



## What to Protect?—Systematics and the Agony of Choice

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### ABSTRACT

*Politicians and scientists alike now agree that a priority list of global centres for preservation of biological diversity is required. Diversity has generally been measured only in terms of species richness, or in the form of indices combining richness with abundance. Such measures are considered inadequate for the task in hand. A novel index, based on the information content of cladistic classifications and giving a measure of taxonomic distinctness, is introduced. This taxic diversity measure, when coupled with detailed knowledge of distribution, can be used in modified analyses of the type previously developed as 'critical faunas analysis' or 'network analysis'. Central to all such analyses is the concept of complementarity of floras or faunas. By employing complementarity, step-wise procedures can identify optimally efficient, single-site sequences of priority areas for a group, taking existing reserves into account or not, as required. For practical planning it is concluded that two basic rounds of analysis are required: first, recognition of global priority areas by taxic diversity techniques; secondly, within any such area, analysis without taxic weighting (as being developed by Margules and his co-workers) to identify a network of reserves to contain all local taxa and ecosystems. The paper concludes with a brief discussion of some immediate prospects for development of a systematic approach to global conservation evaluation.*

### INTRODUCTION

Biological diversity is in crisis. Human activities are destroying the natural world and its biota at an ever increasing rate. Only a few previous mass extinctions, as documented by the geological record, could compare to the

is now occurring. According to Myers (1989), 'we may well be about to witness a major extinction spasm'.

Against this reality, depressing for those who see in biodiversity not only material benefit (Prance *et al.*, 1987) but also spiritual wellbeing (Lovelock, 1990), more and more local, national and international concern over this reversible change is being expressed (Thatcher, 1989; HRH Prince of Wales, 1990). Some concern is translated into action—action to stem the tide of pollution, and action to conserve species or set aside tracts of managed or wild lands, in the hope of saving at least some of the Earth's biodiversity for ourselves and future generations (Chalker, 1990).

Resources for protecting biodiversity through the control of land use will always be limited. Setting aside land for conservation purposes is often in direct conflict with economic pressures that produce environmental destruction. Clearly, resources needed for conservation are both constrained and dependent upon human economy.

Faced with this problem we consider it highly desirable to find effective means of measuring biodiversity, so as to be able to quantify and thereby estimate the contribution of managed areas (both natural and semi-natural: Westman, 1990) to the conservation of the Earth's remaining biological diversity. This objective is in line with previous calls by scientists (Meyerson, 1980; Roberts, 1988) and politicians (the proposed International Convention to Conserve Biological Diversity: Thatcher, 1989; IUCN, 1990). In drawing attention to the proposed Convention, Chalker (1990) has specifically stated that a fundamental requirement is 'agreement on a global network of centres of biological diversity for priority conservation'. Politically, intentions must be translated into actions. Scientifically, in order to identify critical areas for priority action, we consider a vital need to be the effective measurement of biodiversity itself.

Our purpose here is to introduce the idea of a novel index for measurement of biological diversity which, we believe, reflects information coded by *cladistic* (as distinct from phylogenetic) *relationships*, and then to apply this index of *taxic diversity* to wildlife conservation evaluation (Usher, 1990), and specifically to the problem of how to optimise use of resources for conservation of biodiversity (cf. Margules, 1989).

## THE MEASUREMENT OF BIODIVERSITY—ARE ALL SPECIES EQUAL?

When you can measure what you are speaking about, and express it in numbers, you know something about it; but when you cannot measure it, your knowledge is of a vaguer and unsatisfactory kind: it may be the beginning of knowledge, but you have not reached it, in your thoughts, advanced to the stage of *science*.'

William Thompson (Lord Kelvin), *Popular Lectures & Addresses*, 1891–1894

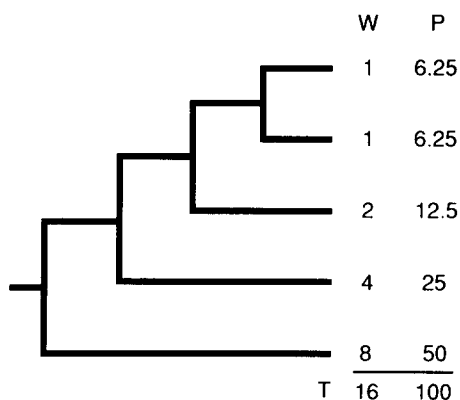
Whittaker (1972), while commenting that 'if diversity is recognised as an evolutionary product, it may cause no surprise that no single measurement serves all purposes', suggested that there are inherent difficulties in measuring aspects such as 'intelligence, organic complexity and *phylogenetic relationship*' (our emphasis added).

How is diversity measured currently? Biologists have tried to measure species richness—the total number of species of a group reliably known to be indigenous to a particular place. Ecologists often wish to include, in addition, information on commonness and rarity, by calculating one or more indices that combine measures of the number of species in a sample together with the relative abundance of those species (Peet, 1974; Taylor, 1978). In a more elaborate system, recently reviewed by Bond (1989), Whittaker (1972) suggested that at least three measures are required: alpha diversity (species richness of standard site samples); beta diversity (differentiation between communities along habitat gradients); and gamma diversity for a geographic area (the product of the alpha diversity of its communities and the degree of beta differentiation amongst them).

