

MEASURING BIODIVERSITY VALUE FOR CONSERVATION

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ABSTRACT

Practical approaches to measuring biodiversity are reviewed in relation to the present debate on systematic approaches to conservation, to fulfil the goal of representativeness: to identify and include the broadest possible sample of components that make up the biota of a given region. Rather than adapting earlier measures that had been developed for other purposes, the most recent measures result from a fresh look at what exactly is of value to conservationists. Although debate will continue as to where precisely these values lie, more of the discussion has been devoted to ways of estimating values in the absence of ideal information. We discuss the current principles by assuming that the currency of biodiversity is characters, that models of character distribution among organisms are required for comparisons of character diversity, and that character diversity measures can be calculated using taxonomic and environmental surrogates.

INTRODUCTION

Over the last two decades almost all arguments about nature conservation have involved the issue of biological diversity and ways to preserve it (23, 31, 48, 64, 107). These discussions culminated in the 1992 Convention on Biological Diversity and its implementation (37). The conservation of biodiversity is a vast undertaking, requiring the mobilization of existing data, huge amounts of new information, and the monitoring and management of wildlife on an un-

precedented scale. From this newly articulated desire to preserve and protect all of nature's variety has arisen a battery of scientific methods to devise a calculus of diversity (57) that can be put to practical use. This account is an attempt to review the key principles that have emerged to date. We describe the various efforts that have been made to provide effective measures of biodiversity within the context of a general strategy for conservation, and how these have been combined with analytical methods of reserve selection for the design of networks of conservation areas capable of satisfying representation goals.

Goals and Representativeness

Extinction of organisms has been increasing at rates that now far exceed the geological background rate (89, 90). Analyses of geological extinction rates have indicated that the present diversity crisis has moved from the abstract to the concrete (71) and that many parts of the globe are losing organisms through pollution, conversion of natural habitats, and environmental degradation due to human overpopulation (87). That conservation intervention is necessary is hardly a new idea; it has been part of environmental policy for more than a century (4). The issues of measuring and conserving wholesale diversity for assessing "ecosystem health" have emerged only relatively recently (70). The future of restoration ecology will depend in large measure on the extent to which the variety of extant organisms is represented in well-managed reserve systems (5).

McNeely et al (61) considered biodiversity to be "an umbrella term for the degree of nature's variety, including both the number and frequency of ecosystems, species or genes in a given assemblage." This can be interpreted as a hierarchy of genes within populations, populations within species and higher taxa, and taxa within functioning ecosystems. Genes and taxa represent the material products of evolution, a process that has been taking place over the last 3.5 billion years, involving millions of diversification events (71). Consequently, organisms represent different combinations of shared and novel genetic systems: While some parts of the genome, such as ribosomal RNA, are as old as life itself and shared by all organisms, the formation of new genetic material has occurred throughout evolution. This historical hierarchy of life is reflected in the taxonomic hierarchy, from kingdoms down to species and infraspecific units (30, 99). The significance of taxonomic relationships for biodiversity measurement has been interpreted in a number of different ways which are discussed in more detail below.

In addition to the wealth of diversity, amounting to estimates of 5–15 million extant species (32, 58, 93, 94, 121) which can be represented in the taxonomic hierarchy, historical relationships are also clearly detectable in biogeography, with distinctive geographical and ecological distributions of genes, species,

and higher taxa evident at global, regional, and local levels (10, 11, 38, 52, 65, 66). As with genealogies, which can be difficult to detect because of homoplasy, geographical patterns are often complicated by stochastic processes of chance dispersals and introductions into non-native habitats (for review see 63). However, we concur with Croizat (11) that life and Earth evolved together to form distinctive patterns that can be uncovered through biogeographic analysis. Biological diversity is thus characterized by taxonomic turnover at all geographical scales, with the result that location of the components of biodiversity is absolutely critical to effective network design for in situ conservation.

In a practical strategy for conserving biodiversity, the minimum survey requirements include analysis of geographical distributions (preferably estimating taxonomic relationships of taxa) and analyzing these relational patterns (42). The aim is to identify particular areas that collectively include all taxa under consideration and then manage these areas as networks of biodiversity reserves, of both natural and semi-natural systems (108), to sustain viable populations of all component taxa. In this way it is hoped to preserve as wide a range of ecosystems, taxa, genes, and other biological features as possible. This strategy recognizes the basic currency of biodiversity as characters, models the distribution of this currency among species, and then compares the spatial distribution of species on various geographical scales. Margules & Austin (55) have noted that new data bases, even for well-known organisms, need to be constructed if accurate ecological and geographical surveys are going to improve on the ad hoc information generally available from existing biological collections. In view of the fact that inventories of only about 1.4 - to 1.8 million of the estimated 5-15 million extant species have been produced (94), it is most likely for many areas of the world that surrogates for character diversity at levels higher than species will have to be used (28, 33). In order of increasing remoteness, these will move to higher taxa, species assemblages, land classes, landscapes, and even whole ecosystems (114). To relate this scale of surrogacy to characters, differential weighting of taxa, based on phylogenetic models for predicting character diversity, provides a quantitative scheme for estimating biodiversity value at its most fundamental level.

