



# The world's biogeographical regions: cluster analyses based on bat distributions

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## ABSTRACT

**Aim** Both floral kingdoms and faunal regions have so far been intuitively defined. This study was conducted to compare these with an analytical regionalization based on cluster analyses in a fairly homogeneous, globally distributed group of organisms: the bats (order Chiroptera). This comparison was used to discuss the possibilities of employing clustering techniques in global biogeography.

**Location** The study considered bat distributions world-wide.

**Methods** Analyses were conducted both for presence/absence of genera and species, and for the number of species in each genus. Clusters distinguished at selected dissimilarity values were mapped.

**Results** A set of *c.* 10 regional clusters recurred in the analyses, broadly corresponding not only to the world's accepted faunal regions and subregions, but also to the floral kingdoms and subkingdoms.

**Main conclusions** This study is an analytical confirmation of the fact that similar global distribution patterns are to be found in different groups of organisms. Cluster analyses can be used to refine global regionalization schemes, and, with the accumulation of such data for different taxa and ecologically defined groups, shared patterns can be used to draft one common global biogeographical regionalization. At the same time, differences between the regionalization schemes derived for different groups can be used to partial out the role of dispersal abilities, body size, evolutionary age, etc., in determining global distribution patterns.

## Keywords

Bats, biogeographical regions, Chiroptera, cluster analysis, floral kingdoms, faunal regions, global biogeography, macroecology.

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## INTRODUCTION

When the early biogeographers (Wallace, 1876; Engler, 1879–1882) started dividing the world map into floral kingdoms and faunal regions, their only guide was their own knowledge, and that of people who, much like them, had travelled broadly, and had noted the composition of floras and faunas. More recently, analytical approaches have worked their way into biogeography (Udvardy, 1969), and clustering procedures are now commonly employed (e.g. Williams *et al.*, 1999; Qian, 2001; Kingston *et al.*, 2003), especially following the realization that biogeographical units are hierarchically arranged (McLaughlin, 1992). However, no attempts have been made to apply such clustering procedures at a global scale.

A few global-scale organism distribution studies (Conran, 1995; Procheş & Marshall, 2001; Procheş, 2001) employed multivariate techniques to establish relationships between various world regions, but without the explicit purpose of proposing global biogeographical regionalizations. Furthermore, two of these studies (Conran, 1995; Procheş & Marshall, 2001) employed previously (and subjectively) defined regions as basic units for analysis, which would make any resulting regional scheme somewhat circular.

Refinements in biogeographical schemes at global (and to a great extent even regional) scales are currently made mainly on the basis of expert knowledge and surrogate variables such as climate, soil types, geology and vegetation types (Thackway & Cresswell, 1995; Adey & Steneck, 2001; Olson *et al.*, 2001).

While the value of such 'ecoregions' for conservation science cannot be denied, these must not be confused with the true biogeographical (faunal/floral) regions, which are determined by the distributions of plant and animal taxa as such.

Where taxon distributions are considered, there are currently gaps between classic (intuitive) biogeography, still used in teaching but never analytically tested, simple multivariate biogeography (generally at the regional scale) and macroecological approaches (at various scales and involving various degrees of methodological sophistication, but which are somewhat forgetful of classical biogeography). In an attempt to bridge these fields, I test here the hypothesis that cluster analyses conducted on the distributions of bat species and genera will largely confirm the world's terrestrial biogeographical regions, as traditionally defined.

## MATERIALS AND METHODS

### The study group

Bats (Order Chiroptera) represent an excellent group for testing hypotheses on global distribution patterns, for at least four reasons: (1) the total number of species (around 1000) is large enough to give reliable results, but not so large as to cause computational problems; (2) they are distributed globally, occurring in all major unglaciated landmasses; (3) taxonomically, they are generally accepted to be a monophyletic group, and (4) ecologically, they represent a well-defined group, little overlap occurring between their niches and those of other organisms (due to the combination of uniquely mammalian characters with the power of true flight – in most species also echolocation and nocturnal life; see Findley, 1993). Fine-scale patterns of bat species diversity have been mapped globally, and even one simple cluster analysis on the presence/absence of genera in predefined zoogeographical regions has been conducted (Findley, 1993); however, defining biogeographical units (at any scale) on the basis of bat distribution has not been attempted.

