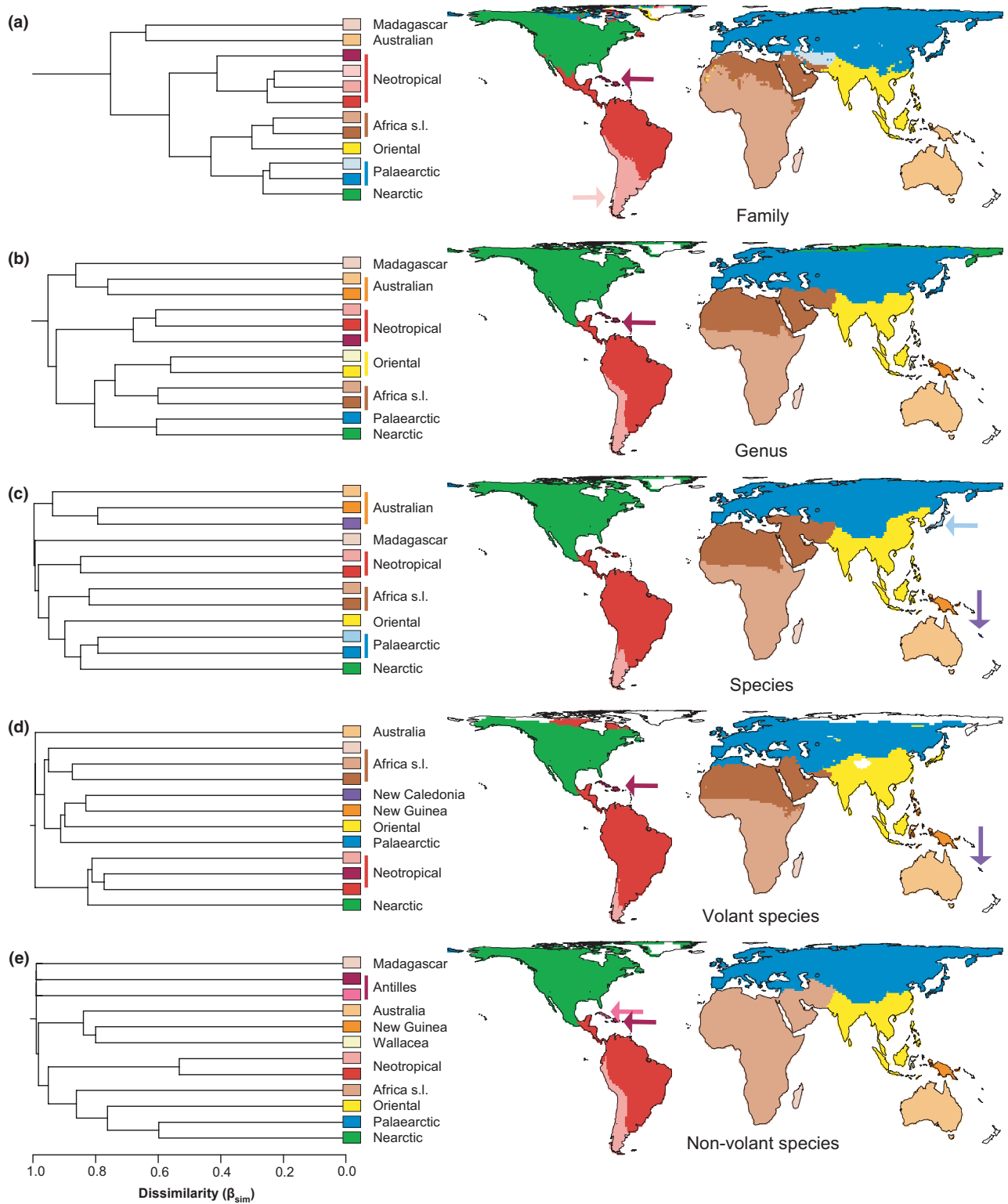
Figure 6 Dendrograms and maps resulting from UPGMA hierarchical clustering of grid cell assemblages based on β_{sim} dissimilarity matrices for mammals at the level of (a) families, (b) genera, (c) species, and for (d) volant and (e) non-volant species. The first 12 cluster groups are shown for each subset of the data to facilitate comparison. Colours used in dendrograms and maps are identical. Coloured arrows in the maps highlight very small cluster groups. Maps are in the Behrmann projection.

