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Mapping biodiversity value worldwide: combining higher-taxon richness from different groups

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SUMMARY

Maps of large-scale biodiversity are urgently needed to guide conservation, and yet complete enumeration of organisms is impractical at present. One indirect approach is to measure richness at higher taxonomic ranks, such as families. The difficulty is how to combine information from different groups on numbers of higher taxa when these taxa may in effect have been defined in different ways, particularly for more distantly related major groups. In this paper, the regional family richness of terrestrial and freshwater seed plants, amphibians, reptiles and mammals is mapped worldwide by combining: (i) absolute family richness; (ii) proportional family richness; and (iii) proportional family richness weighted for the total species richness in each major group. The assumptions of the three methods and their effects on the results are discussed, although for these data the broad pattern is surprisingly robust with respect to the method of combination. Scores from each of the methods of combining families are used to rank the top five richness hotspots and complementary areas, and hotspots of endemism are mapped by unweighted combination of range size rarity scores.

1. INTRODUCTION

How is biodiversity distributed across the land surface of the Earth? The answer to this question is not only of academic interest, but is also important for addressing the urgent need to conserve biodiversity from degradation and extinction (ISCBD 1994). Although it is exceedingly difficult to answer it directly and precisely (Groombridge 1992; Heywood 1995), two factors put useful estimates within reach. First, in practice, many people are interested primarily in the diversity of relatively few groups, particularly higher plants and vertebrates. Secondly, diversity estimates can be obtained at low cost for even some of the more species-rich taxa by using higher-taxon richness as a surrogate for diversity value. Here we explore some of the possible ways of combining counts of higher-taxon richness for different major groups of organisms to provide estimates of large-scale patterns in diversity.

Terrestrial and freshwater plants and vertebrates have retained a disproportionate hold on people's interest over the last two centuries. This preoccupation can be seen from the proportion of space devoted to them by authors from Linnaeus (1758) to Groombridge (1992), and it continues despite the growing knowledge of the far greater numbers of species of smaller organisms in other taxa (Gaston 1991; Hawksworth 1991; Hammond 1992; Lambshead 1993). Unfortunately, the distribution of no one major group of organisms can be assumed to predict the distribution of any other (Prendergast *et al.* 1993; Williams 1993; Williams & Gaston 1994; Gaston *et al.* 1995; Gaston 1996*a*, *b*). Therefore, we seek to cater for the greater popular value given to higher plants and vertebrates by combining available data for their constituent major groups: seed plants, amphibians, reptiles and mammals (a polyphyletic assemblage; there were no data available for birds). This encompasses a total of approximately 316000 species (table 1), 2.3 % of a present estimate of 13.5 million species for all organisms (Heywood 1995).

Complete inventories of organisms are impractical at present because there are far too many for direct enumeration. Therefore, indirect solutions are needed that are effective, inexpensive and quick (May 1990; Ehrlich 1992). Among the many popular choices of surrogate measures for predicting biodiversity value (including indicator taxa, vegetation classes, land classes, patterns in environmental variables, see Williams 1996*b*), one that has received growing attention is the higher-taxon approach (Williams *et al.* 1991; Gaston & Williams 1993; Williams 1993; Prance 1994; Williams & Gaston 1994; Williams *et al.* 1994*b*; Gaston & Blackburn 1995; Gaston *et al.* 1995; Gaston 1996*c*; Balmford *et al.* 1996*a*, *b*; Roy *et al.* 1996; Wright *et al.* 1997). This is an attempt to predict patterns of diversity for species-rich taxa when resources for surveys are very limited. It is based on the view that counts among areas for 1000 families, for example, represent variation within a larger slice of biodiversity value than do counts for 1000 species.

