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The World's Zoogeographical Regions Confirmed by Cross-Taxon Analyses

ŞERBAN PROCHEŞ AND SYD RAMDHANI

The world's zoogeographical regions were historically defined on an intuitive basis, with no or a limited amount of analytical testing. Here, we aimed (a) to compare analytically defined global zoogeographical clusters for the herpetofauna, birds, mammals, and all these groups taken together (tetrapod vertebrates); (b) to use commonalities among these groups to propose an updated global zoogeographical regionalization; and (c) to describe the resulting regions in terms of vertebrate diversity and characteristic taxa. The clusters were remarkably uniform across taxa and similar to previous intuitively defined regions. Eleven vertebrate-rich (Nearctic, Caribbean, Neotropical, Andean, Palearctic, Afrotropical, Madagascan, Indo-Malaysian, Wallacean, New Guinean, Australian) and three vertebrate-poor (Arctic, Antarctic, Polynesian) zoogeographical regions were derived; the Neotropical, Afrotropical, and Australian had the highest numbers of characteristic tetrapod genera. This updated regionalization provides analytically accurate divisions of the world, relevant to conservation, biogeographical research, and geography education.

Keywords: biogeographical regionalization, cross-taxon comparisons, ecoregions, global biogeography, zoogeographical regions

The world's terrestrial zoogeographical regions were originally outlined by Sclater (1858) and Wallace (1876), primarily on the basis of vertebrates, because their distribution records were the most complete at the time. Since then, the completeness of records has improved dramatically for both vertebrates and invertebrates, and although invertebrates represent a far greater proportion of total animal diversity, tetrapod vertebrates remain the best group for comparatively testing biogeographical hypotheses, with a comprehensive data set having become openly available online (WWF 2010). Specifically, where the world's biogeographical regions are concerned, it makes sense to test their accuracy using the same groups of organisms used to delimit them in the first place.

Subgroups of vertebrates have already been used to fine-tune analytical methods for delimiting zoogeographical regions (bats in Procheş 2005, 2006; all mammals in Smith 1983, Kreft and Jetz 2010), and similar procedures have also been employed for some plant taxa (monocots in Conran 1995; bryophytes in Vanderpoorten et al. 2010) and invertebrates (dung beetles in Davis et al. 2002; hawk moths in Beck et al. 2006). In a recent article, Kreft and Jetz (2010) explored at length the methods that can be employed in global regionalization by varying clustering algorithms and taxonomic rank.

Although this incorporation of clustering methods in global regionalization research gives the field much needed credibility, it also tends to remove the focus from the very taxa that produce these patterns. The natural-history value of this work is therefore at least partly lost in the process. However, because both geographical units and taxa can be classified on the basis of distributional data (Holloway and Jardine 1968), it should be possible to devise ways to use the very same data in listing characteristic taxa for each of the regional units that result from the cluster analyses and thus to obtain ideal examples of taxa with distributions characteristic of each region.

The availability of the WildFinder data set (4567 genera of extant tetrapod vertebrates, including freshwater but excluding strictly marine ones, in 821 ecoregions; WWF 2010) and the recently improved understanding of analytical methods create an opportunity to test to what extent biogeographical regions that are similar in number and size across various vertebrate taxa can be derived and to explain any residual differences in terms of macroecological variables, such as body size (Blackburn and Gaston 1994) or dispersal ability (Lester et al. 2007). We address both of these points in the present article and, consequently, explore the possibility of defining a set of regions by combining information derived for analyses on these various taxa, of

listing characteristic taxa for each region, and of linking the number of characteristic taxa to overall regional diversity.

Choice of taxonomic rank and analysis methods

Genus-level data are preferable to species- or family-level data for several reasons: Species-level taxonomy is often debatable, and data are more often incomplete. Familial classification has recently changed substantially (e.g., Alström et al. 2006, Roelants et al. 2007, Kelly et al. 2009). The number of genera is large enough for reliable analyses but not so large as to raise computational problems. Genera also seem to be the most powerful predictors in cross-taxon biodiversity analyses (despite differences in lineage age, and partly because of the previous reasons listed here; see Procheş et al. 2009).

Data for all tetrapod vertebrates and subsets thereof (herpetofauna, birds, mammals) were clustered here using the Jaccard index (“p” distance in the PAUP software package, <http://paup.csit.fsu.edu>; using the unweighted-pair group method with arithmetic mean [UPGMA] option; see Kreft and Jetz [2010] for method comparisons commending UPGMA).

Two equal-value approaches to defining regions could be viewed as ideal: (1) an *equal-dissimilarity* approach, in which sets of clusters are defined on the basis of their percentage dissimilarity (e.g., a cluster is represented by all ecoregions with a dissimilarity of less than 50% from one other but more than 50% dissimilar from any ecoregion not included in the cluster, as in Procheş 2005), and (2) an *equal-numbers-of-clusters* approach, in which one decides a priori that the study region (here, the entire terrestrial realm) is to be divided into, for example, 10 biogeographical regions, and as such, one selects the 10 most dissimilar clusters for each taxon. When we attempted them with the WildFinder data, both of these approaches tended to yield clusters of very uneven geographical coverage, often numerous small clusters in tropical America and large Holarctic or Paleotropical clusters (see supplemental appendix S1, available online at <http://dx.doi.org/10.1525/bio.2012.62.3.7>). Although we note that this outcome indicates a great diversity of biogeographical assemblages in the Neotropics, the fact that we used ecoregions (Olson et al. 2001) as (rather broad and intuitively defined) units for analysis meant that very small clusters would be likely to have imprecise borders relative to their size or that they might even be artifacts of poor ecoregion delimitation. Consequently, we relaxed the equal-dissimilarity and equal-numbers-of-clusters conditions and started manually separating clusters on the dendrograms from high to low dissimilarity levels. Insofar as the top-level dichotomies did not show commonalities across taxa, we progressed to the point at which the sets of clusters showed maximum cross-taxon convergence. Thus, groups of ecoregions were defined as clusters in the analysis for each taxon if they showed an optimal match with the clusters for the other taxa in terms of the percentage of ecoregions included.