Sulawesi and the Philippines. A Holarctic group split at *c.* 0.45 from the Palaeotropics (i.e. Africa and Oriental) and a further split at *c.* 0.3 separated the Nearctic and Palaearctic. In most cases, however, clusterings of grid cell assemblages largely coincided with and thus confirmed the classic Wallace regions. For instance, the boundary between the Neotropics and the Nearctic occurred at *c.* 29° latitude in Mexico, strikingly similar to the one drawn by Wallace. One major discrepancy was the grouping of the Sahara, parts of the Arabian Peninsula and the Near and the Middle East with Tropical Africa. These parts are considered to be closer to the Palaearctic in most biogeographical regionalizations (but see Cox, 2001).

The genus-level dendrogram based on the grid cell assemblages shows similar spatial patterns and similar inter-regional relationships (Fig. 5b). But major splits occurred at higher levels in the dendrogram reflecting the overall smaller geographical ranges of genera resulting in greater dissimilarity. Again, Madagascar and Australia/New Guinea were identified as the most distinctive regions, followed by the Neotropics. The latter was differentiated into the Antilles, a core tropical and a temperate subregion broadly matching Wallace's Neotropical subregions (Wallace, 1876). Africa *sensu lato* and the Oriental were grouped together. In contrast to the family-level clustering, the Oriental was differentiated into the core Oriental region and a region corresponding to the classic Wallacea region plus the Philippines. Notably, boundaries between biogeographical regions shifted. For instance, the Oriental–Palaearctic boundary in East Asia and the boundary between Africa *sensu lato* and the Palaearctic shifted northwards compared to the family results. On the other hand, the boundary between the Nearctic and Neotropics moved southward to the Isthmus of Tehuantepec. Also the boundary between the tropical and temperate Neotropics moved southwards. A potential caveat at the genus level was that genera are often not unambiguously defined and that the definition might not be even across space. Rather, genera might be of vastly different ages and they might be more inclusive in the tropics than in the temperate regions.

Following the general increase in dissimilarity towards lower taxonomic levels, the primary divisions in the species-level dendrogram occurred much deeper in the dendrogram (0.80–1). Again, Australia together with New Guinea and New Caledonia and also Madagascar were the most distinct regions. The next split separated the Neotropical region, which was differentiated into a core tropical (including the Antilles) and a temperate portion. In contrast to the family- and genus-level UPGMA, the Oriental showed here a closer affinity to the Holarctic. The latter was clearly differentiated into Nearctic and Palaearctic (with a further split off separating Japan). The boundaries of the Oriental in East Asia and of Africa *sensu lato* shifted further northwards, but the Nearctic–Neotropics boundary did not change significantly.

The regionalizations of volant and non-volant species both exhibited remarkable differences (Fig. 6d,e). For example, in contrast to non-volant mammals in which the Nearctic was linked to the Palaearctic region, North American volant species showed their strongest association with South America (Procheş, 2005) potentially facilitated by a larger dispersal distance and prevalence of long-distance north–south migrations in this group. Tropical Africa, the Saharo-Sindian region and Madagascar formed a coherent group for volant mammals, whereas Madagascar took a very isolated position for non-volant species. For non-volant species, the boundary between the Oriental and Australia–New Guinea regions followed the classic Wallace Line (Wallace, 1860, 1876). For volant species, the Oriental extended much further north including Honshu Island of Japan as well as most of China and the Tibetan Plateau.