The problem with combining counts of higher-taxon

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richness from different major groups is that they include different numbers of higher taxa that may, in effect, be defined in very different ways, particularly when the major groups are more distantly related. Unfortunately, there is no objective basis for comparing the rank of higher taxa, except in the case of sister groups (Gauthier *et al*. 1988). In the face of this problem, we explore three methods of combining data at the family level to map, worldwide, the diversity of terrestrial and freshwater higher plants and vertebrates. These methods entail summing (i) absolute family richness; (ii) proportional family richness; and (iii) proportional family richness weighted for total species richness of each major group. The robustness of the common pattern among the results and the effects of the different values and assumptions are discussed.

2. METHODS

The spatial distributions of families of each of the four major groups were mapped onto a cylindrical equal-area projection of the world, which was divided into equal-area grid-cells based on intervals of 10° longitude, where the area of each cell was *ca*. 611000 km² (Williams 1993). Data for these groups were obtained as follows: (i) for seed plants, distribution records for Cronquist's (1981) list of 392 non-marine plant families were collected from the literature of floras, checklists and monographs according to Frodin (1984, and personal communication) and from the herbarium of the Natural History Museum, London; (ii) for 38 families of amphibians and (iii) 48 families of reptiles, non-marine distributions were obtained, with some minor modifications, from Zug (1993); and (iv) for mammals, distributions of 120 non-marine families were obtained from Macdonald (1985) and from Anderson & Jones (1984), using the classification of Macdonald (1985). For separate maps of family richness for these groups see Gaston *et al*. (1995).

One difficulty common to all methods of combining data is that data for each group differ in some details of compilation. In particular, the data for amphibians and reptiles do not include distributions of families on oceanic islands. There are also some inconsistencies between major groups in whether records were included for grid-cells containing only a tiny area of a continent. The latter problem is likely to have a negligible effect on the patterns we report, and we address the former by excluding those oceanic islands not scored for reptiles and amphibians.

The three simplest methods of combining family richness are as follows: (i) absolute family richness, achieved by summing local family richness counts for the different major groups; (ii) proportional family richness, reached by summing the local proportion of family richness for the different major groups; and (iii) proportional family richness weighted for species richness, which is calculated by summing the products of the local proportion of family richness with the total terrestrial species richness of the different major groups (table 1). So for each grid-cell:

$$\text{absolute family richness} = f_{\mathrm{p,i}} + f_{\mathrm{a,i}} + f_{\mathrm{r,i}} + f_{\mathrm{m,i}}, \quad (1)$$

$$\text{proportional family richness} = (f_{\mathrm{p,i}}/F_{\mathrm{p}}) + (f_{\mathrm{a,i}}/F_{\mathrm{a}}) + (f_{\mathrm{r,i}}/F_{\mathrm{r}}) + (f_{\mathrm{m,i}}/F_{\mathrm{m}}), \quad (2)$$

$$\text{proportional family richness weighted for species richness} = S_{\mathrm{p}}(f_{\mathrm{p,i}}/F_{\mathrm{p}}) + S_{\mathrm{a}}(f_{\mathrm{a,i}}/F_{\mathrm{a}}) + S_{\mathrm{r}}(f_{\mathrm{r,i}}/F_{\mathrm{r}}) + S_{\mathrm{m}}(f_{\mathrm{m,i}}/F_{\mathrm{m}}), \quad (3)$$

where $f_{\mathrm{p,i}}$, $f_{\mathrm{a,i}}$, $f_{\mathrm{r,i}}$, $f_{\mathrm{m,i}}$ are the numbers of families of terrestrial and freshwater seed plants, amphibians, reptiles and mammals in grid-cell i; F_{p}, F_{a}, F_{r}, F_{m} are the total numbers of families in each group; and S_{p}, S_{a}, S_{r}, S_{m} are the total numbers of species in each group (table 1).