These measures all depend on the size of area sampled (Brown, 1988). They all also depend on good taxonomy to determine the number of species involved. And they all have a third factor in common—all species are treated as taxonomically equivalent, or as equal units. Quite apart from many theoretical and practical problems that continue to affect the species concept and its application, is it appropriate for conservation purposes to regard all species as equal in this manner? To a conservationist, regardless of relative abundance, is *Welwitschia* equal to a species of *Taraxacum*? Is the panda equivalent to one species of rat? Atkinson (1989) answered this question in the following way: 'given two threatened taxa, one a species not closely related to other living species and the other a subspecies of an otherwise widespread and common species, it seems reasonable to give priority to the taxonomically distinct form'. So we now expect still more of taxonomists—not only must they be able to tell various taxa apart, but they must also be able to quantify their distinctness.

Systematics offers two possibilities to measure taxonomic distinctness: similarity measures (phenetic or genetic distance) and group membership (cladistic relationships, often interpreted in terms of ancestry). Two decades of debate have led to an almost universal acceptance of cladistic methods in preference to those based on similarity. Accordingly, we base our approach exclusively on cladistic procedures.

Cladistic classifications are expressed as hierarchies. One possible approach to measuring taxonomic distinctness is to weight equally groups at the same taxonomic rank with respect to the additive weights of their terminal taxa (Fig. 1). This is achieved by giving the terminal members of the group of lowest rank each a weight of one, and then giving the sister group to



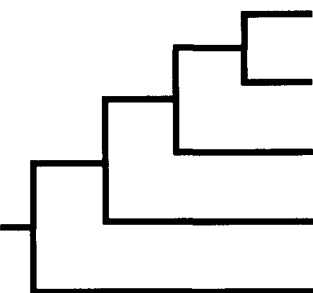
**Fig. 1.** Equal weighting (W) applied to sister groups. Column P gives the percentage contribution for each terminal taxon to the total diversity. See text for explanation.

this group an equal aggregate score, and so on up the tree. This results in every sister group having equal aggregate weight, and thereby gives high relative weight to taxonomically distinct species (such as those comprising monobasic genera or families).

However, this approach has the undesirable effect of overweighting basal taxa: weight accorded to a stem species will be equalled only by summing individual weights of all the subordinate terminal taxa. As a result, taxonomic rank overwhelms the number of species. For example, the two known tuataras (Daughtery *et al.*, 1990) would have a score equal to the combined weight of all 6800 snakes, lizards and amphisbaenians (to which the tuataras are considered to form the sister group amongst living reptiles). While we certainly agree that tuataras are particularly important among reptiles because of ancient divergence of their lineage, and should score highly in any conservation plan, to accord them equal status to 6800 other living reptiles is unreasonable in terms of sustaining *diversity*. What we need is some logically defensible measure sensitive to both taxonomic rank *and* number of species.

The approach we suggest here is based on attempts to measure the amount of information contained or *conveyed* in hierarchic classifications. This complex subject has recently been reviewed by Mickevich and Platnick (1989). Our method involves a variant of two of their primary information measures, terms and components. As discussed by Mickevich and Platnick, application of these measures has the result that the total amount of information conveyed within a hierarchic classification varies with topology, even for the same number of terminal taxa.

To demonstrate the method, consider a pectinate cladogram for five taxa, A–E (Fig. 2). From this cladogram it is possible to make four taxonomic



	I	Q	W	P
A	4	3.5	1	10.7
B	4	3.5	1	10.7
C	3	4.67	1.33	14.3
D	2	7	2	21.4
E	1	14	4	42.9
T	14	32.7	9.33	100

**Fig. 2.** Derivation of index of taxonomic distinctness, or weight. The example is based on a fully pectinate classification for five terminal taxa, A–E. Column I indicates the number of groups to which each terminal taxon belongs within the system, these numbers being the basic measure of taxonomic information. Column Q gives the quotient of the total information for the whole group (in this example,  $TI = 14$ ) divided by the information score for each terminal. Column W gives the standardised *weight* for each terminal, the Q-values for each terminal taxon having been divided by the lowest Q-value (in this case,  $Q_{\min} = 3.5$ ). Column P gives the percentage contribution for each terminal taxon to the total diversity, in terms of the aggregate values for Q or W. The totals row (T) gives the aggregate scores under I, Q, W and P. See text for explanation.

statements about A (it belongs to groups AB, ABC, ABCD and ABCDE), the same for B, three for C (ABC, ABCD, ABCDE), two for D (ABCD, ABCDE), and one for E (ABCDE). This gives a total of 14 ( $4 + 4 + 3 + 2 + 1$ ) informative statements about this taxonomic grouping (Fig. 2, column I). The values (4, 4, 3, 2, 1) could be used directly as weights. However, this not only gives basal taxa low weights, and vice versa—the opposite of what is desired—but it fails also to make the individual values directly reflect the proportion that each taxon contributes to the total diversity (information content) of the group. Both of these problems are overcome by dividing each terminal score into the total—for A,  $14/4$  gives 3.5 and so on—3.5, 4.67, 7 and 14. These quotients are the basic taxic weights (Fig. 2, column Q). For a number of reasons (including ease of calculation by other means), it is convenient to standardise these values by dividing by the lowest value throughout (thus giving the lowest ranking taxon a score of one—Fig. 2, column W). We can also express the contribution of each as a percentage (Fig. 2, column P).