### Data set and data analysis

The world map was divided into 288  $15^\circ \times 15^\circ$  quadrats, and a species data base was compiled for the distributions of the 978 bat species listed by Corbet & Hill (1991) at this scale. Since

1991, several taxonomic changes have taken place, however these are unlikely to affect global patterns significantly. The  $15^\circ$  scale may appear rough, but large scales are in several ways appropriate for analysing global patterns (Blackburn & Gaston, 2002), and they allow for mapping distributions globally with a minimum number of false absence values (Simpson, 1960). Species diversity was mapped, and only the 92 squares with at least five species each were considered in further analyses, both to maintain a reasonably small data set, and to concentrate on those world areas with substantial bat faunas.

The quadrats were clustered on the basis of a Bray–Curtis dissimilarity matrix (group average linkage, PRIMER 6.2.4, 2001; PRIMER-E Ltd, Cambridge, UK). In biogeographical analyses, Kulczynski's index is normally employed (e.g. Conran, 1995); however, Bray–Curtis dissimilarity (in its presence/absence form identical with Sørensen, also used in e.g. Kingston *et al.*, 2003), while differing in actual dissimilarity values, results in the same clusters, and allows for species numbers to be further used untransformed. Three different data sets were used: (1) genera presence/absence, (2) number of species in each genus, untransformed, and (3) species presence/absence. The clusters defined at 50% and 75% dissimilarity were mapped.

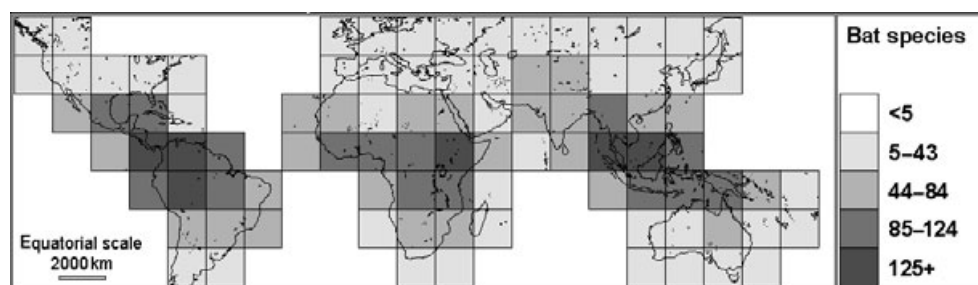
### Terminology

The use of the word 'region' in the following sections broadly follows faunal regionalizations (Darlington, 1957). Floral regions are finer units, representing subdivisions of kingdoms or subkingdoms (Good, 1974); this sense of the word will be avoided. The subdivisions of regions or subregions will be referred to as provinces.

## RESULTS AND DISCUSSION

### Diversity patterns

Global patterns of bat species richness (Fig. 1) are fairly typical of terrestrial biodiversity, with three centres of highest species concentration ( $> 125$  species/quadrat), in tropical America, tropical Africa and Southeast Asia (the Indochina – Sumatra – Borneo region). All these are limited to the equatorial band  $15^\circ$  N to  $15^\circ$  S. High species numbers ( $> 85$  species) can be found in the  $30^\circ$  N to  $15^\circ$  S band, moderate values (44–84 species) in the  $45^\circ$  N to  $30^\circ$  S band, and low diversity values



**Figure 1** Global patterns of bat species diversity at the  $15^\circ$  scale. For patterns using a finer grain size, see Findley (1993).

(5–43 species) extend as far as 60° N and 45° S. Very low values (0–4 species) are characteristic of high latitudes or of isolated oceanic islands. The 92 quadrats with at least five bat species each form two distinct areas (Old and New World) not sharing any resident species, but sharing several genera in Molossidae and Vespertilionidae.