A second difficulty was related to obtaining clusters with a certain degree of geographic contiguity. For all of the data sets, when we included all ecoregions, the clusters with disjunct distributions comprised genus-poor ecoregions geographically distant from one another but sharing similar assemblages of widespread genera (mostly islands and highlands, often in mixed clusters; see also Smith 1983). We avoided this result by sequentially eliminating genus-poor ecoregions in each analysis until all major clusters were conterminous or nearly so. As a rule, we accepted geographically disparate clusters if no more than one ecoregion excluded from a cluster intervened between two included ones (if only clusters that are conterminous on land were included, too many ecoregions had to be excluded, which reduced the comprehensiveness of the analyses).

Sets of clusters obtained in this manner, showing maximum similarity in ecoregional composition across the four selected vertebrate groups, were mapped. Genus diversity at the ecoregional level was plotted for each of the clusters in the form of histograms (which also indicated the ecoregions excluded from each analysis) to illustrate the general shape of the distribution of generic diversity values in each group and to indicate which of the clusters contain the ecoregions with the highest generic diversity. The resulting dendrograms, maps, and histograms are presented in figure 1.

Zoogeographical regions and subregions

The clusters of ecoregions that were found to be consistently congruent and were well defined across the four analyses (or across those analyses among the four where the number of genera for the ecoregions within that cluster was sufficient to include them in the analysis; figure 2) are recognized here as *zoogeographical regions*. The clusters that were derived in the most-relevant analyses or in all analyses but that differed substantially in geographic extent (more than 50% of the ecoregions included) or that were poorly defined in at least one analysis (e.g., the cluster was separated from other clusters only by less than 1% similarity) are recognized as *subregions* of the zoogeographical region that represented the cluster that was most similar to them in all or most analyses. The assignment of marginal ecoregions to a zoogeographical region followed a majority-rule allocation (out of four analyses; figure 2), with the analysis for all tetrapods taking precedence over the others in the case of a tie.

Following this protocol, 11 clusters were recovered consistently across taxa (figure 1), with limited variation in extent partly attributable to the different sets of ecoregions analyzed in each case. This had to do with the inclusion or exclusion of ecoregions on the basis of the number of genera present in the analyzed taxon (see the white bars at the low-generic-diversity end of the scale in the histograms in figure 1, which indicate the ecoregions excluded from the analysis). Note that, with the exception of the herpetofauna, generic diversity across ecoregions was weakly bimodal, and the ecoregions that had to be excluded in order to obtain contiguous clusters were those forming the first peak of