Difference in Diversity

A simple count of species is still perhaps the most common approach used by both ecologists and systematists for measuring diversity to yield species-richness values for assemblages in areas (56, 77, 88). Species-richness measures depend on the size of the area being sampled (9). For comparisons between areas, accurate identifications of the taxa are considered fundamental because the species of each area are treated as having equal weight, whatever the range occupied. For decades this approach has been used to compare patterns of

diversity at global, regional, and local scales (39). However crude such a measure might be, species richness is the one most widely used for a variety of purposes. For example, extinction rates are calculated either in absolute terms as a rate loss or as an estimate of a ratio of species lost in relation to amounts of transformed habitat (39). Each species constitutes a unit (89, 90) such that loss of one species means that the world is poorer by one unit species or a defined area is poorer by one locally extinct taxon.

Regarding species as equally represented in different areas under comparison is considered insufficient by ecologists, who often want to know about species, beyond their presence or absence, including such information as commonness or rarity (33). Besides the number of species in a particular area, it is also necessary to know how individuals are apportioned within it (54, 77), for example the Shannon index (48, 54, 76, 96). In a more elaborate system (see 7, 59), Whittaker (109–111) suggested that at least three measures are required to determine diversity: alpha diversity (species richness of standard site samples), beta diversity (differentiation between samples along habitat gradients), and gamma diversity for a geographic area (differentiation between areas at larger scales). Various modifications to these concepts have resulted in considerable variation in precise definition of alpha and beta diversity in the modern literature (52).

Over the last five years biologists and economists have begun to question seriously whether we can afford to treat all species equally. The panda logo of the World Wide Fund (WWF) is a reminder that human beings have always intuitively considered that some organisms are more important than others and should receive higher priorities in assessments and choices among conservation areas. One could ask whether one species of panda is equivalent to one species of rat. We suppose that the WWF chose the panda as a symbol because it is a rare, threatened, and large charismatic animal guaranteed to evoke interest and draw large quantities of charitable funds. Rats are more important in the economy of nature, but they lack appeal for more than a few people.

The 1994 Chambers Dictionary defines diversity as “the state of being diverse; difference; dissimilarity; variety.” Thus, when choosing to prioritize one area for conservation against another, the one containing the most unlike taxa would be more diverse than the one containing similar taxa. For example, if comparing one area containing two sibling species of daisy with another area containing a columbine and a daisy, the latter area would be more diverse and could warrant a higher priority than the former area (see 41). Such a decision is justified in terms of the number of character differences or higher taxa being represented by the component taxa of each area (100, 120). Thus, as a basic rule of thumb, the taxonomic hierarchy can be used for an inclusive measure of diversity, including genetic diversity (44). However, there is a problem now that the taxonomic hierarchy has come to mean a variety of

different things, ranging from traditional classifications simply aggregating species into genera and families, to highly corroborated phylogenetic hypotheses with detailed data on tree topology and branch lengths (25).

CLADOGRAM MEASURES OF TAXONOMIC DIFFERENCE

The use of phylogenetic history in assessing diversity has been interpreted in different and sometimes conflicting ways (47, 48). For example, Erwin (19, and 8) valued areas for conservation that could cater for future evolution in so-called "species-dynamo" areas. Erwin suggested that in areas with many closely related species, members of rapidly evolving clades ("evolutionary fronts") make greater contributions to future diversity than do species-poor lineages. There are a number of problems with this approach if we accept that areas with a greater number of different taxa are more diverse than those that contain actively evolving clades. In terms of characters, or degrees of difference between taxa, choosing "dynamo areas" could result in selection for low character diversity, and such a choice further makes the unwarranted assumption that we know something about future patterns of evolution (112, 116).

There are a number of ways to justify the choice of one area over another. In contrast to Erwin's approach, for example, one could assume that evolution of characters was clock-like, either implicitly or explicitly. In this model, character richness could be maximized for a restricted set of organisms by choosing representatives of earliest diverging taxa. Vane-Wright et al (in 57, 100) were the first to provide an explicit quantitative method, *root weight*, which provided an absolute measure that scored basal clades with higher weights as compared to the trivial clades higher in rooted trees. A similar approach, the *phylogenetic diversity* method, using weighted and unweighted binary ranking procedures to give diversity scores to terminal taxa in cladograms (43, 67, 117), appeared shortly thereafter. By assigning weights in terms of the number of taxa from a particular node and the position of the node in a tree, Nixon & Wheeler's (67) two procedures performed in a manner similar to root weight by giving highest weights to early diverging taxa. Stiassny & de Pinna (92) noted that basal taxa within lineages of freshwater fishes (i.e. groups that are species poor when compared to their sister groups), are particularly vulnerable to environmental pressures (notably due to range-size rarity). Because known freshwater groups and 25% of all vertebrates fall within this category, the authors considered loss of such taxa would cause disproportionate character loss. Contrary to Erwin, they suggest that all threatened basal lineages should receive higher weights in biodiversity assessments than their species-rich sister clades.