3. RESULTS

Correlations between grid-cell scores show that, with the present data, all three methods of combining family richness give very similar results at a coarse-grained scale (table 2). The maps in figure 1 show a consistent pattern of a strong latitudinal gradient (interrupted in Africa by the Sahara desert), and a consistent longitudinal pattern with maximum richness in the Americas (figure 2). Indeed, the same hotspot of overall maximum richness (Central Colombia) is shared between two of the maps (figure 1 *a*, *b*) and the

Table 2. *Spearman's rank correlation coefficients for grid cell scores among the three methods of combining family richness for the four major taxa* ($p < 0.0005$ *in all cases*)

	absolute family richness	proportional family richness	proportional family richness weighted for species richness
absolute family richness	1		
proportional family richness	0.979	1	
proportional family richness weighted for species richness	0.991	0.949	1

Table 1. *Estimates of total terrestrial richness for the four major taxa*

(Numbers of families from Cronquist (1981); Macdonald (1985); Zug (1993); numbers of described species from Groombridge (1992).)

	terrestrial and freshwater families (F)	described species	total species	marine species	terrestrial species (S)	mean S/F
seed plants	392	250000	300000	50	299950	765
amphibians	38	4000	4500	0	4500	118
reptiles	48	6550	7000	50	6950	145
mammals	120	4327	4500	100	4400	37

third hotspot (Oaxaca) is in close proximity (figure 1*c*). Broader differences between the maps are slight, but the proportional family richness method gives particularly high scores in central Africa (figure 1*b*) because of the higher weight this method gives to the mammalian families which are relatively numerous there (Gaston *et al*. 1995, fig. 1*e*).

Table 3 lists the top five complementary areas for each of the three methods of combining major groups, along with the top five hotspots, by absolute richness. Complementarity is not only more effective in representing diversity within the limited areas available for conservation management (Vane-Wright *et al*. 1991; Williams *et al*. 1996), but when applied to these data it tends to select for areas within a greater variety of regions (for all three methods, 5/5 areas are in different biogeographic regions, table 3) than do sets of richness hotspots (mean of 2.7/5).

4. DISCUSSION

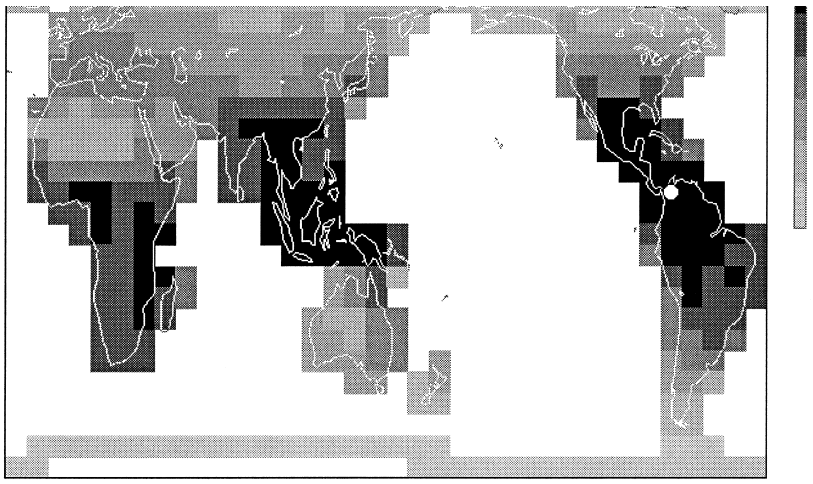
Ideally, the choice of method for combining higher taxa from different major groups should depend on where value is seen to lie in biodiversity. Different underlying values call for different models linking value with family richness, and therefore require different methods for combining data sets.

The simplest approach is to sum absolute family richness (figure 1*a*). This gives equal weight (value) to each family and assumes that the family–value relationship is acceptably consistent among major groups. Although there is no special theoretical justification for this at present, higher taxa have been viewed simply as larger slices of the biodiversity cake than species (Gaston & Blackburn 1995; Gaston *et al*. 1995). From this perspective, families may be treated like species to the extent that higher richness yields higher diversity value at the chosen rank. Problems might arise if family richness was viewed instead as a surrogate for other value 'currencies', such as species richness, or genetic or character richness (see below). However, if families were monophyletic and if most of the genetic or character differences were between rather than within families, then absolute family richness could still provide a simple, powerful and inexpensive measure of this diversity value when more detailed information is unavailable.