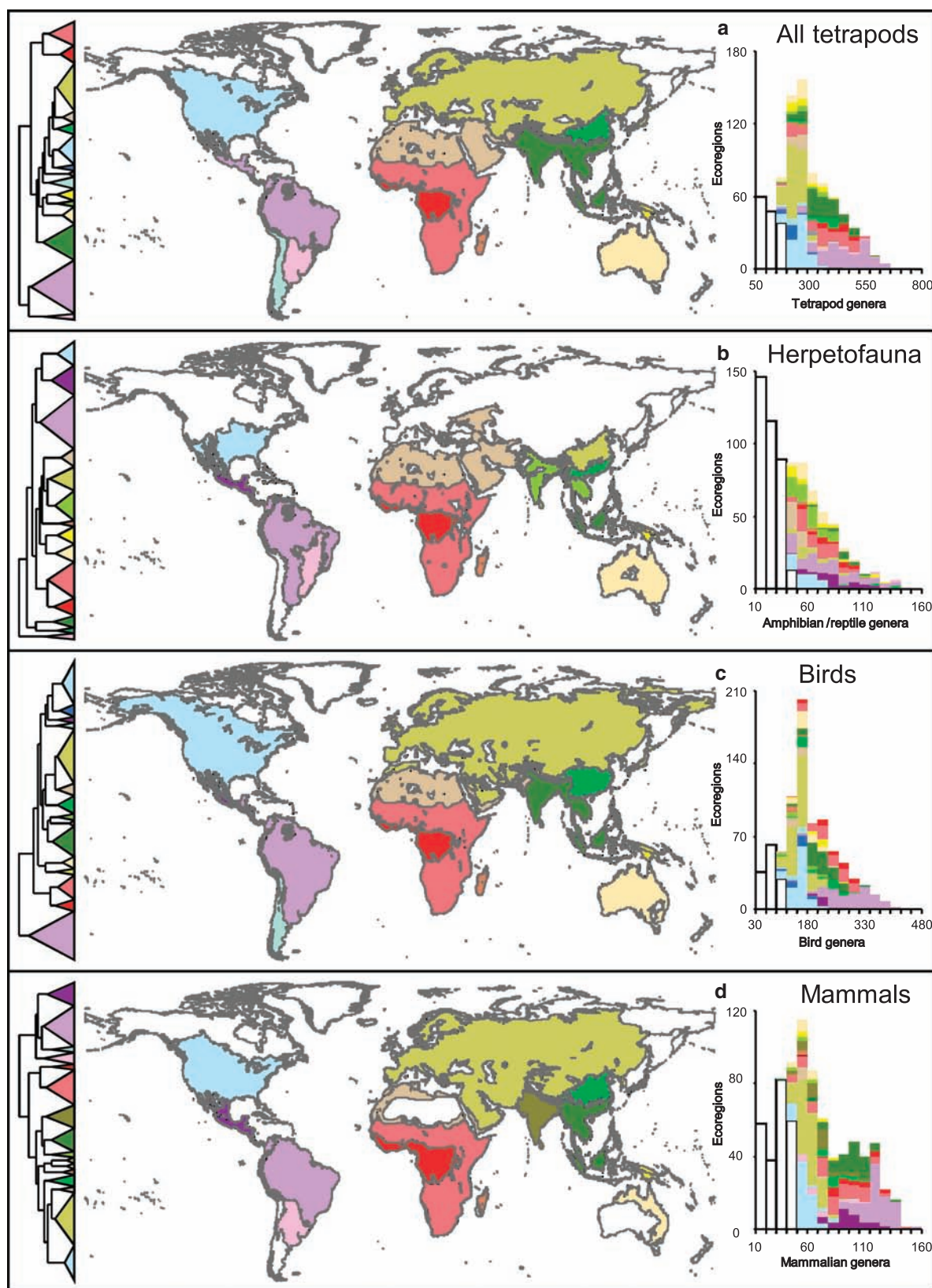


Figure 1. A synopsis of the clusters obtained in analyses for different vertebrate groups. Presented are the relationships between the clusters of ecoregions (see the text for details), maps of the clusters, and histograms of generic diversity across clusters for (a) all tetrapod vertebrates, (b) herpetofauna, (c) birds, and (d) mammals. The blocks not in color on the maps and in the histograms refer to ecoregions with low generic diversity left out of those respective cluster analyses.

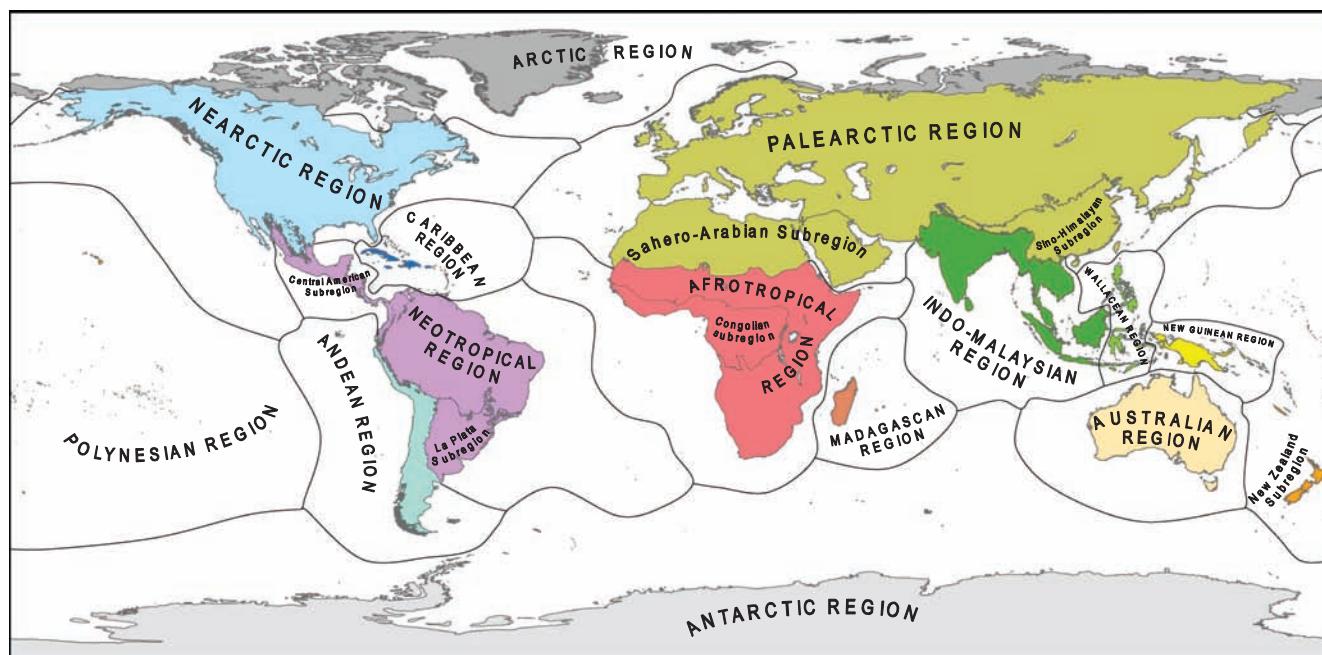


Figure 2. Vertebrate zoogeographical regions and subregions as derived from the four analyses presented in figure 1 (see the text for details).

values in the bird and all-tetrapod analyses. It can be argued, therefore, that the ecoregions excluded from the analyses were, in fact, quasinatural regions of low generic diversity. The variation in the geographic coverage of each cluster was generally low in genus-rich regions. Among these regions, the most unusual pattern was that observed in Southeast Asia in the herpetofaunal analysis, with the inclusion of the Indian subcontinent and Indochina in a transitional cluster that included only Wallacea in the other analyses (strict adherence to the contiguity rule would have produced a twelfth cluster here, but this was not supported by ecoregional assignment in the other analyses). In genus-poor areas, notable differences were (a) the inclusion of southeastern Europe in the Sahero-Arabian cluster in the herpetofauna analysis, where the Palearctic proper is restricted to temperate China; (b) the absence of the Caribbean and temperate South American clusters in the herpetofaunal analysis (both falling entirely below the cutoff number of genera); and (c) the absence of the Caribbean cluster in the mammal analysis (the temperate South American cluster is present in this case but is reduced to only six ecoregions in coastal Peru and Ecuador and is less than obvious in figure 1).