Grid cell versus whole-region assemblage area dendrograms

In grid-based analyses, the high occupancy of wide-ranging species is likely to dominate biogeographical patterns (Jetz & Rahbek, 2002; Lennon *et al.*, 2004; Beck *et al.*, 2006a; Kreft *et al.*, 2006; Šizling *et al.*, 2009). The spatial pseudo-replication that comes along with the relatively fine grain of our study may thus potentially distort areal relationships (Morrone & Escalante, 2002). We thus assessed differences in the UPGMA area dendrograms based on grid cell assemblages versus whole-region taxa lists. The latter is less affected by the geographical heterogeneity of species geographical range sizes and weighs occurrences independent of grid cell occupancy within a region. The two approaches yielded remarkably different topologies (Fig. 7). For instance, the Nearctic and Palaearctic regions were grouped together across all taxonomic subsets in the grid-based approach, but the Nearctic was merged with the Neotropics in the approach based on whole-region lists. This difference highlights the influence of taxa blending into different biogeographical regions. In this particular case, patterns of faunistic interchange between North and South America were reflected in the clustering of regional assemblages. On the other hand, the high-arctic and temperate faunas of the Nearctic and Palaearctic were clearly related and very homogeneous. In these high-latitude regions spatial turnover of species across grid cells is much lower (and geographical range sizes much larger) than, for example, near the equator (Orme *et al.