Such terminal scores or weights, based directly on an information measure of the hierarchic classification, have the type of properties we desire. Taxonomic equivalence (equal rank) results in the same score. Taxonomic

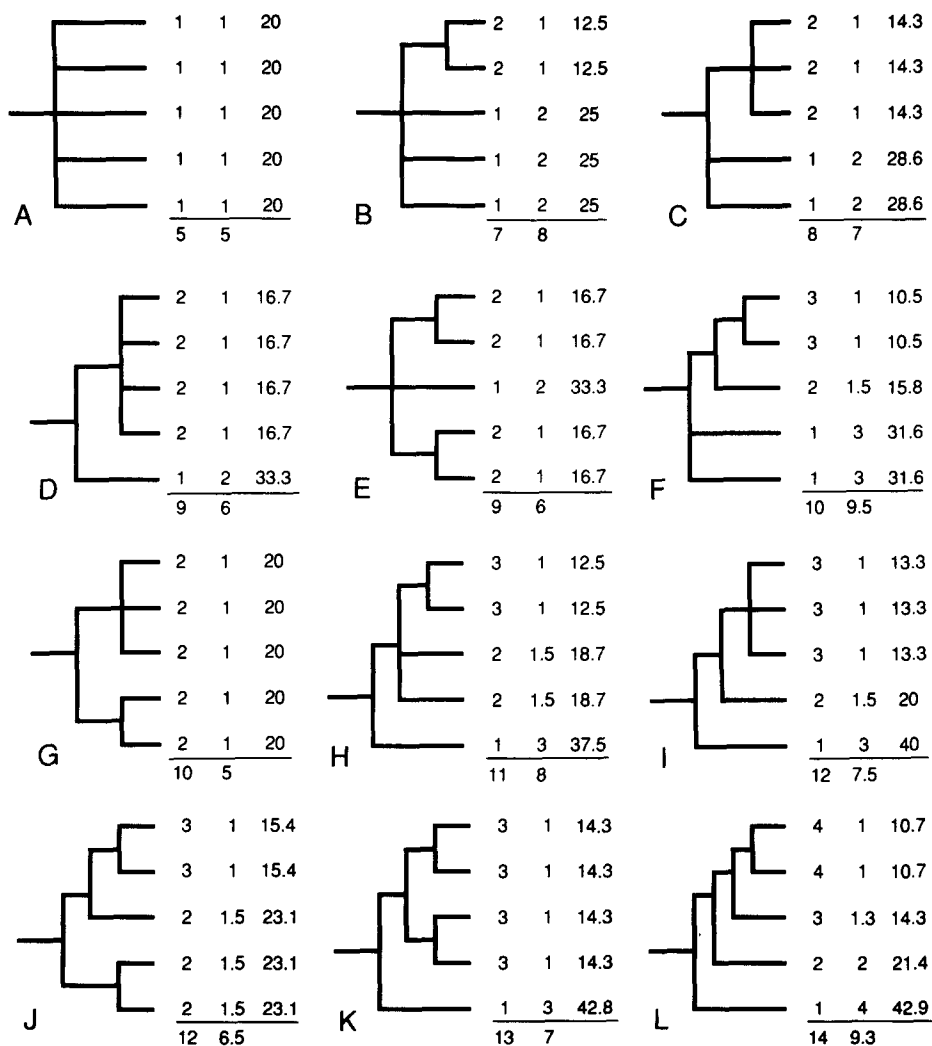


Fig. 3. The twelve cladistic topologies possible for five terminal taxa (designated A-L, corresponding to Mickevich and Platnick, 1989). Against each diagram the left-hand column gives the information value for each terminal taxon and the total information for the whole topology; the central column gives the standardised *weight* for each terminal taxon and the aggregate total; and the right-hand column gives the percentage contribution for each terminal taxon to the total diversity (cf. columns I, W and P in Fig. 2). See text for explanation.

distinctness results in a graded variation of score—not all species are equal. For unequal sister group pairs, the group with the higher number of terminal taxa will always have a higher aggregate score than the smaller group. Aggregated diversity scores of (monophyletic) groups of species will thus depend on both rank and number.

We have already noted that the amount of information in a classification

depends on its topology. There are 12 different topologies available to describe all possible cladistic relationships for five taxa, including the fully pectinate form already discussed, and the totally unresolved tree (or 'bush'). All 12 are shown in Fig. 3, with information values, weights and percentages for each. Note that polychotomies do not offer any difficulties, and that use of percentages enables the different results to be compared. Note also that the total information measure is different for many, but not all, of the topologies.

The fact that some information measures are the same is not just a curiosity. Compare Fig. 3(A) and 3(G). Although Fig. 3(G) has exactly twice the information content of Fig. 3(A), the weights and percentages are all the same. While this makes sense because all terminal taxa have equivalent rank, clearly there is some information that we have failed to encode.

May (1990) has proposed a modification of our index which takes account of the number of lineages arising at each node. All nodes are scored by counting the number of branches arising from them. Each terminal taxon is then scored by summing the values for all subtending nodes. Standardised indices are then derived by dividing the score for each terminal, in turn, into the maximum score. This procedure produces identical results to our method when applied to fully resolved or completely unresolved hierarchies, but does affect the values for partially resolved trees. This is an interesting suggestion, and could be of special value when dealing with the vexed problem of evaluating subspecies, utilising it as a reducing factor for terminal polychotomies of strictly allopatric taxa.

However, we consider that a more radical solution is almost certainly needed. Consider Fig. 3(G) again, in which the group of five species is just divided into two subgroups. For conservation purposes, we might well wish to give first priority to conserving one member of each. We thus consider that some procedure for sampling 'across' the cladogram, to ensure that as wide a range of clades as possible is sampled in addition to identifying highly distinct groups, is desirable. We are currently evaluating other information measures of taxic diversity which make use of this approach (Williams, Humphries & Vane-Wright, in prep.). Our main purpose here is to establish the idea that meaningful taxic diversity measures can be developed, and that they can be applied to assessment of conservation priorities.

### ARE ALL PLACES EQUAL?

We now consider the second systematic aspect of the problem of conserving biodiversity—distribution and biogeography of taxa. The conservation of nature is intimately affected by distribution and biogeography. If a taxon is restricted to one place or region, it is there that you must preserve it, or it is

from there that you must normally obtain it if you plan *ex situ* conservation or introduction.