Nine of these 11 clusters were largely equivalent to regions or subregions already recognized in prior intuitive or analytical regionalization studies (Sclater 1858, Wallace 1876, Darlington 1957, Udvardy 1975, Smith 1983; see table 1): the Nearctic, Caribbean (i.e., West Indian or Antilles), Neotropical, Andean (i.e., Argentinian or Patagonian), Palearctic, Afrotropical (i.e., Ethiopian), Madagascan (i.e., Malagasy), Indo-Malaysian (i.e., Malesian or Oriental), and the transitional zone usually termed *Wallacean* (in honor

of Alfred Russel Wallace; in our analyses, this zone was established approximately as the region between Huxley's modification of Wallace's line and Lydekker's line; see Holloway and Jardine 1968). The two remaining clusters (one comprising Australia and Tasmania, the other New Guinea and neighboring islands)—often, but not always, most similar to each other in the analyses—could be equated to the previously recognized Australian region only if they were combined. These 11 clusters are recognized here as *zoogeographical regions* (figure 2).

Among the clusters with lower stability in terms of coverage, one that included the Sahara; the Arabian Peninsula; and in some taxa, parts of South and Central Asia is similar to the Mediterranean Subregion of Smith (1983). Other clusters with lower stability were (a) a transitional zone between the Nearctic and the Neotropical region, (b) a transitional zone between the Neotropical and the Andean region, and (c) a transitional zone between the Palearctic and the Indo-Malaysian region. In addition, a cluster consistently derived with almost identical coverage but minimal distinctness from the most similar other cluster (the Afrotropical cluster) was represented by the rain-forest-dominated ecoregions of Central and West Africa (this was nevertheless very distinctive in the nonvolant mammal analysis; appendix S1). These five clusters are recognized here as *subregions* (retaining Wallace's [1876] hierarchy of biogeographical units) and are termed the *Central American* and *La Plata* clusters (in the Neotropical region), the *Sahero-Arabian* and *Sino-Himalayan* clusters (in the Palearctic region), and the *Congolian* cluster (in the Afrotropical region). This naming system coincided

Table 1. Summary of the zoogeographical regions and subregions recognized here, as compared with other zoogeographical schemata.

Region in the present article	Sclater (1858)	Wallace (1876)	Darlington (1957)	Udvardy (1975)	Smith (1983)	Kreft and Jetz (2010)
A. Arctic Region	-(B,F)	-(B,F)	-(B,F)	-(B,F)	-(BF)	-(B,F)
B. Nearctic Region	B	B	B	B	b (BF)	B
C. Caribbean Region	- (D)	c (D)	c (M)	- (D)	c (M)	- (D)
D. Neotropical Region	D	D	D	D	d (DE)	D
d1. Central American Subregion	- (D)	d1 (D)	d1 (B/D)	- (D)	- (DE)	- (D)
d2. La Plata Subregion	- (D)	- (D)	- (D)	- (D)	- (DE)	- (D)
E. Andean Region	- (D)	- (D)	- (D)	- (D)	e (DE)	- (D)
F. Palearctic Region	F	F	F	F	f (GI)	F
f1. Sahero-Arabian Subregion	- (F)	f1 (F)	- (F,G)	- (F)	f1 (GI)	- (G)
f2. Sino-Himalayan Subregion	- (I)	- (I)	- (F,I)	- (F)	- (GI)	- (I)
G. Afrotropical Region	G	G	G	G	g (GI)	G
g1. Congolian Subregion	- (G)	g1 (G)	- (G)	- (G)	- (GI)	- (G)
H. Madagascan Region	- (G)	- (G)	h (M)	- (G)	h (M)	H
I. Indo-Malaysian Region	I	I	I	I	I (GI)	I
J. Wallacean Region	- (I,L)	- (I,L)	j (I/L)	- (I)	- (GI,M)	- (I)
K. New Guinean Region	- (L)	- (L)	- (L)	- (M)	- (M)	- (L)
L. Australian Region	L	L	L	L	I (M)	L
M. Polynesian Region	- (L)	m (L)	M	M	M	- (L)
m1. New Zealand Subregion	- (L)	m1 (L)	m1 (M)	m1 (N)	- (M)	-
N. Antarctic Region	-	-	n (M)	N	-	-

Note: This table simply indicates rough equivalence between units, even if the names differed. The letter M, assigned here to Polynesia, is also used for worldwide island assemblages. Capital letters indicate region status, lowercase letters indicate subregion status, a dash indicates no recognition, and the other region in which the unit was largely incorporated is specified in parentheses. If two large regions were lumped together, this is indicated by having no comma between the letters designating them; elsewhere, a forward slash indicates transitional status.

of marine affinities (see Procheş 2001). For delimiting the other two regions (the Arctic and Polynesian regions), one additional analysis was necessary (the complete results are not shown) in which all tetrapod genera were included without excluding any ecoregions. This analysis was used to determine the borderlines between the Arctic and the Nearctic–Palearctic regions and those between the Polynesian region and the Australian, New Guinean, Wallacean, Palearctic, Nearctic, and Andean regions. The Arctic region formed one distinct cluster in this analysis. The Polynesian region appeared as several separate subclusters of a broader “islands worldwide” cluster, and its validity, as far as vertebrates are concerned, would presumably need to be tested at the species level. One subcluster derived here is recognized as a New Zealand subregion on the basis of its much higher Holocene generic diversity, although this diversity has now been partly obliterated by human hunting and alien-species introductions (see McDowall 2008). All of the regions and subregions accepted here, and presented in figure 1, are also listed for convenience in table 1. In addition, the assignment of Olson and collaborators’ (2001) ecoregions to our regions is given in supplemental appendix S2, and this list can be used as an update to the assignment (which was partly based on Udvardy [1975]) that was already provided by Olson and colleagues (2001).

with—where it was possible—the ecoregional names of Olson and colleagues (2001).