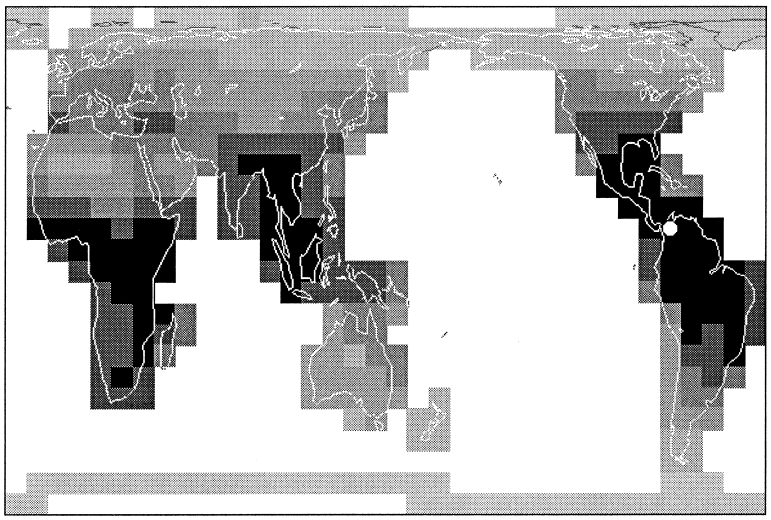
The proportional family richness approach (figure 1*b*) is an obvious alternative that differs by giving equal weight (value) to each major group (seed plants, amphibians, reptiles and mammals). While this may be expedient in the face of sectoral interests (ICBP 1992; WWF & IUCN 1994), it depends strongly on which major groups are accepted at the outset as being of equal value (for example, accepting as one unit either seed plants, flowering plants, or monocotyledonous plants). This approach is also likely to depart even more strongly than absolute family richness from measures of more fundamental value currencies, such as genetic or character richness, if there is any relationship among major groups between family richness and scores for these values.

The proportional family richness weighted for the species richness approach (figure 1*c*) differs by seeking to give equal weight (value) to each species. This depends upon a frequently observed relationship between higher-taxon richness and species richness (Gaston & Williams 1993; Williams 1993; Williams & Gaston 1994; Williams *et al*. 1994*b*; Gaston & Blackburn 1995; Balmford *et al*. 1996*a*,*b*; Roy *et al*. 1996; Wright *et al*. 1997). There are potential pitfalls in seeking to exploit this relationship (for a discussion, see Williams & Gaston 1994) and many of these remain inadequately studied. However, Prance's (1994) objections appear to stem from misapprehensions. First, his observation that relative family richness fails to mirror species richness between Malesia and the neotropics does not take into account the large differences in the extent of the area between these regions (and therefore the confounding effects of spatial turnover of taxa within them), whereas our investigations of the family–species richness relationship have largely been made on a per unit area basis, using equal-area grid-cells. Second, his criticism that data for species should be used because they are better predictors of conservation value is groundless because we suggest using family data only in situations where there are insufficient resources available for good species data to be a realistic alternative. Assuming that family richness may (if used with care) predict species richness, there is a consensus that higher diversity value does tend to reside in greater species richness (or in some currency that is reasonably and consistently related to species richness across major groups). In effect, the proportional species richness approach differs from the absolute family richness approach in accepting that species–family richness relationships cannot be assumed to be consistent among major groups (as shown by the mean S/F ratios in table 1). When better models (e.g. regression models) for predicting species richness from family richness become available from empirical studies, they could then be substituted.