### Geographical clusters

The clustering procedures on genera presence/absence, number of species in each genus (untransformed) (clusters defined at 50% dissimilarity), and species presence/absence (clusters defined at 75% dissimilarity), resulted in *c.* 10 (between nine and 11) clusters (Figs 2 & 3).

Among these, the clusters were best defined in the genera presence/absence analysis, any dissimilarity value between 47% and 62% resulting in the same nine clusters [tropical South America, Patagonia, North and Central America, Caribbean, tropical Asia (including Sulawesi and New Guinea), Africa (including Madagascar), temperate Eurasia, Australia and Melanesia]. The first dichotomy was the one separating the New and Old World from one another. In the New World, tropical South America and Patagonia separated early from North and Central America and the Caribbean, while in the Old World the most distinctive grouping was represented by Australia and Melanesia (Fig. 2a).

The analysis on numbers of species in each genus showed generally similar clusters, with the following differences: (1) it placed North America and Patagonia in one 'temperate American' cluster; (2) it separated Madagascar from Africa; (3) it separated New Guinea (together with Sulawesi and the Philip-

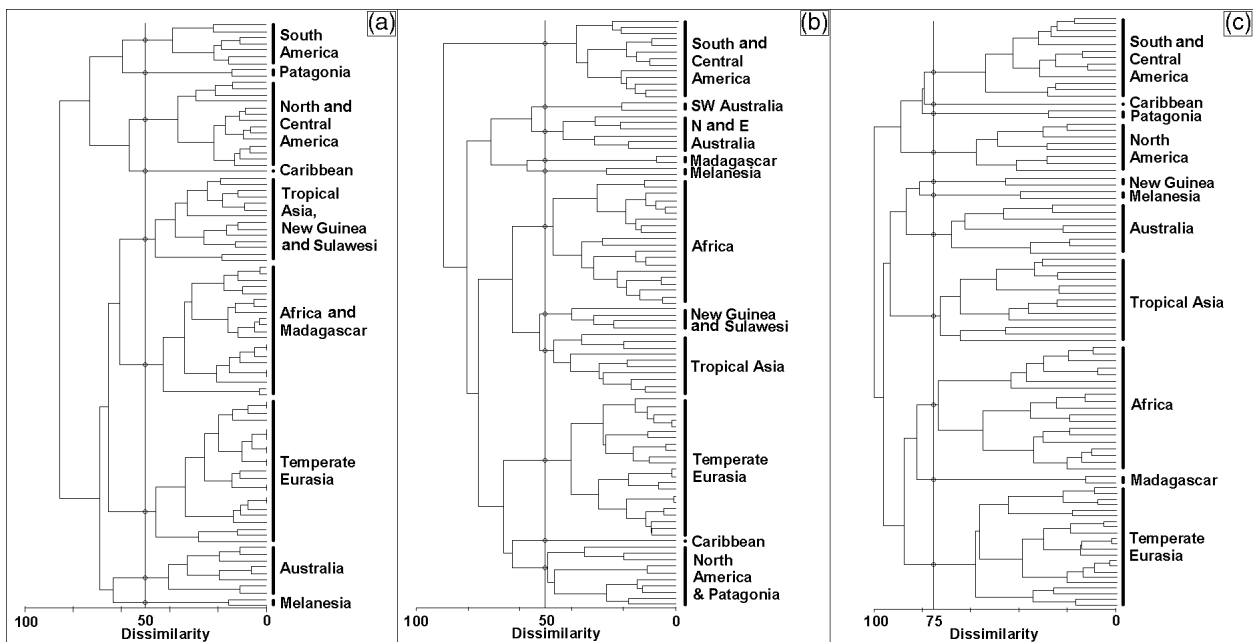
pinus) from tropical Asia; and (4) it separated SW Australia from the rest of the continent. Despite this general resemblance with the previous analysis, the early dichotomies were different, with tropical America breaking off first, followed by an Australia-Oceania-Madagascar grouping, and by an extended northern temperate-Patagonia-Caribbean one (Fig. 2b).

In the analysis on species presence/absence (75% dissimilarity), North America and Patagonia were separated from each other, and the New Guinea cluster was reduced to two quadrats. Sulawesi and the Philippines clustered with tropical Asia. The main disjunction here was again the one between the New and Old World, however, the groupings within each of these were different from the ones in the genera presence/absence analysis (Fig. 2c).