*, 2006; Buckley & Jetz, 2008). The potential number of linking species is therefore necessarily lower. The resulting geographical variation in similarity of grid cell assemblages has direct effects on the clustering and estimates of regional similarity. We note that the grid cell-based approach identifies delineation and similarity among regions based on the composition of all their grid cell assemblages, while a whole region approach draws only on one single regional assemblage. The choice of data for the area dendrogram will depend on the specific inference (e.g. ecological versus historical) and application. Further research is necessary to integrate the delineation of biogeographical regions and the analysis of its historical relationships into one coherent framework (but compare Szumik *et al.*, 2002; Szumik & Goloboff, 2004).
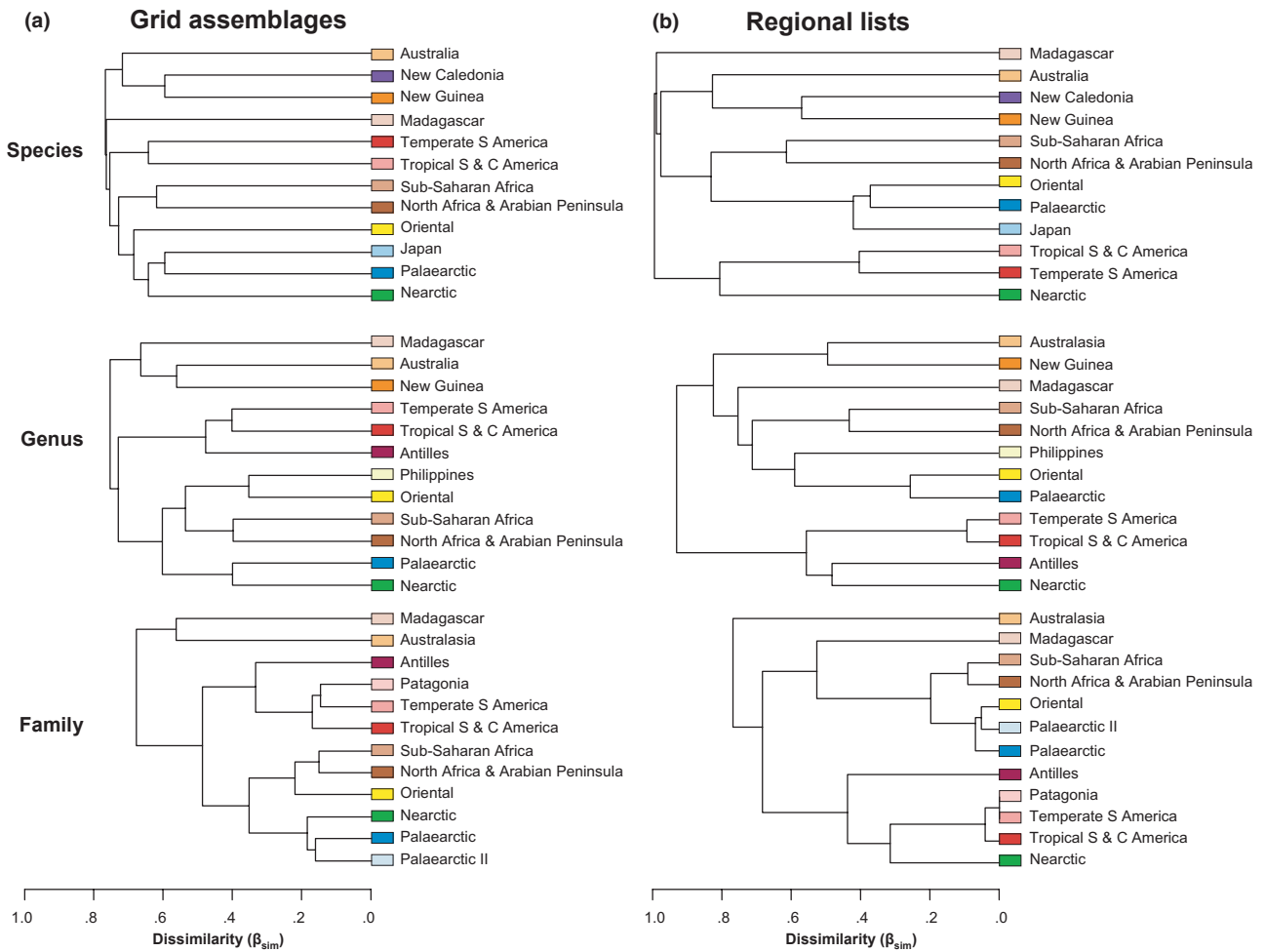
Figure 7 Comparison of dendrograms from UPGMA hierarchical clustering of mammals based on (a) grid cell assemblages and (b) regional taxa lists. An arbitrary number of 12 cluster groups at family, genus and species level is shown (see Fig. 6a–c). Regional taxa lists were extracted across the 12 regions derived from grid cell assemblages. Then β_{sim} distances were computed and UPGMA clustering reapplied. Note the differences in the topology of both classifications. Most markedly, the relative topology of the Nearctic, Neotropical and Palaearctic regions changes.