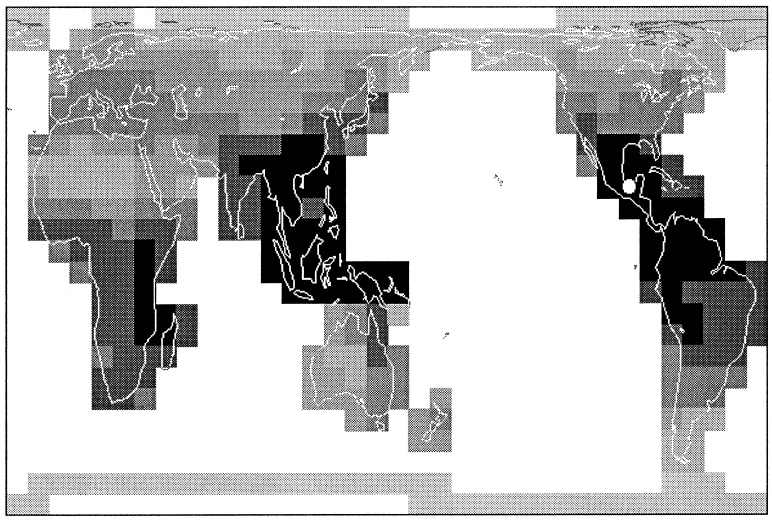
Arguably a more fundamental value of diversity lies in giving equal weight (value) to different expressed or expressible genes or characters (Williams *et al*. 1994*a*). Although not attempted here, this approach would lead us to consider modifying the method by applying taxonomic or phylogenetic measures of diversity to families (Williams *et al*. 1991; Williams 1993). Simple models are used to predict the distribution of character or expressed genetic changes from estimates of phylogeny so that the length of a subtree spanning a biota can be used to predict its relative character or genetic richness (Faith 1992, 1994; Humphries *et al*. 1995). However, application of these measures would be much more demanding of monophyly in families than the other approaches, and would require good quantitative knowledge of phylogenetic relationships. Although this information is rapidly becoming available, there is still considerable difficulty in choosing among alternative reconstructions of phylogeny (Graur 1993). Another potential problem is in measuring the great and poorly known divergences between major groups (particularly between seed plants and verte-



(a)



(b)



(c)

Figure 1. Maps of combined family richness of terrestrial and freshwater seed plants, amphibians, reptiles and mammals worldwide on an equal-area grid map (grid-cell area *ca.* 611 000 km², for intervals of 10° longitude; Williams 1993, 1996*a*). Data compiled from sources in Gaston *et al.* (1995) and combined by summing: (*a*) absolute family richness; (*b*) proportional family richness; and (*c*) proportional family richness weighted for species richness. Maximum scores are shown in black, other scores are divided into five grey scale classes of approximately equal size by numbers of grid-cells. Although the units and numerical values differ, the frequency classes remain comparable among maps.