Three further zoogeographical regions recognized in prior regionalization studies could not be confirmed here because of the nature of our data set and methods. These are tentatively accepted here without following the same empirical methods applied for the other regions. An *Antarctic* region can be recognized as the region represented by all southern polar and subpolar ecoregions in which all vertebrates are

Characteristic genera

After we finalized the boundaries of the zoogeographical regions, the characteristic genera for each region were identified on the basis of the match between their distribution (at the ecoregion level) and the extent of the zoogeographical region. The degree of match was calculated by multiplying a measure of occupancy (the percentage of the ecoregions in a zoogeographical region where a genus occurs) by a measure of endemism (the percentage of ecoregions where a genus

occurs located in that zoogeographical region). A match of 0.5 was considered sufficient for a genus to be listed as characteristic for a zoogeographical region (e.g., a genus occurs only in that region and occupies at least 50% of the ecoregions in it; a genus occurs in all ecoregions in a region and in at most an equal number of ecoregions outside that region; or, most often, intermediate cases).

There were both commonalities and differences between generic diversity across clusters (see the histograms in figure 1) and the number of genera characteristic to the corresponding zoogeographical regions (table 2, supplemental appendix S3). Unsurprisingly, the ecoregions with the highest generic diversity across all taxa fell in the Neotropical, Ethiopian, and Indo-Malaysian clusters, which comprise the largest tropical rainforest areas (see Prentice et al. 1992). In the bird analysis, the top 10 ecoregions were all Neotropical, whereas in the mammal analysis, they were Afrotropical, and in the herpetofauna analysis, Indo-Malaysian ecoregions were also represented. The Neotropical and Ethiopian regions (as delimited here) also had the highest number of characteristic genera but

were followed by the Australian and New Guinean regions, and the Indo-Malaysian region remained relatively poorly defined. The Nearctic, Palearctic, and Andean clusters comprised low generic diversity ecoregions. The zoogeographical regions with the lowest numbers of characteristic genera were the Arctic, Andean, Polynesian, and Antarctic regions (which all had zero characteristic genera), followed by the Wallacean region (which had four such genera). The Nearctic and Palearctic regions, however, had substantial numbers of characteristic genera (table 2).

Limitations: Data and protocols

It can be argued that the World Wide Fund for Nature ecoregions (Olson et al. 2001) are far from perfect as units of analysis. It has been highlighted before that, ideally, a study of this nature should be based on equal-area units free of predetermined biogeographical meaning (Procheş 2005). It can also be argued that the distributional data in the WildFinder database, albeit comprehensive, are not complete. However, despite these shortcomings, it is the only database available for global analyses of this nature

Table 2. Characteristic tetrapod genera for the zoogeographical regions recognized here.

Region in the present article	Amphibia	Serpentes	Other Squamata	Passeriformes	Other birds	Chiroptera	Other mammals
Nearctic (35)	<i>Pseudacris</i> (Hylidae) 72%	<i>Thamnophis</i> (Colubridae) 57%	—	<i>Junco</i> (Emberizidae) 86%	<i>Colaptes</i> (Picidae) 55%	<i>Lasionycteris</i> (Vespertilionidae) 69%	<i>Ondatra</i> (Muridae) 77%
Caribbean (12)	<i>Osteopilus</i> (Hylidae) 52%	<i>Alsophis</i> (Colubridae) 65%	<i>Cyclura</i> (Iguanidae) 58%	<i>Spindalis</i> (Emberizidae) 63%	<i>Saurothera</i> (Cuculidae) 58%	<i>Monophyllus</i> (Phyllostomidae) 79%	—
Neotropical (208)	<i>Leptodactylus</i> (Leptodactylidae) 76%	<i>Micrurus</i> (Elapidae) 60%	—	<i>Myiodynastes</i> (Tyrannidae) 83%	<i>Chloroceryle</i> (Cerylidae) 85%	<i>Glossophaga</i> (Phyllostomidae) 90%	<i>Eira</i> (Mustelidae) 85%
Palearctic (33)	—	<i>Natrix</i> (Colubridae) 51%	—	<i>Prunella</i> (Prunellidae) 74%	<i>Alectoris</i> (Phasianidae) 61%	<i>Plecotus</i> (Vespertilionidae) 50%	<i>Apodemus</i> (Muridae) 81%
Afrotropical (138)	<i>Kassina</i> (Hyperoliidae) 80%	<i>Dasypeltis</i> (Colubridae) 79%	<i>Agama</i> (Agamidae) 59%	<i>Sylvietta</i> (Macrosphenidae) 87%	<i>Plectropterus</i> (Anatidae) 88%	<i>Eidolon</i> (Pteropodidae) 87%	<i>Loxodonta</i> (Elephantidae) 84%
Madagascan (38)	<i>Boophis</i> (Mantelliidae) 55%	<i>Langaha</i> (Lamprophiidae) 55%	<i>Zonosaurus</i> (Gerrhosauridae) 73%	<i>Foudia</i> (Ploceidae) 91%	<i>Coracopsis</i> (Psittacidae) 82%	—	<i>Cryptoprocta</i> (Eupleridae) 64%
Indo-Malaysian (43)	<i>Fejervarya</i> (Ranidae) 54%	<i>Bungarus</i> (Elapidae) 51%	—	<i>Hypothymis</i> (Monarchidae) 68%	<i>Phaenicophaeus</i> (Cuculidae) 76%	<i>Cynopterus</i> (Pteropodidae) 76%	<i>Lutrogale</i> (Mustelidae) 78%
Wallacean (4)	—	—	<i>Hydrosaurus</i> (Agamidae) 53%	—	<i>Tanygnathus</i> (Psittacidae) 69%	<i>Acerodon</i> (Pteropodidae) 69%	—
New Guinean (68)	<i>Hylophorbus</i> (Microhylidae) 65%	<i>Aspidomorphus</i> (Elapidae) 80%	—	<i>Mino</i> (Sturnidae) 75%	<i>Lorius</i> (Psittacidae) 81%	<i>Syconycteris</i> (Pteropodidae) 60%	<i>Echymipera</i> (Peramelidae) 80%
Australian (119)	<i>Pseudophryne</i> (Myobatrachidae) 78%	<i>Suta</i> (Elapidae) 92%	<i>Egernia</i> (Scincidae) 100%	<i>Pardalotus</i> (Pardalotidae) 97%	<i>Chenonetta</i> (Anatidae) 100%	<i>Vespadelus</i> (Vespertilionidae) 97%	<i>Pseudomys</i> (Muridae) 95%