McNaughton (1989) has observed that we have to 'determine what should be conserved and how it is to be conserved. A *critical places* strategy... could accomplish this objective'. McNaughton is an ecologist, and his 'critical places' refer to representative ecosystems. As systematists we think instead of areas of endemism, or critical faunas and floras for particular taxonomic groups.

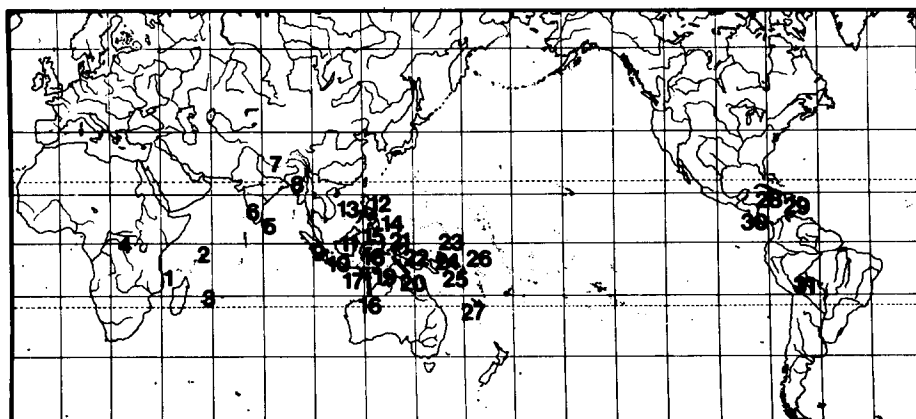
'Critical faunas analysis' was introduced by Ackery and Vane-Wright (1984) in an account of milkweed butterflies of the world. The distributions of all 157 species then recognised (many of which are polytypic) were examined on a global basis, divided amongst more than 350 countries, regions and islands. Species richness varied in these samples from one species up to about 35. Some species were narrow endemics, occurring in only one sample area, but most were widespread. Given that the idea of individually conserving representative populations of all 157 species was considered unrealistic, the following question was asked: what is the minimum set of areas, or faunas, which would contain at least one population of every species? To cover all 157 species, distributed through 350 sample areas, the answer was found to be 31 (Fig. 4). Parsons (1989) has since added a 158th species, a new *Parantica* from New Britain, one of the areas identified.

How was this shortlist of 31 faunas determined? All faunas with one or more endemic were placed in sequence, those with the highest number of endemics first, those with only one endemic last (this procedure is justifiable in terms of the recommendations put forward in Raven (1980); 'give priority to areas containing the richest and most highly endemic biota...'). The highest number of endemics (nine) was found on the island of Sulawesi. This island has populations of 24 other, more widespread, milkweed butterflies.

Thus a programme to conserve the entire milkweed butterfly fauna of Sulawesi could preserve representatives of 33/158, or 21% of the world species. The next highest number of endemics was found on Biak, an island in Irian Bay, New Guinea. It has a total of 18 species, four of which are not found anywhere else. Of the other 14, five occur on Sulawesi, but nine do not. So conserving Sulawesi + Biak could preserve a total of  $33 + 4 + 9 (= 46)$  separate milkweed butterfly species—29% of the world fauna. For all narrow endemics, 24 regions are recognised as essential—but these 24 regions do not include representatives of all 158 species. A minimum of seven further regions is needed to complete the list—the 31 critical faunas for milkweed butterfly conservation (Fig. 4).

Collins and Morris (1985), in their IUCN Red Data Book, applied critical faunas analysis to all 573 world species of swallowtail butterflies they recognised. Unlike milkweed butterflies, swallowtails are strongly represen-





**Fig. 4.** The minimum set of faunal regions, or critical faunas, that includes at least one representative population of all known species of milkweed butterflies (Lepidoptera: Danainae). Countries or islands listed in *italics* include species only found in those particular regions; the list is not in priority order. 1, *Comoro Islands*; 2, *Seychelles*; 3, *Mauritius*; 4, *Zaire*; 5, *Sri Lanka*; 6, *southern India*; 7, *Nepal*; 8, *Burma*; 9, *Sumatra*; 10, *Java*; 11, *Borneo*; 12, *Luzon*; 13, *Negros*; 14, *Mindanao*; 15, *Sulawesi*; 16, *Sumbawa*; 17, *Sumba*; 18, *Flores*; 19, *Timor*; 20, *Seram*; 21, *Biak*; 22, *New Guinea*; 23, *New Ireland*; 24, *New Britain*; 25, *Guadalcanal*; 26, *San Cristobal*; 27, *New Caledonia*; 28, *Hispaniola*; 29, *Cuba*; 30, *Costa Rica*; 31, *Bolivia*. It should be noted that the New World has a danaine fauna of 14 species, the Afrotropical Region has 21, and the Indo-Pacific has 126 (world total 158 species; original data from Ackery and Vane-Wright (1984) and Parsons (1989)). Over 350 separate islands, regions or countries were surveyed; the site conservation efficiency (Pressey & Nicholls, 1989a), for minimum representation, is better than 0.91.

ted in Palaearctic, Nearctic and Neotropical regions as well as Old World tropics. Although not based on strictly comparable geographical units, the top Old World tropical elements in their list of 51 critical faunas for swallowtails are closely matched by the first part of the milkweed list (Table 1)—strongly suggestive that it may indeed be possible to recognise areas of endemism common to a number of different groups (so-called ‘hot spots’).