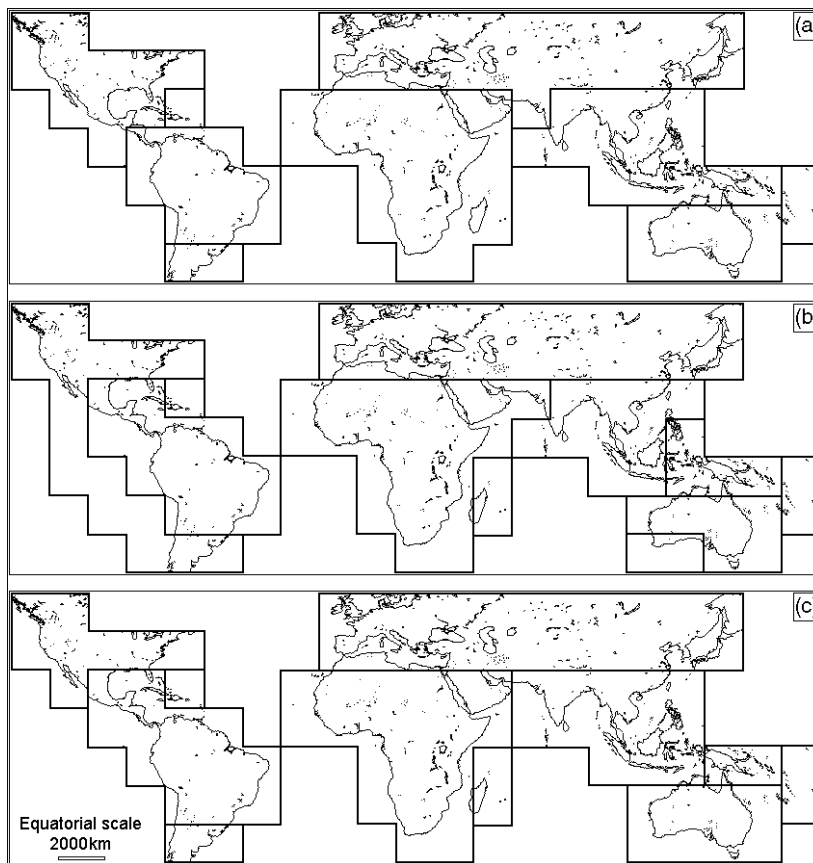
The quadrat including the western parts of the Indian subcontinent had a labile position, clustering with temperate Eurasia in one analysis, with Africa in the second one, and with tropical Asia in the third. The clusters in the last two analyses were not as well defined as in the first one, as shifting the dissimilarity values by only a few per cent resulted in losing or adding several clusters. It must be noted that although the two to four major clusters separated in each analysis were different (Fig. 2), the analyses converged towards a common pattern around the dissimilarity values that separated *c.* 10 (nine to 11) clusters in each case (Fig. 3).

### Comparisons with classic regionalizations

These *c.* 10 clusters correspond fairly well with world's accepted biogeographical units [faunal regions and subregions (Darlington, 1957); floral kingdoms and subkingdoms (Good,



**Figure 2** Three global clustering procedures (group average linkage, Bray–Curtis dissimilarity) based on bat distributions. (a) Genera presence/absence (nine clusters separated at 50% dissimilarity); (b) number of species in each genus, untransformed (11 clusters separated at 50% dissimilarity); (c) species presence/absence (11 clusters separated at 75% dissimilarity).



**Figure 3** Three global regionalizations based on clustering procedures performed on bat distributions. (a) Genera presence/absence (nine clusters separated at 50% dissimilarity); (b) number of species in each genus, untransformed (11 clusters separated at 50% dissimilarity); (c) species presence/absence (11 clusters separated at 75% dissimilarity).

1974)] (Fig. 4a,b). A remarkably similar regionalization was derived by mapping the nine clusters obtained at 50% dissimilarity by Conran (1995) using the distributions of *Liliiflorae* (although considering different taxonomic ranks) (Fig. 4c). These similarities and differences are discussed below, region by region.