Note: The total number of genera meeting the 50%-match criterion is given in parentheses after each region's name (there are no characteristic terrestrial genera for the Arctic, Andean, Polynesian, and Antarctic regions). Also given are the genera in each taxonomic group with the highest match values (percentage match; the families they belong to in parentheses; see the text for the calculation of match values). The family assignment was according to the data set (WWF 2010), except where taxonomic changes were recognized in recent years (e.g., Alström et al. 2006, Kelly et al. 2009).

that incorporates all tetrapod vertebrates (Lamoreux et al. 2006, Funk and Fa 2010). We were able to detect only a few instances in which these problems were reflected in our results (ecoregions are probably too coarse of a scale to accurately reflect species distributions in the Andes, where presumably continuous patterns appeared fragmented in some of the analyses, and the lack of bird data from the Korean Peninsula in the database resulted in a blank spot on the relevant map, which should in all likelihood be incorporated in the Palearctic cluster; figure 1c).

Beyond these data-related caveats, the statement that the world's biogeographical regions can indeed be confirmed across taxa following rigorous analyses—our main proposition in this article—needs to be dissected further.

First, we have to clarify the concept of *taxa* as it is applied here. One of the three groups separated here (the herpetofauna) is paraphyletic to the other two (birds and mammals; Hugall et al. 2007). Analyses of monophyletic subsections of this group (Amphibia, Squamata; the results are not presented here) failed to show any results resembling the overall patterns. However, this is clearly just a taxon-size effect; the distribution of the herpetofauna as a whole is virtually identical to the sum of those of the other two groups. Furthermore, the Amphibia and Squamata subgroups are also linked by other characteristics, such as poikilothermy and limited dispersal abilities (at least compared with birds; see Mehranvar and Jackson 2001). Therefore, we consider herpetofauna to be a valid group for biogeographical and macroecological analysis.

Second, two of the procedures we followed here involved a certain degree of subjectivity: One was the selection of the cutoff point (the number of genera) beyond which an ecoregion was included in the relevant analysis, and the second was the selection of cross-taxon matching clusters in each dendrogram. Multitaxon biogeographical analyses in which such procedures are avoided (e.g., Rueda et al. 2010) do show great similarity across taxa, albeit not quite to the extent illustrated here. But true biogeographical commonalities may simply be more complex than what current computational algorithms can handle. Our search for common patterns across taxa is consistent with current approaches in systematics; more specifically, they are akin to defining monophyletic taxa on phylogenetic trees on the basis of different criteria (e.g., nuclear DNA, mitochondrial DNA, morphology), without imposing the condition that all taxa at one given level (e.g., families) must be of comparable evolutionary age or that each taxon must contain equal numbers of lower taxa (e.g., 10 genera in each family). It is quite likely that a “consensus tree” approach to the study of regionalization will soon be available to further reduce subjectivity, without a loss in meaningful patterns.

Here, we tried to standardize both of the potentially subjective procedures in a way that would make our work repeatable, and we believe that, to a great extent, we succeeded. Although it can be argued that the very process of standardizing these methods was a subjective one and one

potentially influenced by knowledge of prior regionalization studies, it was certainly not subjective enough to prevent us from recognizing distinct and novel patterns.

Cross-schemata comparisons

Although our regionalization study comprises a number of units similar to those of prior studies, there are several novel aspects (see table 1). The recognition of a New Guinean region is new under a global zoogeographical perspective, although it has been pointed out repeatedly both that the island is home to a host of unique lineages and that these lineages result in substantial overall differences between its fauna and those of Australia, the Indo-Malay archipelago, and the Pacific islands (Gressitt 1958, Holloway and Jardine 1968, De Boer and Duffels 1996). The latter claim is supported by our combined analyses but even more poignantly by a separate analysis on bats (appendix S1), in which New Guinea is more distinct from tropical Asia than Australia is (New Guinea and Wallacea in this case qualify as 2 of the 10 most distinctive clusters, whereas Australia groups with Madagascar and most of tropical Asia). It can also be argued that the uniqueness of the island's biota was already recognized in the sheer fact that its zoogeographical and geobotanical assignments differed markedly (grouped with Australia in zoogeography [see above] but with tropical Asia in geobotany [see Engler 1879–1882, Good 1974]). A transitional area between the tropical and temperate parts of South America has been discussed before (Morrone 2006) but is, to our knowledge, a new concept as a subregion in a global context. The subregional status of the Sahero-Arabian and Sino-Himalayan transition zones, which has been suggested before (Udvardy 1975, Smith 1983) but has not been widely accepted, is recognized here with more solid grounding, on the basis of both their distinctive assemblages (figure 1) and unstable previous assignment (table 1).