A closely similar step-wise approach to the critical faunas procedure has been developed independently by Margules and his co-workers (Margules *et al.*, 1988; Pressey & Nicholls, 1989a,b), based on an original idea of Kirkpatrick (1983) and Kirkpatrick and Harwood (1983). Margules and his colleagues are concerned with evaluation procedures which will lead to maximum efficiency in establishment of nature reserve ‘networks’ to conserve all or most species or land systems within a given area.

In both the network approach and the critical faunas procedure, all species are treated as taxonomically equal. A minimal list is obtained by recognising that all narrow endemics (species restricted to just one of the sample areas) have to be included if all the species are to be taken into

TABLE 1

Some Critical Faunas<sup>a</sup> for Milkweed and Swallowtail Butterflies

The table lists the first four regions in each of the original critical faunas analyses of Ackery and Vane-Wright (1984) for the Danainae, and of Collins and Morris (1985) for the Papilionidae. Note that the milkweed butterflies are mainly distributed in the Indo-Australian tropics, whereas the swallowtails are far more evenly distributed on a global basis. Note also that Sulawesi, Biak and New Guinea are all effectively included in the political division Indonesia, and that Mindanao is the main southern island of the Philippines (see also text).

<i>Milkweeds (Danainae)</i>		<i>Swallowtails (Papilionidae)</i>	
1. Sulawesi	(9 endemics)	1. Indonesia	(53 endemics)
2. Biak	(4)	2. Philippines	(21)
3. Mindanao	(3)	3. China	(15)
4. New Guinea	(3)	4. Brazil	(11)
Total: 69 species		Total: 296 species	
(over 40% world total)		(over 50% world total)	

<sup>a</sup> All 31 critical faunas for the Danainae are listed, unordered, in the legend to Fig. 4; the 51 critical faunas list for the Papilionidae, as given by Collins and Morris (1985), is completed thus: 5, Madagascar; 6, India; 7, Mexico; 8, Taiwan; 9, Malaysia; 10, Papua New Guinea; 11, USA; 12, Cuba; 13, Ecuador; 14, Colombia; 15, Australia; 16, Andamans and Nicobars; 17, Jamaica; 18, Zaire; 19, Cameroon; 20, USSR; 21, Tanzania; 22, French Guiana; 23, Japan; 24, Canada; 25, Sri Lanka; 26, Haiti; 27, New Caledonia; 28, Comoro Islands; 29, Peru; 30, Bolivia; 31, Venezuela; 32, Gabon; 33, Bhutan; 34, Ghana; 35, Solomon Islands; 36, Afghanistan; 37, South Africa; 38, Iran; 39, Vanuatu; 40, Mauritius; 41, Réunion; 42, Fiji; 43, Western Samoa; 44, Burma; 45, Laos; 46, Honduras; 47, Argentina; 48, Uganda; 49, Ethiopia; 50, Mozambique; 51, Italy. Site conservation efficiency (Nicholls & Pressey, 1989a) for minimal representation of Papilionidae: 0.7 (about 170 countries analysed by Collins and Morris (1985)).

account. The network or critical faunas list-sequence is highly dependent, therefore, on according, *a priori*, high values to endemics. Given that we may be able to save only a *portion* of the Earth's biota, and that many *existing* reserves are not in optimal areas (and often largely duplicate each other, in terms of species representation; cf. Pressey & Nicholls, 1989a, b), the critical faunas or network step-wise procedures do not offer a sufficiently flexible strategy at a global level. Nonetheless, both procedures are based on a basic guiding principle—which we call *complementarity*.

In carrying out a simple critical faunas analysis, once the first choice has been made, all further considerations of species included within that region are eliminated. The second area is then drawn from the taxonomic complement of the first—the remaining fauna with the highest number of endemics, and all additional non-endemics that the area happens to contain.

Once the first two faunas have been added, the reduced complement is then searched for the third area. This algorithmic procedure is repeated until all species are accounted for (the total complement).

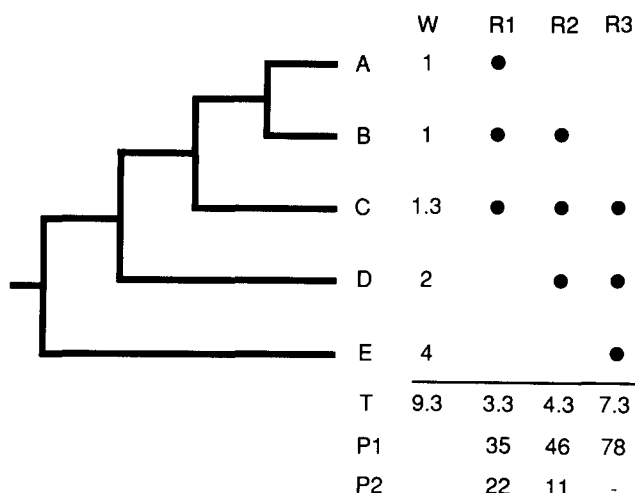
Both methods proceed by choosing a single site, ideally with a maximum score, at each step. Once a step has been taken the site is fixed, and only the distribution of the remaining taxonomic complement is considered at the subsequent step. However, a more optimal strategy for obtaining higher average diversity scores per site is possible if multiple-site choices are considered. At the limit this involves selection in one step of a set that contains the entire complement in the smallest possible number of sites. Such multiple site-sets are much more difficult to calculate (indeed, exact methods may not be available for large data matrices, this task being a variant of the 'travelling salesman' problem), and the procedure does not identify a priority sequence of sites, but only a priority *set*. The difference between priority sequences and priority sets could be profound for conservation planning. In particular, optimisation of diversity for a larger set of sites could well involve redeploying some, conceivably all sites identified by a previous analysis for a smaller set of sites.