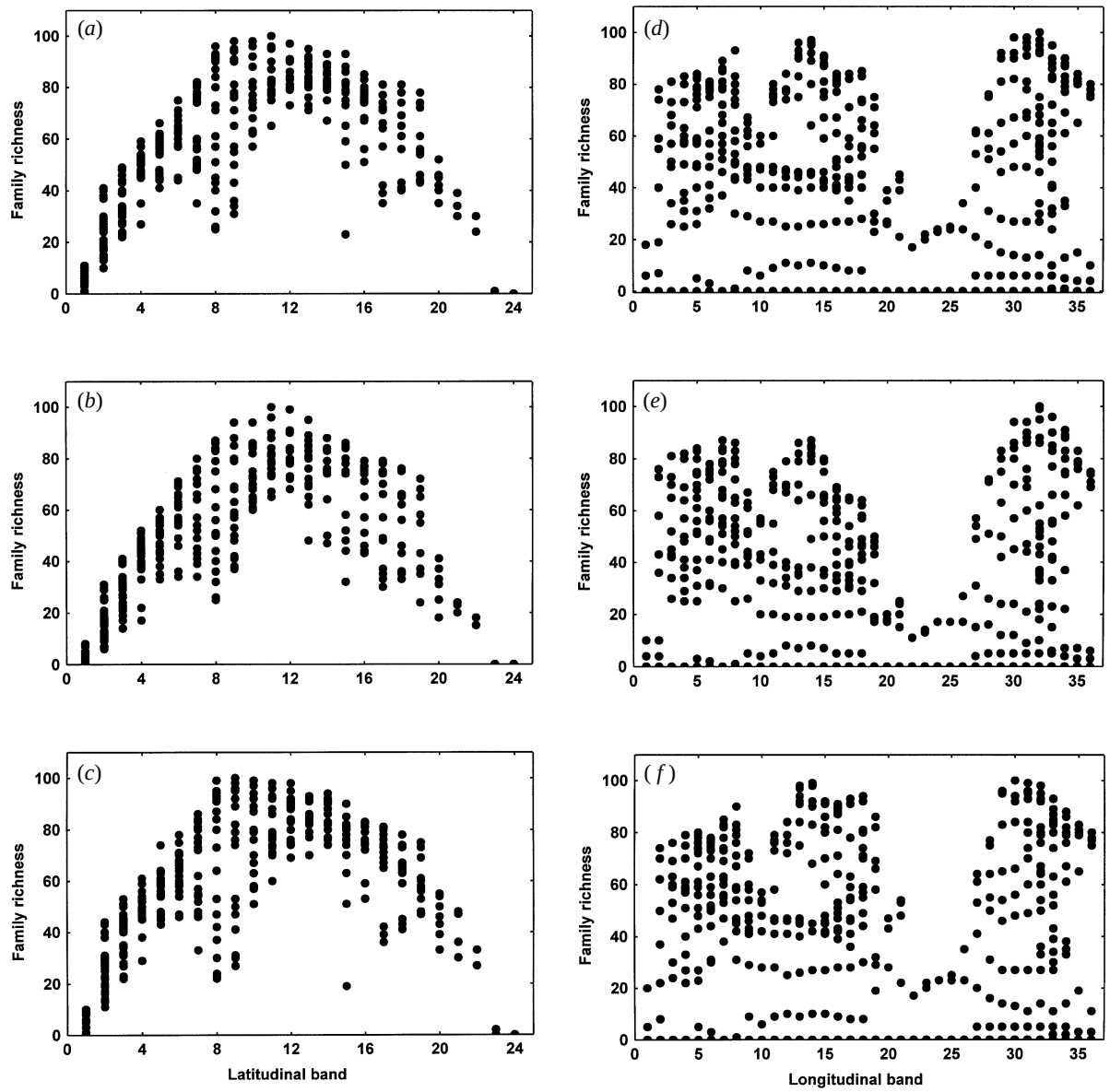


Figure 2. Plots of combined family richness of terrestrial and freshwater seed plants, amphibians, reptiles and mammals worldwide against latitudinal band and longitudinal band from the maps in figure 1. Data compiled from sources in Gaston *et al.* (1995) and combined family richness scores are re-scaled to percentages of the observed maximum value for a grid-cell. For latitudinal bands (1–24, north to south), data are combined by summing: (*a*) absolute family richness; (*b*) proportional family richness; and (*c*) proportional family richness weighted for species richness. For longitudinal bands (1–36, west to east), data are combined by summing: (*d*) absolute family richness; (*e*) proportional family richness; and (*f*) proportional family richness weighted for species richness.

brates), although if the analysis was restricted to grid-cells containing at least one representative of each of the major groups, then this would become a constant in the calculations that could be ignored.