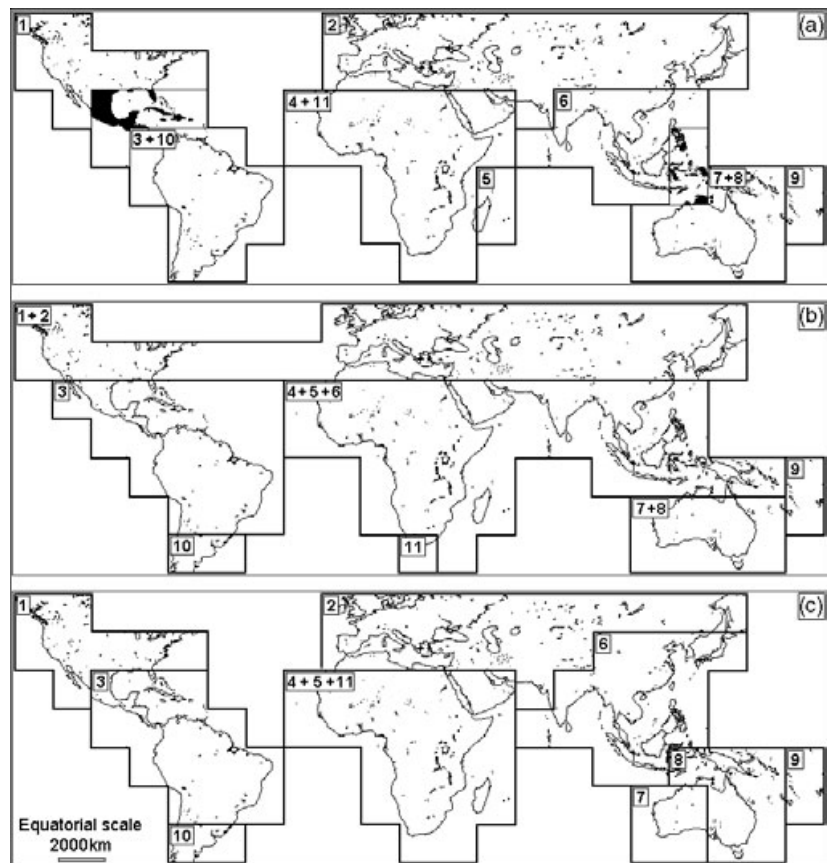
North America is recognized as the Nearctic subregion in Darlington's (1957) faunal regional scheme, with Central America defined as a transitional region towards the Neotropics. It also emerges as a cluster in Conran's (1995) study, although Good (1974) includes it in the Holarctic Kingdom, even denying it the subkingdom rank. In the present study, North America represented a distinct cluster in the genera presence/absence analysis (incorporating continental Central America), as well as in the species presence/absence analysis (where Central America clustered with South America, in a Neotropical cluster, as accepted in geobotanical regionalization; Good, 1974). The Patagonian cluster, which emerged here in two out of three analyses, was also recognized in Conran's (1995) analysis, and it also corresponds to Good's (1974) Patagonian Region. According to Good (1974), the Patagonian Region is part of a border Antarctic Kingdom. No other parts of this kingdom (e.g. New Zealand) were included in the bat analyses, and there are no bat taxa with a broad Antarctic distribution, that would parallel plant or invertebrate distributions. The most unusual feature amongst the New World clusters derived in the present study is the Caribbean cluster, recognized in two out of three analyses,

but not having received such high recognition in any previous biogeographical regionalization. It has been acknowledged recently though, that the Caribbean has distinct species assemblages in several other plant and animal groups (Dávalos, 2004).

Temperate Eurasia (the Palearctic, Darlington, 1957, or part of the Holarctic in Good, 1974) appeared as a well-defined cluster, almost identical in all three analyses on bat distributions. Slightly different contours were derived in Conran's (1995) study, where East Asia clustered with tropical Asia. This can be explained by the strong Mediterranean-climate affinities of the geophytes, dominant in *Liliiflorae* (Procheş *et al.*, in press), which make the Mediterranean-Central Asian flora clearly distinct from the East Asian one.