Whichever analytical method is ultimately adopted, by applying the taxic weighting procedure we can still employ complementarity while removing the emphasis on endemics. We look first at a hypothetical example based on the pectinate five-taxon statement elaborated in Fig. 2, using the single-step-sequence optimisation method.

## PRIORITY AREA ANALYSIS USING TAXIC WEIGHTING

In Fig. 5 the five taxa, A–E, are given distributions in three regions (R1, R2, R3), such that each area has just three species. Based on species richness alone, we could not choose between the three areas. Based on endemism, we would be unable to choose between Region 1 and Region 3 (each has one endemic; Region 2 has no endemics). What percentage of the total weighted diversity is represented in each of the three areas?

Region 1 scores  $(1 + 1 + 1.3)$ , or 35% of the total of 9.3 units. Region 2 scores  $(1 + 1.3 + 2)$ , 46%. Region 3 scores  $(1.3 + 2 + 4)$ —78%. Note that, because of sympatry, the three scores add up to more than 100%. Thus Region 3 becomes the first choice. What is the second choice? Region 2 scores 46%, whereas Region 1 scores only 35%. But if we take complementarity into account, we can see that Region 2 as second choice is not the correct answer. If we regard Region 3 as a conserved ecosystem or set of ecosystems supporting taxa C, D and E, we are now only interested in the fate of species A and B. On this basis Region 1 can contribute  $(1 + 1)$ , or 22%



**Fig. 5.** Theoretical priority area analysis, based on topology and taxic weighting given in Fig. 2. Three of the five terminal taxa occur in each of three areas, R1–R3, according to the three-column matrix at the right. Column W gives the taxic weights (cf. Fig. 2). Row T gives the total (aggregate) scores for all five taxa, and for each of the three regions; row P1 gives the percentage diversity scores for each of the three regions at the first step, indicating that R3 is the top-priority region; row P2 gives the percentage diversity scores for the remaining two regions with respect to the taxa *complementary* to those occurring in R3, and indicates that R1 is the second priority; finally, the fact that the highest values of the first two steps sum to 100% indicates that the analysis is complete (Pressey & Nicholls' site efficiency value: 0.33).

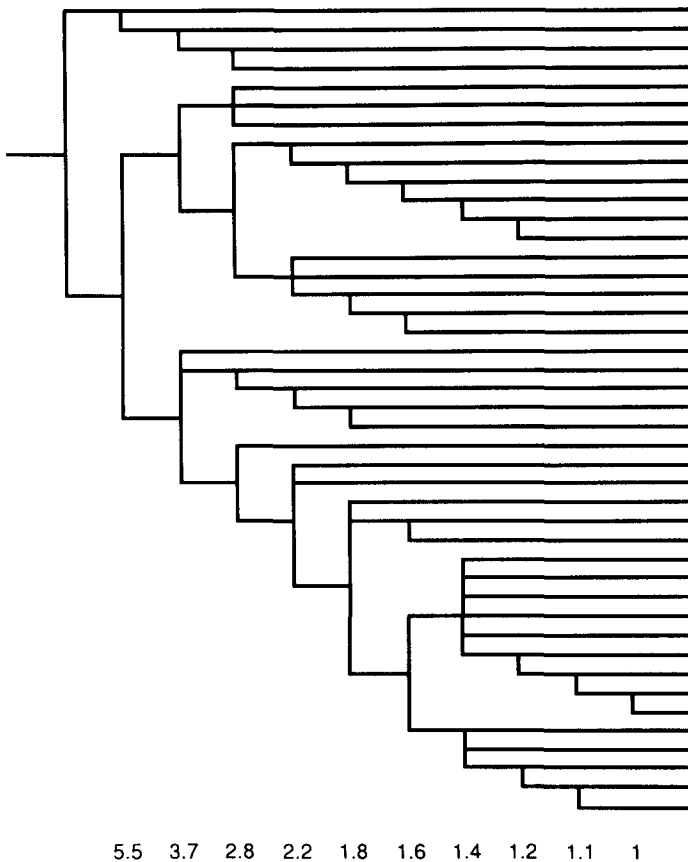
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additional taxic diversity, whereas Region 2 offers only one unit (11%). Thus, despite being least diverse in terms of weighted scores, Region 1 is the second priority. And note now that Regions 3 + 1 give a combined or complementary taxic diversity score of  $(78 + 22) = 100\%$ . This indicates that the weighted step-wise analysis is complete.

By securing Regions 1 and 3, all five taxa are represented. But this is not to say that Region 2 is of no value, or is unimportant in other respects—merely that in this initial analysis it is not required to achieve 100% representation of the group in question.

Figure 6 shows the topology of a current classification of the bumble bees of the *Bombus sibiricus*-group (Williams, in press). Taxic weight for each terminal taxon can be read, from the bottom line, against the node subtending the terminal taxon in question. Williams has modified his WORLDMAP computer program to carry out priority area analysis on the group. Representatives of the 43 species occur in 120 of the 250 equal-area grid-squares employed in the map projection (Williams, in press; Fig. 7).