Number of clusters and biogeographical detail

As expected, the optimal number of clusters based on the L-criterion applied to the evaluation graphs differed with taxonomic level (Fig. 8). Based on our three different indices and the L-method, the optimal numbers of clusters for the species-level UPGMA were at $k = 30$, 28 and 20 for node height, mean regional endemism and total endemicity, respectively. Optimal numbers of clusters at genus level were at $k = 7$, 8, 10 and at family-level at $k = 6$, 8, 8. All evaluation graphs showed a relatively smooth curvature. The L-criterion tends to somewhat underestimate the number of optimal clusters in such cases (Salvador & Chan, 2004).

This assessment facilitated the final aim of this study, i.e. to provide an appropriately detailed global biogeographical regionalization of all mammal species. In Figure 9 the world is separated into 30 differently coloured biogeographical

regions. These 30 regions were themselves nested in six major realms: Australian (including New Guinea and New Caledonia), Neotropical (including the Antilles), African (including North and sub-Saharan Africa, the Arabian Peninsula, and parts of the Near and Middle East), Oriental (including Wallace), Palaearctic, and Nearctic. The boundaries of a further 60 nested regions were indicated with lines. The line width was set proportionally to the merging height of the clusters, and along with the combination of colours and boundaries used, enhanced the visualization of different regions. The combination of colours and boundaries used allowed for the increase of the biogeographical detail (Fig. 9). The 30 regions differed greatly in size, with New Caledonia being the smallest (one 110 × 110 km grid cell) and the Temperate and Boreal Euro-Siberia being the largest (2065 grid cells). The median size of a biogeographical region was 188 grid cells or roughly 2.3×10^6 km². The average proportion of endemics was 30%
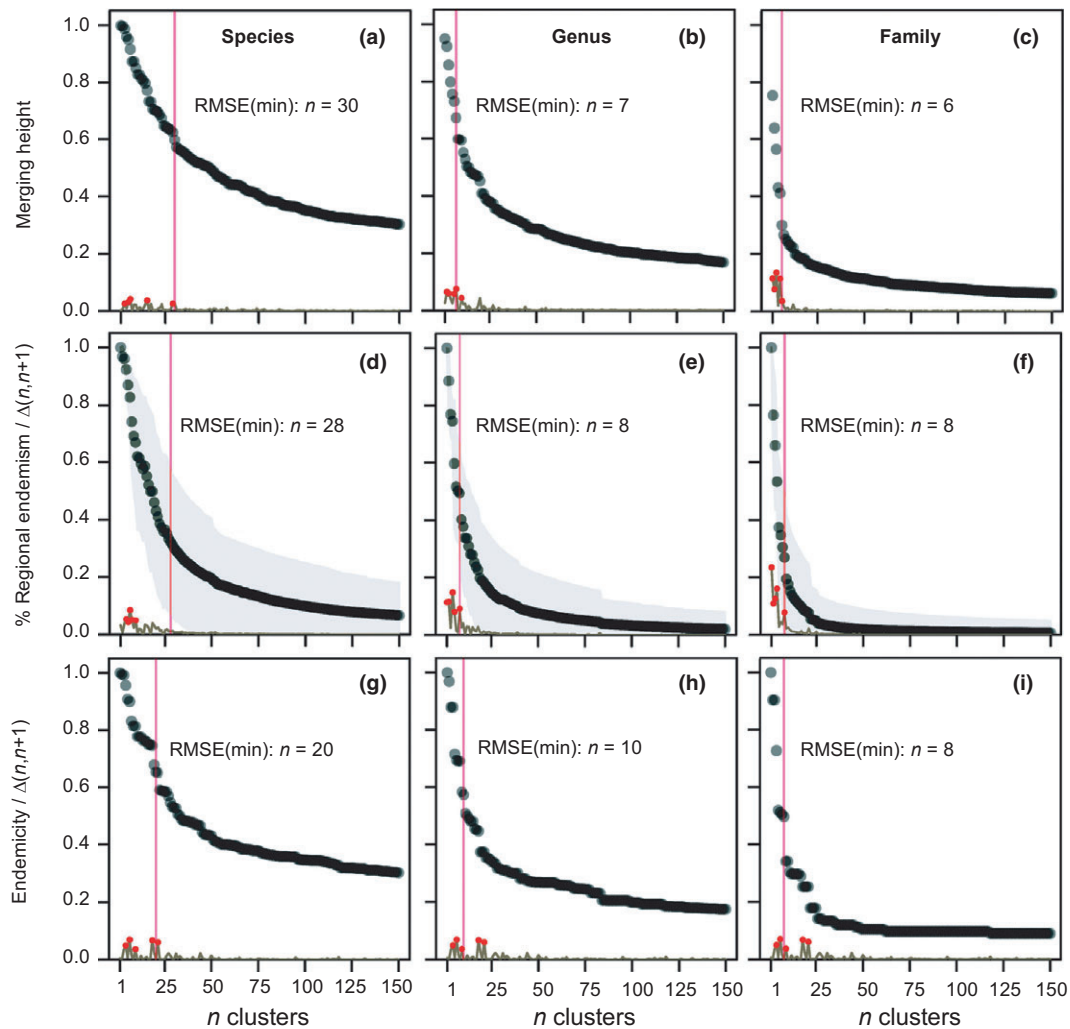
Figure 8 Evaluation graphs for UPGMA hierarchical clustering of mammals based on β_{sim}. Three different evaluation criteria are compared: (a–c) merging height, i.e. the height of nodes in the dendrogram; (d–f) average proportion of endemic taxa per region; (g–i) total endemicity (number of taxa endemic to a single biogeographical region divided by the number of non-endemic taxa). Graphs are shown for three different taxonomic levels: species (a, d, g), genus (b, e, h) and family (c, f, i). Grey shading in (d–f) indicates standard deviations from the mean. Vertical red lines mark the optimal number of clusters determined with the minimum root mean square error criterion (RMSE$_{min}$) of the L-method (Salvador & Chan, 2004; see text for details). Grey lines indicate the $\Delta_{n,n+1}$, i.e. the drop in the evaluation metric from n to $n + 1$ cluster groups, and red dots highlight the top five steepest drops.