Sub-Saharan Africa was recognized as the Ethiopian Region by Darlington (1957), including a Madagascar Subregion. Very similar results were found in the bat distributions, with Madagascar separating from Africa in two of three analyses. In Good's (1974) geobotany, both of these are included in the Palaeotropical Kingdom, however, a South African Kingdom is separated (with a single region: the Cape). The Cape does not show a high dissimilarity from the rest of Africa in terms of its bat fauna. Interestingly enough, neither does it in terms of higher taxa in *Liliiflorae* (Conran, 1995), despite the huge number of endemic species (cf. Procheş *et al.*, in press).

All three analyses on bat distributions recognized a tropical Asian cluster, an Australian cluster, and a Melanesian cluster. To these, a New Guinean cluster was added in two analyses, in



**Figure 4** Three classic global regionalizations, approximately adapted to the analysis units used in the present study. (a) Darlington's (1957) faunal regions and subregions, indicating the Celebesian and Caribbean transitions (solid); (b) Good's (1974) floral kingdoms and subkingdoms; (c) the nine clusters separated at 50% dissimilarity in Conran's (1995) study on families/sub-families of Liliiflorae. Regional units: 1, Nearctic; 2, Holarctic (1 + 2 = Boreal/Holarctic); 3, Neotropical; 4, African (Ethiopian); 5, Madagascan; 6, Indo-Malaysian (Oriental); 7, Western/Central Australian; 8, Northern/Eastern Australian (7 + 8 = Australian); 9, Polynesian (as illustrated here, Melanesian); 10, Patagonian; 11, South African (Cape).

one of which this included the Celebesian transition (Sulawesi). In the analysis on species numbers for each genus, a SW Australian cluster was also recognized. These results best compare with Darlington's (1957) scheme, with the difference that here New Guinea is part of the Australian Region [as in Conran's (1995) analyses], a fact not confirmed by bat distributions. In this respect, Good's (1974) floral scheme appears closer to chiropteran ones, with New Guinea being a part of the Palaeotropical Kingdom, thus closer to tropical Asia, than to Australia. While New Guinea and Australia may share a common evolutionary history, present-day climatic conditions are overwhelmingly different, and distinct sets of ancient Australasian taxa persist in the two regions, although this is less obvious in Liliiflorae and non-flying mammals.

Overall, the regional schemes derived from bat distributions (Fig. 3) are not necessarily closer to the faunal regions as traditionally defined (Fig. 4a), presenting common points with regionalizations derived from classic or analytical studies of plant distributions (Fig. 4b,c).

### Biogeographical regions, diversity and endemism centres

By comparing the species diversity map (Fig. 1) with the cluster-derived regionalizations (Fig. 3), it becomes obvious that some of the resulting regions are species rich (tropical America, Africa, tropical Asia), while others are species poor (North America,

Patagonia, temperate Eurasia, Melanesia). Some (Patagonia, SW Australia) almost completely lack endemics. With the clustering procedure employed here, regions are not necessarily defined around high diversity areas, neither following the distribution of endemic taxa, but rather as different species assemblages, some including endemics, some not. In this respect, the method used here is in disagreement with most of the traditional approaches to biogeographical regionalization, which call for an endemic element, if not for a diversity centre, to characterize a biogeographical region. To understand this situation, a short historical note is in order.

The origin of Engler's (1879–1882) floral regions can be traced back to de Candolle's (1820) areas of endemism. After Handlirsch's (1913) endemism analysis for Wallace's (1876) regions, the percentage of endemic species has been used, more implicitly than explicitly, to characterize biogeographical regions (i.e. an area can only achieve regional status if a certain percentage of its taxa are endemic). Ever since, the concept of biogeographical regions has largely obliterated the diversity/endemism centres, until Myers *et al.* (2000) popularized their 'biodiversity hotspots' – which are centres of both diversity and endemism (although still intuitively selected and delimited). Currently, the concepts of 'diversity centres' and 'biogeographical regions' run at almost equal strength, and both approaches have led to sophisticated applications in conservation planning (e.g. Thackway & Cresswell, 1995; Rodrigues *et al.*, 2004). However, a review of these for purely biogeographical purposes

is still lacking. In the following paragraphs, I will discuss a few methodological issues regarding global biogeographical regionalizations and diversity/endemism centres.