Note that, although the clusters recognized here as regions are remarkably stable with respect to the vertebrate groups contained within them, larger groupings are not (see the dendrograms in figure 1, in which cluster relationships vary widely from one taxon to another). Some common but not universal patterns are the close relationships (a) among the Palearctic, Indo-Malaysian, and sometimes the Madagascar clusters; (b) among the Nearctic, Caribbean, and Andean clusters; and (c) between these two broader groupings taken together. These patterns can be explained by the Palearctic and Madagascar clusters' having relatively impoverished faunas (Smith 1983) compared with the neighboring Indo-Malaysian and Afrotropical clusters. Likewise, the Nearctic, Caribbean, and Andean clusters have impoverished faunas when compared with the Neotropical cluster (see the histograms in figure 1). These patterns suggest that their relationships are based on shared absences rather than on shared presences and raise the question of whether such patterns can also dictate grouping at the level of regions.

To answer this question, the analysis in which the characteristic genera are sought for each region (genera whose distribution matches the shape of the region well) failed to show any terrestrial genera in the case of the Arctic, Antarctic, Polynesian, and Andean regions, and showed only four genera for the Wallacean region (table 2). The first three of these regions are indeed genus impoverished, but the Andean and Wallacean regions certainly contain numerous endemic vertebrate genera, although these genera are localized within the region (e.g., distributions in the Valdivian rainforests, but not in the high Andes or Patagonia; in the Philippines but not in Sulawesi and vice versa; Crisci et al. 1991, Jones and Kennedy 2008). Therefore, it is apparent that these regions are defined primarily on the basis of shared absences (missing Neotropical genera in the case of the Andean region; missing both Indo-Malaysian and New Guinean genera in the Wallacean region). This need not disqualify them as regions (see Smith 1983 for a discussion of islands), since all of them represent unique complements of vertebrate genera that merit recognition.

Higher numbers of characteristic genera indicate higher regional cohesion, irrespective of the presence of more-localized endemism hotspots (see Mittermeier et al. 2004) in the case of broad regions. It is unsurprising that the Neotropical region should have the highest number of such genera, given that it contains the largest proportion of Earth's vertebrate diversity (see the histograms in figure 1; also see Newton and Dale 2001). It is however notable that the Afrotropical region has more characteristic genera than the Indo-Malaysian region, despite the two holding similar total numbers of genera, and this reflects Africa's longer and more-complete biogeographical isolation (Kingdon 1989). The impressive number of genera that characterizes the novel New Guinean region and the Australian and Madagascan regions may appear to be a reflection of these regions' present insular state, although historically New Guinea and Australia were connected until very recently (Williams et al. 2009), and their intermittent separation is not responsible for the differences between them (also note that these differences are lower at the family level; Kreft and Jetz 2010). Tropical Africa and Australia are the only two regions so well defined that they have characteristic genera in each of the seven major groups considered in table 2. Australia also holds the genera best matching in their distribution the regional borders, which indicates the presence of habitats (such as semiarid wattle and eucalyptus-dominated systems; Mackey et al. 2008) ubiquitous throughout the region (table 2, appendix S3).

So what is a zoogeographical region?

Biome borders can easily be predicted from environmental variables (Prentice et al. 1992), but biogeographical regionalization has a lot more to do with history, although historical biogeography hypotheses are often limited to describing the rather ancient sequence of tectonic events in the splitting of Gondwana and Laurasia (e.g., Boyer et al. 2007).

Our regionalization study does confirm the importance of history, although it can be argued that some environmentally determined boundaries, when they are maintained for sufficiently long periods, act as historical barriers as well (see Brown et al. 1996). Thus, it could be argued as a matter of convention that where a regional boundary separates two regions dominated by different environmental conditions, this separation should be described as an environmentally determined boundary. Even so, the distinctness of Madagascar from nearby Africa, which has similar environmental conditions, is clearly driven by historical isolation (Yoder and Novak 2006; as are the differences between the Caribbean, Wallacean, and Polynesian regions and their neighbors). The borders viewed here as environmentally determined are either caused by humid-dry contrasts (Afrotropical-Paleartic, New Guinean-Australian) or, more often, by differences in temperature (tropical-temperate in the case of the Neotropical-Andean, Neotropical-Nearctic, and Indo-Malaysian-Paleartic differences, although humidity differences also play a role along parts of these borderlines, and temperate-polar for all borders in the case of the Arctic; see Prentice et al. 1992). Irrespective of the factors determining these borderlines, some regions and especially subregions have faunas that are transitional between two neighboring regions (Wallacean, Central American, La Plata, Sino-Himalayan), albeit still characterized by strong endemic components (see, e.g., the "hotspot" status of some such regions; Mittermeier et al. 2004). In the case of the Sino-Himalayan cluster, its inclusion in the Palearctic region was a truly borderline one, because it could be almost equally well incorporated in the Indo-Malaysian region, although its subregional status in a global context is less questionable.