in the 30 biogeographical regions, and the total proportion of species that are endemic to only one was 52.7%.

DISCUSSION

Framework and methods

The results of this study demonstrate that multivariate statistical methods are able to reveal sensible biogeographical patterns and provide quantitative, transparent and replicable biogeographical groupings that allow multiple uses and novel inference. The main strength of ordination methods [Materials and Methods, point (5)] is their straightforward ability to reduce the complexity of the distance matrix and to visualize the continuous transitions between biogeographical regions. In

fact, all biogeographical regions except Australia are more or less continuously connected to other regions. Abrupt and drastic changes in faunal composition at this geographical scale appear to be relatively scarce. A drawback of NMDS was the relatively high stress values for two dimensions, indicating that the overall information contained in the distance matrix could only be imperfectly reduced to two axes. Additionally, our mapping technique was constricted to a two-dimensional colour space. Although colour spaces of up to three dimensions are generally conceivable [e.g. mixing red, green, blue (RGB) values by assigning the colours red, green, blue to one of three ordinal axes, respectively], the visual capability of the reader's eye remains a strong constraint. Given the imperfect reduction of multidimensionality, some apparent artefacts, and the fact that most biogeographical regions are visually
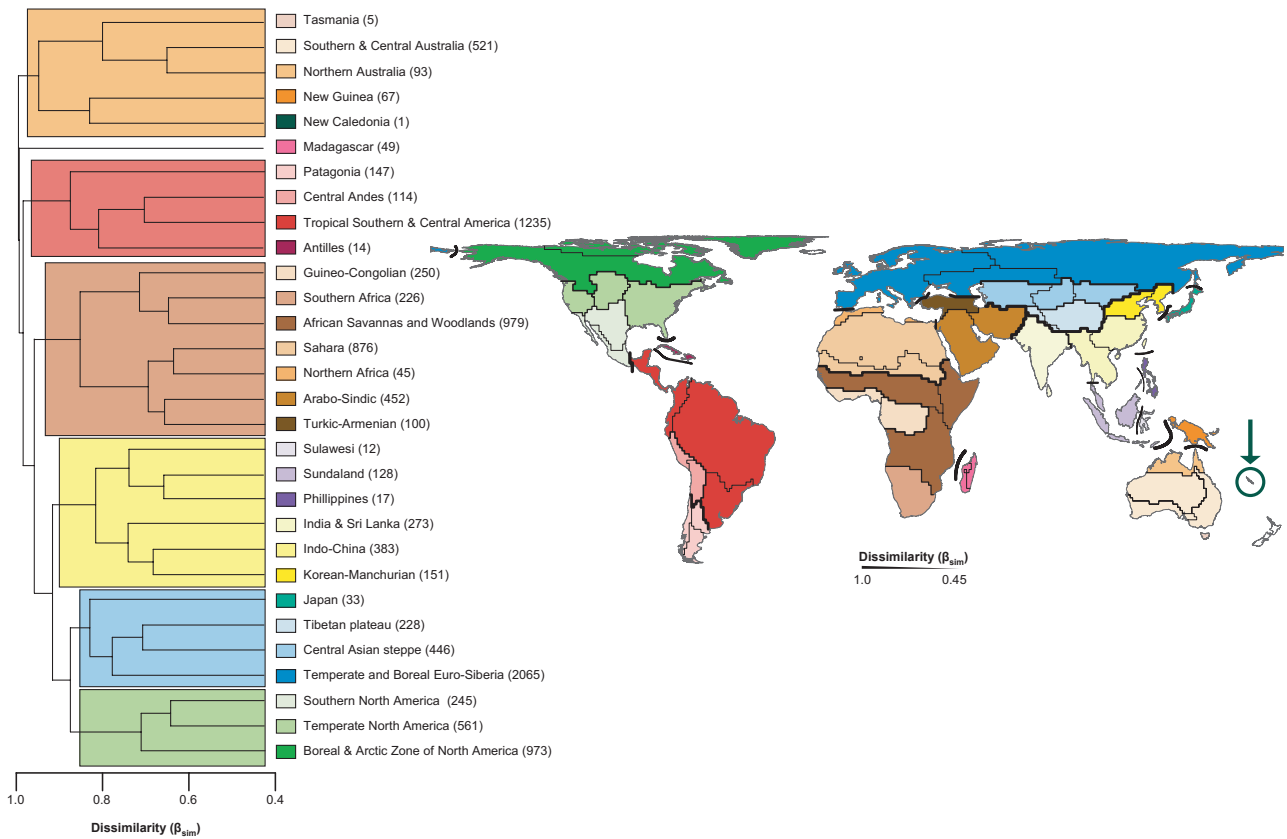
Figure 9 Dendrograms and maps resulting from UPGMA hierarchical clustering of grid cell assemblages of mammals based on a β_{sim} dissimilarity matrix at the species level. The six major biogeographical divisions are highlighted in the dendrogram with large coloured rectangles: orange, Australian; red, Neotropical; brown, African; yellow, Oriental; blue, Palaearctic; green, Nearctic. The first 30 groups in the dendrogram (small rectangles) and in the map are displayed in different colours. Additionally, the first 60 groups are indicated with black boundaries in the map. Boundary widths are proportional to the height in the UPGMA dendrogram where adjacent groups merge. For visual clarity, the land area of excluded coastal grid cells is filled with the colours of adjacent cells and the oceanic portions of grid cells are not shown. The map is in the Behrmann projection.

inseparably interconnected, NMDS results are not easy to interpret, and a direct translation into discrete groups is problematic. The need to classify regional faunas into discrete groups, however, is a central prerequisite for their distinction and naming (Simpson, 1961) and dramatically facilitates synthesis. However, it has also been argued that only the centres of biogeographical regions should be considered as such and that interjacent transition zones should be treated and named differently (Mayr, 1944). But given the large degree of overlapping taxa and the breadth of transition zones, this challenge is likewise difficult to accomplish using ordination techniques.