### *Contiguity*

Regionalizations are land classifications that take location into account (Grigg, 1965), in other words each of the resulting land classes has to represent one contiguous area. This is in opposition to other land classifications, whereby one land class can be represented by archipelagos of points in the middle of another. In this sense, the procedure presented here is not a regionalization, as no specific constraint of adjacency (see Margules *et al.*, 1985) was imposed. Nevertheless, the resulting regions were continuous – if not as land masses (which were not selected as working units), at least in terms of latitude and/or longitude (one obvious non-contiguity was in the ‘temperate American’ cluster; Fig. 3b). Several intuitive regionalizations have included provinces which were not contiguous [e.g. White’s (1983) ‘Afromontane’ – although recent analytical approaches do not confirm this as one valid biogeographical unit; see Linder *et al.*, 2004, also Williams *et al.*, 1999]. It must be observed that discontinuous classes are more likely to result as the grain (quadrat) size considered gets smaller. However, to the extent that discontinuous classes are still obtained, even at large grain sizes, it may be necessary to separate the concept of biogeographical regions from the logical region concept, as the key criterion in the former has to be, ultimately, the degree of similarity in organism assemblages. No contiguity constraint needs to be imposed on diversity or endemism centres, although these are also intuitively easier to accept if contiguous.

### *Comprehensiveness and transition zones*

The very concept of diversity centre precludes comprehensiveness. Centres are defined in opposition to the rest of the world’s areas, which are comparatively species-poor; a set of diversity centres should concentrate the highest possible number of species (or higher taxa, clades, etc.) in a minimum total surface area. At the opposite end of the spectrum, regionalizations should be comprehensive, therefore able to assign an inclusive region to any precise location. Most published regionalizations fulfil this requirement [but see Cox (2001), where Wallace’s (1876) Celebesian transition is excluded from both the Oriental and Australian regions].

In a cluster-based regionalization (for one given dissimilarity value), it is impossible to identify transitional zones, all identified regions having equal status. One can recognize as transitional those regions that have an unstable position between different clustering methods (e.g. western India, Central America, and the Celebesian zone in Fig. 3), or between different groups of organisms. However, accepting a special status for transition zones is a step towards defining diversity centres, as all of the world’s areas not included in a

centre are, ultimately, transitional between centres, sharing some species with one, others with another. Endemism centres, on the contrary, allow for no gradations, as all the species used to define such a centre are confined there.

If transitional zones are of special interest, clustering analysis in itself is insufficient. Multidimensional scaling (MDS) techniques have been used to illustrate gradations in the relationships between regions (Conran, 1995; Procheş & Marshall, 2001; Procheş, 2001); more sophisticated techniques are also available (Williams, 1996).

### *Grain size*

The 15° × 15° quadrats used here may be seen as rather rough, especially considering that geographically discrete units (like Madagascar) were partly confounded with neighbouring ones (Africa). Madagascar only received recognition at a regional scale when parts of it occurred in quadrats where the fauna of continental Africa was absent. To avoid such problems, one can repeat the analysis while shifting the position of the quadrats. Large grain size may be seen as a drawback, but when one is testing for the world’s biogeographical regions (*c.* 10), as was done here, large quadrats are appropriate. Reducing grain size would only relegate problems to a different scale (if grain is small enough, tiny islands with high endemism would receive regional-level recognition). Conceptually, one solution is to set a cut-off size for biogeographical regions and/or a cut-off species number (as was done here by using 15° × 15° quadrats with five or more bat species).