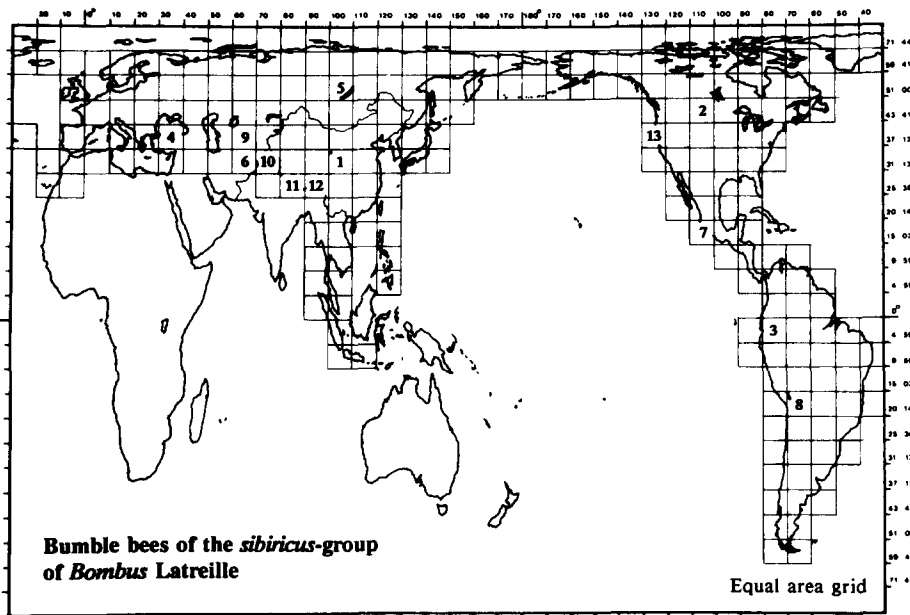
Although the greatest number of species in one area occurs in the grid-square centred on Ecuador, the 10 species found in that square contribute



**Fig. 6.** Cladogram topology for the *Bombus sibiricus*-group (based on Williams, in press and unpublished) which forms the basis for the analyses shown in Figs 7 and 8; the row of standardised taxic weights (bottom) applies to the terminal taxa arising at the corresponding nodes. See also text for explanation.

less than 15% of the total weighted diversity score, whereas the Gansu area of China, with nine (more high-ranking) species in the grid, contributes almost 23%. The highest complement to Gansu is the Big Horn region of North America, which, although it has only four species, can add more than 15% weighted diversity to the Gansu total. The third complement is then added by the Ecuador square, with 14% (i.e. this means that none of the 10 species in Ecuador is found in Big Horn or Gansu). Thus, the first three squares out of the total of 120 score 52% of the weighted diversity index for the group (and also happen to include more than half of the world species). By this method, all species (100% diversity score) are represented within a minimal set of 13 grid areas, arranged in priority sequence (Fig. 7).

Figure 8 plots the step-wise accumulation of weighted diversity, together with theoretical bounds that would describe total sympatry at one place (i.e.

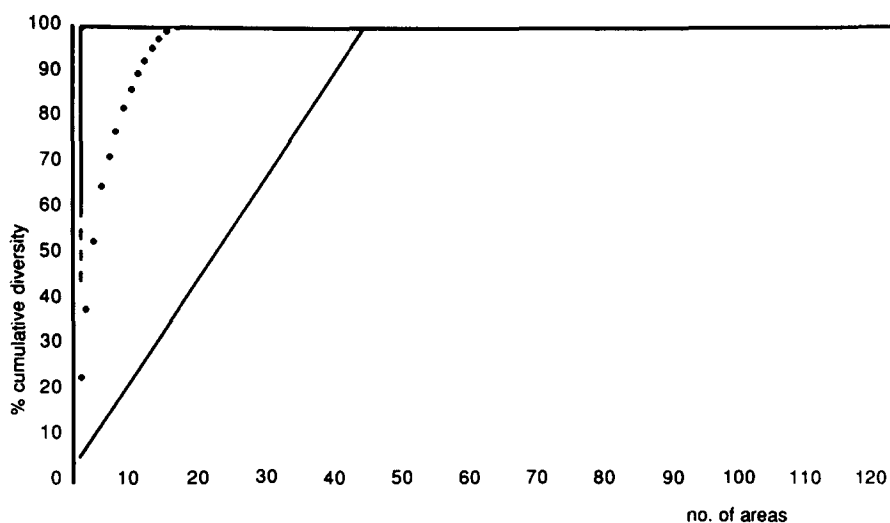


**Fig. 7.** Sequence of critical faunas for the bumble bees of the *Bombus sibiricus*-group, giving the highest successive scores for taxically weighted complementary diversity. The areas are labelled by reference to major geo-political features near the centre of the particular grid-squares, as follows: 1, Gansu (China); 2, Big Horn (USA); 3, Ecuador; 4, Turkey; 5, Baikal (USSR); 6, Hindu Kush (Afghanistan); 7, Michoacan (Mexico); 8, La Paz (Bolivia); 9, Samarkand (USSR); 10, Kashmir (India); 11, Nepal; 12, Arunachal Pradesh (India); 13, Northern California (USA).

The map (Williams, in press) is based on a cylindrical, equal-area projection, orthomorphic at 45° N/S (where bumble bee records are particularly numerous). The grid is calculated from intervals of 10° Longitude to provide equal areas that appear as squares on this projection.

The portion of the grid shown covers the known native distribution of all bumble bees.

one square with all 43 *sibiricus*-group species contained within it), or complete allopatry with all species regarded as taxonomically equal (this line starts at 2.3%, one species out of 43, and reaches 100% at area 43). The shape of the cumulative diversity curve for the priority sequence (which in this analysis, as already noted, reaches 100% at area 13) gives a measure of the geographic dispersion of taxic diversity for the group, worldwide. We believe that this measure, once properly quantified, will be of use in ecology and conservation planning. The 100% point in Fig. 8 corresponds to the (site) efficiency measure of Pressey and Nicholls (1989a) ( $E$ , efficiency, is defined by the formula  $E = 1 - (X/T)$ , where  $X$  is the minimum number or extent of sites needed to contain all attributes required [taxa], and  $T$  is the total number or area of sites sampled; Pressey & Nicholls, 1989a). Different patterns of dispersion and accumulation will call for quite different actions if conservation plans are to be effective.