Cross-taxon comparisons

The differences between clusters derived for the herpetofauna, birds, and mammals (figure 2b, 2c, 2d) need to be explained case by case. Mammalian patterns have been discussed in detail in a recent paper by Kreft and Jetz (2010). The bird analysis is the most complete (figure 2c; with sufficiently high generic diversity at high latitudes) but is also the closest to mirroring purely environmental schemata, such as biome-based ones (Prentice et al. 1992). This result clearly reflects birds' better dispersal abilities, which allow them to optimize their distributions according to environmental variables (Lester et al. 2007; also cf. the clusters obtained for bats, where islands are more prominently featured, in appendix S1). However, bird clusters are also most similar to previous zoogeographical regions (e.g., North Africa is part of the Palearctic region). The world's zoogeographical regions have indeed been first determined on the basis of bird-distribution patterns (Sclater 1858), and biome borders (which birds follow) also influenced regional thinking. The least complete and most unusual clusters were derived in the case of the herpetofauna, which is poorly represented in most temperate regions (figure 2b) and is also characterized by the

lowest dispersal abilities. Two of the clusters derived here deserve special mention for their distinctive faunas: one in eastern South America (eastern Brazil and Uruguay but including only part of the Mata Atlântica hotspot and only moderately similar in extent to the La Plata cluster observed in the mammal analysis and that for all tetrapods; figure 2b) and one in southern China and northern Indochina (largely included in the Indo-Burma hotspot; it is more similar in terms of herpetofaunal genera to the one represented by the main western Indonesian islands than it is to others, but is nevertheless substantially distinctive from it). Both of these clusters have large numbers of characteristic herpetofaunal genera (21 and 11, respectively; supplemental appendix S4) and deserve a special conservation focus on amphibians and reptiles. Although both of these regions are currently the subjects of substantial herpetological research, mostly motivated by their high species diversity (e.g., Bain and Truong 2004, Carnaval et al. 2009), their recognition as units in a global context is, to our knowledge, novel.

Approaches similar to the global regionalization approach presented here are starting to be possible for higher plants, although the taxonomic units of analysis in that case are more likely to be families (Stevens 2010). To date, Kier and colleagues (2005) looked at floristic knowledge in the world's ecoregions, and Giam and colleagues (2011) examined the potential conservation applications of an ecoregional framework for higher plants. More accurately, for both plants and animals, it will soon become possible to employ shared phylogenetic branch length (Pagel 1994) rather than shared taxa, in calculating similarity values for broad animal groups. Previous analyses (Procheş et al. 2009) in which the biogeographical and ecological explanatory power of phylogenetic and taxonomic measures were compared suggest that the resulting clusters will not be notably different. However, listing characteristic lineages for each region will undoubtedly be a lot more meaningful than listing characteristic genera. Distinctive patterns are likely to be observed in narrower and especially in dispersal-limited groups, as was the case here for the herpetofauna. However, the remarkable similarity between our results and intuitive descriptions of regionalization, as well as analytical ones in which various methods, groups of organisms, and levels of taxonomic resolution are considered, suggests that our results are likely to remain largely stable. Nevertheless, in a context in which biogeographical regionalization research seems to be going through a revival (Kreft and Jetz 2010, Rueda et al. 2010), we would certainly welcome any further developments.

The final point we would like to make in the present article refers to general versus specialized biogeographical schemata. We purposefully sought commonalities across taxa in an attempt to test whether these commonalities truly agree with prior intuitive knowledge. Other recent articles (Mackey et al. 2008, Kreft and Jetz 2010) have, on the contrary, highlighted the diversity of approaches that one can take in delimiting biogeographical regions, and there has

been wide support (Procheş 2008, Cox 2010) for the need for such specialized approaches. At the same time, one cannot ignore the success of well-marketed single takes on global biogeography, such as biodiversity hotspots (Mittermeier et al. 2004) and ecoregions (Olson et al. 2001), despite their being largely intuitive and often imprecise, in focusing global conservation initiatives. In the same way, we feel that the study of regionalization, to establish its recently found new life, needs to find a central common ground. In this context, the next steps would have to involve the incorporation of additional taxa, such as higher plants and selected invertebrates, besides vertebrates, in single comprehensive exercises.

Conclusions

In brief, numerical methods can be used to delimit zoogeographical regions very similar to those based on pure intuition, although some notable differences remain if any degree of repeatability is to be preserved. On one hand, the extensive similarities between numerical and intuitive approaches commend the visionary thinking and broad understanding of our natural world by the pioneers of this field—primarily by Alfred Russel Wallace. On the other hand, the complex series of steps needed to reproduce these regions, although these steps are largely repeatable, involves at this stage a number of questionable decisions, and substantial progress in biogeographical cluster analysis techniques will be needed to eliminate these. One important development would be the global-scale use of nonhierarchical clustering (likely to deal better with the problems of transitional and low-diversity areas; Jardine and Sibson 1968; Beck et al. 2006) and R-mode and Q-mode analyses (which would permit the definition of regions and characteristic groups at the same time; Birks and Deacon 1973, Thuiller et al. 2006). The rapid progress made in phylogenetic analysis suggests, however, that such steps could be achieved relatively quickly, should regionalization research gather similar momentum, and indeed, phylogenetic and regionalization analyses could be integrated (very promising steps were recently made by Pavoine et al. 2011). Although we looked only at animal distributions in this article, and the term *zoogeographical* is used throughout, we acknowledge here that the differences between plant and animal regions are not as poignant as was previously argued (but see van Steenis 1950, Woodruff 2010) and that the ultimate goal of global regionalization efforts would be to integrate the two, over and above any genuine and substantial plant–animal differences. On the basis of the available analyses, the high level of agreement between plant and animal regionalization schemata, both intuitive and numerical, can be viewed only as strong support for their accuracy and value in understanding life on Earth.

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