The apparent strength of hierarchical clustering algorithms is the hierarchy of discrete groups they produce. Our clustering approach maximizes the homogeneity within clusters so that grid cell assemblages in the same cluster group are as similar as possible. Simultaneously, it maximizes the heterogeneity between clusters so that grid cell assemblages belonging to different clusters should be as dissimilar as possible. We found that different hierarchical clustering algorithms varied greatly

in their capability to achieve these two general aims and to result in meaningful biogeographical regionalizations. The different algorithms tested here showed vastly different performances, expressed by a great variation in co-phenetic correlation coefficients. Among all algorithms and across all investigated subsets of the data, UPGMA consistently performed best. Other frequently used algorithms, namely Ward and NJ (Table 1), performed significantly worse, and clustering results from single linkage retained only very little of the original information in the distance matrix (Fig. 5, Appendix S1). No perfect method exists to delineate biogeographical regions, but the selection of an appropriate method needs to be guided by data type, quality and research question. Our findings clearly stress the need for a careful selection and evaluation of an appropriate clustering algorithm. There is no a priori justification for using a particular method, and our results show that multiple algorithms should be compared. There is also no guarantee that UPGMA will perform best in other data sets, as the data structure probably changes for different taxa, geographical extents and scales.

Although β_{sim} is little affected by differences in richness (Lennon *et al.*, 2001), the family-level UPGMA demonstrates that low richness nonetheless had an effect on the results. In the family-level UPGMA, spatially incoherent clusters did appear, with, for example, low-richness grid cells in high-arctic regions of North America placed into the Neotropical, Oriental or African region. Faunas in such low-diversity regions are usually composed of a few, but very widespread, near-cosmopolitan families, which provide little useful biogeographical information. Furthermore, species lists of low-richness areas are more strongly affected by stochastic processes (Lennon *et al.*, 2001), which further complicates placing them using unsupervised clustering methods. The family UPGMA further shows that clusters become fuzzy with increasing detail and hard to interpret (for instance the subdivision of the Palaearctic, Fig. 6a). This is probably a consequence of the relatively low overall number of mammal families compared with the number of genera and species.

Mammal biogeography

Generally, there is a broad congruence between our grid-assemblage based UPGMA clustering results and the classic Wallace regions (Fig. 9). Our findings confirm that the six biogeographical regions – Palaearctic, Nearctic, Africa, Oriental, Neotropics and Australia – represent useful biogeographical entities characterized by a homogeneous taxonomic composition useful for describing modern-day distributional patterns of mammals. We also observe a good congruence between our quantitative regionalization and Wallace's subregions. For instance, the boundaries of the Manchurian, the Boreal and Arctic zones of North America and the Guineo-Congolian regions (Fig. 9) match well with Wallacean subregions. However, some noteworthy differences from the commonly used Wallace scheme or derivates also surfaced.

Madagascar, traditionally considered as a subregion of the Ethiopian realm, was placed close to the African mainland fauna only for the case of volant species (Fig. 6d). At the family and genus level, Madagascar was grouped close to Australia (albeit at very high dissimilarity levels). This is explained by the extraordinary high levels of endemism, especially for non-volant species (Goodman & Benstead, 2004; Vences *et al.*, 2009). The few existing links in the distribution of modern taxa to other regions only occurred for volant families such as Pteropodidae, which is widespread throughout the tropics of the Eastern Hemisphere, and thus only provide limited biogeographical inference. A large number of Malagasy taxa show sister-group relationships to mainland African counterparts (Yoder & Nowak, 2006). However, these occur mostly at higher taxonomic ranks and are not reflected at the rank of genera or even families. A similar issue was also apparent for the Greater Antilles (Cuba and Hispaniola), where all extant non-volant species are endemic (Morgan & Woods, 1986). Consequently, these islands were identified as distinct groups by the UPGMA analysis (Fig. 6e).

Second, the boundary between the Ethiopian and the Palaearctic region as identified here (Fig. 9) is clearly different from most traditional expert-based biogeographical regionalizations. Classically, the boundary was drawn along the Tropic of Cancer with the Ahaggar Mountains being part of the Palaearctic region (Wallace, 1876). We found consistent evidence across taxonomic levels and for both grid assemblages and regional species lists (Fig. 7) that this boundary should be drawn much further north to reflect natural faunistic resemblances. Instead, a broader African or Ethiopian realm should also include the Sahara, northern Africa, the Arabian Peninsula and significant portions of the Near and Middle East. Especially in plant geography, the latter region is sometimes referred to as the Saharo-Sindian region (Wickens, 1976; Brenan, 1978), a region with extensive biotic interchange between core African and Asian floras and faunas after the closing of the Tethys Straits (Vermeij, 1991). Only in the case of the family-level and volant species UPGMA are the parts of Morocco, Algeria and Libya with mediterranean-type climate placed into the Palaearctic region, possibly reflecting the greater dispersal abilities of bats. Together these results reaffirm the arguments of Cox (2001) that the Sahara and northern Africa should be regarded as impoverished parts of the African realm.