**Fig. 8.** Weighted taxic diversity accumulation histogram for the 43 bumble bee species of the *Bombus sibiricus*-group. The abscissa represents the number of sample areas (the *sibiricus*-group occurs in 120 of the 250 grid-squares shown in Fig. 7). The ordinate scales percentage diversity (based on the aggregate of the 43 weights for the terminal taxa given in Fig. 6). The 13 points correspond to the sequence of grid-squares listed in the legend to Fig. 7, the 13 priority areas. Thus the first point is area 1, Gansu, contributing 22.95% of the total weighted diversity; area 2 is Big Horn, contributing an additional 15.25% of complementary weighted diversity, and so on up to area 13, Northern California, which contributes the last 2.19% of weighted diversity, and brings the accumulation to 100% (the cumulative number of species taken into account at each successive step, up to the total of 43 at the 13th, is 9, 13, 23, 28, 30, 32, 35, 38, 39, 40, 41, 42, 43). The (incomplete) vertical straight line indicates how the histogram would look if there was at least one grid-square containing all 43 species; the sloping straight line is a bound indicating how the histogram would look if all 43 species occurred in different grid-squares and all were treated as taxonomically equal. See also text for explanation.

## PLANNING NATURE RESERVE NETWORKS WITHIN CRITICAL AREAS

Identification of whole countries, geographic regions, islands or large grid squares as critical faunas or floras is a basic step, but such units rarely represent practically conservable areas in terms of current economic resources. Furthermore, within critical areas, all species of interest rarely coexist at single localities. It is therefore necessary to undertake further rounds of analysis, within each priority region, to develop effective action plans for conservation.

Fundamental to secondary analyses is the view that all animal and plant species within a critical area, regardless of general abundance or local endemism, should be (insofar as it is possible) equally and adequately

protected. This is because rare or endemic taxa, together with common or widespread species, do not exist in isolation—they exist within more or less well-defined ecosystems or communities, on which they are dependent, and to which they make their own unique contributions. Thus, once identified, the whole biota of a priority reserve area needs adequate protection as a functional ecological system, or set of such systems.

As already noted, ecologists and conservationists working for national and state wildlife services in Australia are developing step-wise analyses intended to serve this particular function (Margules, 1986; Margules & Nicholls, 1987; Margules *et al.*, 1988; Margules & Stein, 1989; McKenzie *et al.*, 1989; Pressey & Nicholls, 1989*a,b*). Their analyses can take into account the desire to protect all species and representative ecosystems within a region. By planning multiple representations wherever possible, they also make allowance for population effects, such as possibilities of local extinction. Their approach appears capable of accommodating any theoretical or practical developments affecting the size, shape and design of nature reserves. For optimising efficiency, however, they will also need to address the analytical problems associated with the potential advantages and disadvantages of set-wise versus step-wise methods.

We believe, nonetheless, that these analytical methods designed to identify efficient nature reserve networks within specified or local regions are well-suited to the needs of secondary analyses. However, the primary analyses should involve the identification of priority areas on a global scale, or measurement of the global contributions made by existing national parks, through use of priority area analyses, as already outlined. Only by an approach of this type can requirements for the proposed International Convention (Chalker, 1990) be met with an efficient systematic perspective.

## GLOBAL PROSPECTS

Many biologists, especially non-systematists, may take exception to introduction of taxonomic weighting into conservation procedures. Such a reaction is likely because to do so could be seen to add a new level of uncertainty. It has often been argued that higher taxa are artificial, whereas species are natural or 'stable' units. On a world scale this is certainly not the case: higher taxa are no more difficult to recognise or define than species level taxa. Indeed, in many cases (e.g. Mammalia versus many species of *Mus*, or *Rubus* versus many of its 'species'), higher taxa are much more stable and easily delimited.

If conservation evaluation is to be based on concepts of diversity, then we believe that imperfections of our knowledge of the divergence of taxa



through time (classification) and distribution in space (biogeography) have to be accepted, and continual adjustments made as our understanding of both changes and improves. The current estimate of the world number of biological species is uncertain by an order of magnitude or more (Wilson, 1989; May, in press). Of those 1.5–1.8 million plant and animal species named to date, only a small fraction can be considered well-known in terms of species-limits, higher classification, distribution, and basic ecological requirements. Thus the global analyses can be based, for the immediate future at least, only on those plant and animal groups which are already well-known, or for which suitable study material already exists.

Our next concern, apart from refining taxic information measures and their application to priority area procedures, is to assemble a federation of systematists willing to pool data on particular and appropriate groups. Initially at least we intend to confine our attention to terrestrial organisms. Within our own institution we are currently able to commit work on danaine, ithomiine and papilionid butterflies, sphingid moths, and Coniferales. Through collaboration with the Royal Botanic Gardens, Kew, we anticipate major analyses of the tree families Chrysobalanaceae and Lecythidaceae. As the leading specialist on these groups is already deeply involved in considerations of priority areas for conservation (Prance, 1990), this particular initiative will provide unique opportunities to develop and test our methods.

Within the near future we hope to secure potential collaboration with workers on many more groups. Scientifically, a further task will then emerge as to how best to evaluate information generated from such disparate groups for the major task in hand—recognition of priority areas, and the assessment of the contribution that existing national parks and other reserves make. Politically, if we are to be effective, we will also need to ally our federation and system to one or more of the major international agencies concerned with the conservation of wildlife.

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