It is reassuring for biodiversity studies that, in practice, all three methods for combining family richness used here give very similar results at a coarse-grained scale with the present data. Of course, it is known that latitudinal patterns of family richness (high in the tropics, low near the poles) are broadly shared among the major groups of higher plants and vertebrates (Gaston *et al.* 1995). And although there are strong differences in the longitudinal distribution of family richness among these groups (Gaston *et al.* 1995), there is still an apparently sufficient shared pattern (figure 2, no doubt dependent in part on variation in the extent of land area at low latitudes) to make the results in figure 1 surprisingly robust to the precise method of combining major groups. This is also aided in the first and third methods (figures 1*a* and 1*c*) by the dominating effect of the particularly high total plant family and species richness on these scores (table 1).

In view of the consistency in the general pattern, we may tentatively conclude that the first method could be used when species numbers are not available. When species numbers are available, it would be advisable to check for consistency in the results. Circumstances likely to result in differences between methods include strong differences among major groups in (i) total numbers of higher taxa; (ii) total numbers of species; and (iii) distribution of richness, whether this be due to

Table 3. *Top five hotspots of richness and top five complementary areas using each of the three methods for combining family richness for the four major taxa*

(For hotspots, the top five areas are chosen for their highest scores independent of one another, whereas the complementary areas are chosen for the highest cumulative scores among areas at each step, although in both cases it is the cumulative scores that are shown for comparison. Complementary areas are selected using a simple greedy algorithm, which results in a rank order of areas for near-maximum representation of diversity in cases requiring the choice of from one to five areas (see Williams *et al*. 1996; Csuti *et al*. 1997). Numbers of biogeographic regions show the spatial and biotic dispersion of the areas, using regions from Udvardy (1975), identified by abbreviations: AF, Afrotropical; PA, Palaearctic; IN, Indomalayan; AU, Australian; OC, Oceanian; NA, Nearctic; NT, Neotropical. Column abbreviations: (*a*), cumulative scores from 598 families; (*b*), cumulative scores from four major groups; (*c*), cumulative scores from 316000 'species equivalents'.)

	method of combining families					
	absolute family richness	(*a*)	proportional family richness	(*b*)	proportional family richness weighted for species richness	(*c*)
hotspots of richness (areas ranked by independent scores)						
1	NT Central Columbia	276	NT Central Colombia	1.62	NA Oaxaca	166000
2	NT Nicaragua	292	NT Southern Colombia	1.68	NT Nicaragua	172000
3	NA Oaxaca	304	NT Central Venezuela	1.70	PA Southern Yunnan	208000
4	NT Southern Colombia	309	NT Ecuador	1.71	IN Cambodia	218000
5	IN Southern Peninsular Malaysia	390	NT Nicaragua	1.85	IN Southern Peninsular Malaysia	224000
no. of regions	3 (NT, NA, IN)		1 (NT)		4 (NA, NT, PA, IN)	
complementary areas (areas ranked by complementary scores)						
1	NT Central Columbia	276	NT Central Colombia	1.62	NA Oaxaca	166000
2	IN Southern Peninsular Malaysia	361	IN Southern Yuunan	2.22	IN Southern Peninsular Malaysia	206000
3	NA Arizona	404	AF Lake Victoria	2.53	PA Southern Sichuan	225000
4	AF Northern Madagascar	439	OC Southern Irian Jaya	2.74	AF Eastern Cape	241000
5	AU Tasmania	463	NA Texas	2.92	NT Southern Guyanas	252000
no. of regions	5		5		5	

differences in ecological habitat association or historical biogeography. The latter effect is likely to become more pronounced at finer spatial grain sizes.

Nonetheless, consistency in the general pattern is no guarantee that by using family richness the maximum richness hotspot can be identified with precision for any other currency. This is because of the approximate nature of surrogacy relationships (which may be regarded as an effect of taxonomic scale; see Williams & Gaston 1994; Balmford *et al*. 1996*a*). Similarly, the location of the maximum richness hotspot is highly dependent on the grain size (spatial scale) of a survey (Stoms 1994), through species–area effects. For example, with these very large grid-cells (*ca*. 611000 km^2), not all of the families recorded within a grid-cell necessarily coexist locally (indeed, many doubtless do not). There may be spatial turnover of taxa at a finer scale between localities, so the location of the maximum richness hotspot measured for a finer grain size could be quite different. Furthermore, the data used here remain preliminary and will undoubtedly require revision as knowledge of the taxa improves.