### *Taxonomic rank*

In the present study, both genus and species-level analyses produced acceptable regionalizations. When bat families were used in clustering procedures, the geographical clusters disintegrated, with many distinct regions sharing the same set of families, and often these were represented by similar numbers of species/genera, irrespective of geographical location. For example, southern Australia clustered together with parts of Central Asia (data not presented). Thus, the classification no longer satisfied the contiguity condition. The ideal taxonomic level is, however, likely to be a group-specific characteristic, as taxonomic ranks are arbitrarily defined. Biogeographically, genera in one group may well correspond to families in another, as illustrated by Conran’s (1995) analysis, where families, subfamilies and tribes were used – resulting in clusters similar to the species- and genus-based ones presented here. This can, at least partly, be explained by the limited dispersal of the Liliiflorae, compared with bats. Between groups with similar dispersal abilities, evolutionary age could be important in determining how taxonomic rank affects geographical regionalizations. More insights in this direction can be attained by perusing Good’s (1974) treatise, thoughtfully divided into parts dealing with the distribution of families, genera and species.

### Analysis methods revisited

The easiest way to define centres of diversity or endemism is to map absolute diversity values or the number/proportion of endemics, and select the areas above a certain critical value. To define biogeographical regions, the clustering method used here (in particular for presence/absence data) appears to be both reliable and relatively easy to apply, although by no means the only possible analysis to use towards this goal, a whole range of multivariate analyses being available (see Williams *et al.*, 1999). Here, I used arbitrarily chosen dissimilarity values for separating regions (and these values were partly dictated by the number of accepted regions). However, analytical procedures can be used to recognize more natural clusters – in a fashion that would be independent of both predefined dissimilarity values and predefined cluster numbers. Cluster analyses using species numbers per higher taxon, rather than presence/absence data, are hybrid between regionalizations and defining diversity centres (see Fig. 3b, where all of low-diversity temperate America formed one cluster).

### CONCLUSION

This paper was not intended to propose a new regionalization scheme or amend existing ones. Being based on one single group of organisms, the results presented here have limited applicability, as representative as that one group may be for the entire picture of global biodiversity. However, the remarkable convergent patterns presented by purely descriptive and analytical approaches to regionalizing organism distributions, whether they may be plants or animals, gives hope that a common global biogeographical scheme is within reach. Analyses on distribution patterns in other groups are likely to clarify this point further.

Comprehensive global distributions data sets that are already digitally available, include species-level ones for mammals, amphibians, threatened birds (IUCN partnership, see Rodrigues *et al.*, 2004), and bumblebees (Williams, 1993). At family level, data are available for higher plants [Williams *et al.*, 1994 – although this would need an update considering that a new familial classification is available; see Angiosperm Phylogeny Group II (APG II), 2003], and at genus level, for termites (Eggleton *et al.*, 1994). The distributions of many other groups can be digitized with a reasonable amount of effort. Picking up convergent distribution patterns among taxonomic groups can ultimately result in selecting the most natural global regionalization scheme.

At the same time, separate schemes for individual groups can be of interest for more specific purposes. These need not be phylogenetically defined groups (of central interest to evolutionary biology); macroecology is equally interested in groups defined on other criteria (e.g. body size, dispersal abilities). From this perspective, the current separation between plant and animal biogeography is probably one of the least fortunate options, with both groups including large and small, well and poorly dispersed taxa, with diverse climatic requirements. For

example, a regionalization based on daktling beetles (Coleoptera: Tenebrionidae) will presumably be closer to Conran's (1995) one, based on Liliiflorae, than to the broadly mammalian one, accepted as 'zoogeographical'. Differences between terrestrial and even freshwater (Bănărescu, 1990–1995) groups are expected to be small, when compared to marine groups (Briggs, 1995), which show different global patterns – essentially governed by seawater temperatures, as better dispersal allows for ecological factors to overcome historical limitations. These patterns are replicated even by marine organisms of relatively recent terrestrial ancestry (Procheş, 2001; Procheş & Marshall, 2001).

To end with, there is plenty of scope for applying analytical methods to global biogeographical regionalization. The use of analytical tools, such as cluster analysis, in describing global biogeographical patterns could make classical biogeography and macroecology join forces towards a better understanding of our living world.

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## BIOSKETCH

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