The primary geographical divisions in the global mammal fauna clearly coincide with geology and plate boundaries (Cox, 1974; Briggs, 1989; Cox & Moore, 1993). For instance, the southern boundary of the Nearctic coincides with the North American plate, the Neotropics consist of the Caribbean and South American plates, the African plus the Arabian plate form a distinct region, the Indian plate is clearly reflected at a subregional level and islands and archipelagos as isolated landmasses emerge as distinct regions. At a finer geographical scale the divisions increasingly reflect broader zones of similar climate and vegetation (e.g. Guineo-Congolian, divisions in the Patagonia region, in the Central Asian steppe region, or in the temperate North American region; Fig. 9).

Taxonomic scale and the potential and promise of implementing phylogenetic data

We observe that the location of boundaries obtained from UPGMA is sensitive to taxonomic scale. Interestingly, discrepancies between taxonomic levels partly coincide with some long-standing problems in zoogeography. For instance, boundaries between the Neotropics and Nearctic, the Palaearctic and Ethiopian, as well as the Oriental and Palaearctic regions shifted considerably depending on the taxonomic level considered. Taxonomy represents a strong limitation in comparing grid cell assemblages based on presence and absence of taxa. For instance, the inclusiveness and the age of genera and families vary between taxa and regions (Avise & Johns, 1999; McKenna & Bell, 2000; Bininda-Emonds *et al.*, 2007), but also species-level analyses based on standard presence–absence dissimilarity indices do not correct for differences in age and degree of evolutionary separation of

species. This taxonomic predicament can be resolved by comparing assemblages using distribution data in combination with phylogenies and phylogenetically inclusive and continuous measures of phylogenetic beta diversity (Graham & Fine, 2008).

CONCLUSIONS

Multivariate approaches offer a transparent and replicable toolkit for the delineation, analysis and interpretation of unique regions in biogeography and macroecology. For instance, they can provide quantitative guidance for identifying the position and strength of boundaries between regional assemblages or they can be starting points for the analysis of environmental versus historical controls on the distribution of species assemblages. For historical biogeography, quantitative regionalizations may serve as geographical templates to construct area or PAE cladograms. Therefore, these approaches might be useful in resolving many of the long-standing debates about biogeographical divisions. However, our results also suggest that there is no perfect biogeographical regionalization that will fit all purposes and none that will satisfy all aspects of historical and ecological biogeography. Conversely, the different ecological and evolutionary approaches to an understanding of broad-scale distribution patterns have led to an artificial separation of regionalizations into ecological and historical biogeography. Future progress towards a more synthetic understanding of global biogeographical patterns will be made at the interface between both branches (Ricklefs, 2004; Wiens & Donoghue, 2004). In this context, quantitative tools such as the ones presented in this study might be useful for reconciling historical and ecological dimensions of species distributions.

A further strength of multivariate biogeographical approaches arises from their potential to provide dynamic insights into changes of species assemblages through space and time. The increasing performance of hind- and forecasting niche modelling techniques (e.g. Pearman et al., 2008) may shortly provide suitable data sets that, together with palaeontological data, might be incorporated into a clustering framework to analyse spatial responses of whole species assemblages in time and space (Graham et al., 1996; Riddle, 1998).

We foresee an exciting next step for data-driven approaches as presented here in the light of a growing number of well-resolved complete phylogenies. Comparing grid assemblages and regions in their phylogenetic similarity rather than just presence/absence of taxa is likely to facilitate an array of novel, probably deeper, evolutionary interpretations (Graham & Fine, 2008). At the same time, increasing availability of global species distribution data will probably allow the extension of the presented methods to many new taxa. This may bring a renewed and bright future for global-scale biogeographical regionalizations that will be increasingly rigorous, inclusive and with an increased potential for evolutionary interpretation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Co-phenetic correlation coefficients for nine different clustering methods and five different subsets of the global mammal data.

Appendix S2 Scatter plots illustrating the relationships between the original pairwise distances (β_{sim}) of species-level grid cell mammal assemblages and pairwise distances in the dendrogram (co-phenetic distance) resulting from nine different hierarchical clustering methods.

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