One of the advantages of using higher taxa to estimate the distribution of biodiversity is that this approach retains some information on the complementarity of biotas, which itself depends on the spatial turnover of taxa (Gaston & Williams 1993; Williams 1993; Williams & Gaston 1994; Williams *et al*. 1994*b*; Gaston *et al*. 1995). However, a limitation of their use is that because there are fewer higher taxa than species, a minimum representative set of areas also tends to be smaller. This leads to the result that all of the 'species equivalents' (table 3) obtained by the third method may be represented in far fewer grid cells than would be needed to represent all real species. Consequently, complementary areas based upon higher taxa are most useful when considering the maximum coverage problem (*sensu* Csuti *et al*. 1997) for numbers of areas that are much lower than the minimum representative set. This is not a serious limitation because it is the more realistic case for conservation questions regarding large-scale biodiversity. The precise implication of these area sets for complementary richness in terms of real species remains unclear, but their value is presumed to lie in the strong likelihood that they include more complementary species than do sets of randomly selected areas or even sets of richness hotspots (see Williams 1993; Balmford *et al*. 1996*b*).

Higher taxa can also be used to investigate hotspots of endemism (Williams *et al*. 1994*b*). Endemism can be measured as range size rarity, using the local sum (by the absolute method) of the inverse range size for each family represented in a grid-cell (discussed in Williams

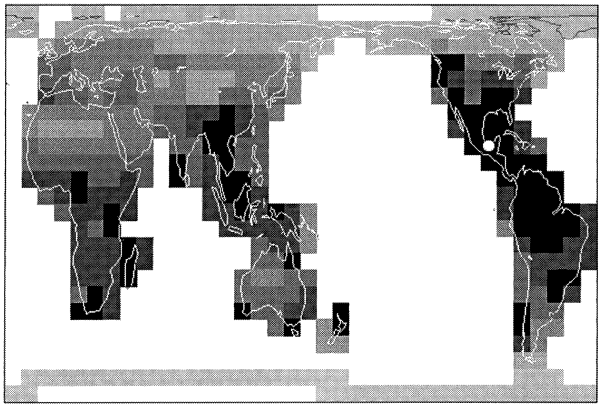


Figure 3. Map of combined family endemism of terrestrial and freshwater seed plants, amphibians, reptiles and mammals worldwide on the grid from figure 1. Data compiled from sources in Gaston *et al.* (1995) and combined by summing the inverse of the family range sizes (numbers of grid cells with records). Scores are represented by a grey scale, as in figure 1.

et al. 1996). Grid-cell scores by this measure are correlated with absolute family richness (Spearman's rank correlation $\rho = 0.918$, $p < 0.0005$), but endemism scores differ in being particularly high in the Western Ghats of India, the Pacific north-west of North America, South Africa, Madagascar, Australia, New Zealand, Chile and the Atlantic coast of Brazil (figure 3). These results show encouraging similarities to the hotspots of richness, endemism and threat identified by Myers (1988, 1990) for species. He used a compilation of data sources, although some of these he described as inadequate for drawing quantitative conclusions.

Using higher taxa to measure biodiversity value in any sense requires considerable care because of the complexities of interpretation. The choice of which approach is best for combining higher taxa from different major groups depends on where value is seen to lie in biodiversity (which in turn depends on the purpose for which it is being measured), and on the limitations of available data. Although they have evident limitations, all three of the methods used in this paper provide a promising route to overcoming some of the enormous sampling problems encountered in assessing large-scale biodiversity at low cost.

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