The root weight and phylogenetic diversity methods (99, 154) are both

capable of selecting early-diverging and basal taxa by using information about the position of all taxa within a clade to assign absolute scores to each terminal taxon relative to its position in the branching topology. Williams et al (119) showed that such approaches had consequences that might seem undesirable. For example, considering all vertebrates using root weight or higher taxon richness (119, 120) would preferentially favour selection of basal groups of fishes as first choice subsets. The implications of considering the whole tree of life would give a perverse result of selecting several lineages of bacteria, while eukaryotes could be represented by one protist (116). Williams et al (119) proposed new ways for assessing taxonomic diversity of faunas and floras based on pairwise differences between taxa in cladograms. They noted that diversity considered as relative genealogical divergence, even in a restricted sense, was open to different interpretations.

For the first concept, their higher taxon richness measure was implemented to search for a flora or fauna in which species diverged closest to the root of the cladogram, to capture areas richest in highest taxa. However, seen from another perspective, different floras and faunas might contain samples of species that could be highly clumped or regularly dispersed across a cladogram. In the second concept, regular dispersion of species (terminal taxa) across a fully resolved pectinate cladogram would show more of a different kind of diversity than a clumped selection of an equal number of terminal taxa within the cladogram. Williams et al (119) were thus seeking to define diversity in terms of a pattern of relationship. Subsequently, the higher taxon measure selecting for early diverging taxa has been shown to increase the likelihood of capturing character-rich biotas, while the dispersion measure capturing the most regularly dispersed faunas and floras samples the richest combination of characters (25, 116). As diversity was assessed by the numbers of nodes between each pairwise comparison, the advantage of these methods was that any available branching diagram could be used for large numbers of species in the absence of branch length data.

SAMPLES OF CHARACTERS

Branch Lengths

The earliest reaction to Vane-Wright et al (in 57, 100), by Altschul & Lipman (4), suggested that in addition to nodes on cladograms, lengths of branches should also be taken into consideration in biodiversity measures. Vane-Wright et al (100) and Williams et al (119) emphasized that the best estimates of genealogy should be used, and they concentrated on node-counting measures because of the lack of reliable branch-length information for most taxa. Whereas cladograms are estimates of the most robustly supported relationships be-

tween taxa, branching diagrams interpreted as phylogenetic trees that incorporate branch length information, require more exacting interpretative models of character distributions (112) to calculate and predict accurately the pattern of diversity value.

Characters cannot all be counted directly, but their distribution among organisms can be predicted from their genealogy (22) by using a model of how character distributions may be related to the genealogical pattern. Different biotas can then be compared by using a taxonomic measure to predict or model differences of representation in these underlying characters. It is important to note that different classes of characters show very different patterns of distribution among organisms. If one class of characters is considered to be of real value, then it becomes important to identify that class of characters appropriate for diversity comparisons. Special cases have been made for interspecific genetic diversity (39), ecological and functional characters (86, 102), morphological diversity, and phenotypic characters (116). Attention has tended to converge onto valuing interspecific genetic diversity (23–25, 78, 91, 103–105), albeit in some instances to suit particular kinds of data such as molecular sequences and genetic distance data (12, 13).

“Phylogenetic diversity” has been used as a term most frequently by Faith (20, 25) to measure feature richness by using a spanning-subtree length technique. Unfortunately, the term, “phylogenetic diversity” had been used by Nixon & Wheeler (67) for their node-counting measure, and the term “feature richness” was already in use by conservationists to include cultural sites, geological structures etc. Nonetheless, Faith correctly recognized the most appropriate general measure of what we shall call “character richness.” Phylogenetic diversity is intended to identify floras and faunas with the greatest representation of individual genetic or morphological characters (20). It is based on genealogical classifications of organisms that use measures of character differences as estimates of character distance along all branches (see also 20, 21, 26, 91, 103–105). These approaches show that phylogenetic pattern has the potential to quantify and estimate biodiversity at a range of resolutions, from branching patterns in tree topologies to variation among characters, to cater for almost all available information within any kind of classification or topology. Faith (25) characterized this range at three levels; existing hierarchies that may or may not reflect phylogenies, classifications concordant with phylogenies, and well-corroborated phylogenetic estimates with both topological and branch-length information.

Models of Character Change

Predicting character distributions requires a well-corroborated estimate of the phylogenetic tree and selection of an explicit process model as to how character changes are distributed on phylogenetic trees. At its simplest there are three

cladistic models (116), although several variations have been described (25 for example). The most popular of these is the empirical model, which assumes any sample of characters to be representative of the entire universe of valued characters. More contentious are anagenetic or cladogenetic models. The clock-like anagenetic model is most appropriate for selectively neutral character changes, so that actual branch lengths on an ultrametric tree are assumed to be representative of character diversity. The cladogenetic model on the other hand suggests that character change is under stabilising selection and is primarily associated with the nodes of trees (43, 117).

If we had complete knowledge of the character universe, this could be used directly in diversity measures (78, 91, 103, 119). However, complete knowledge is never available. The empirical model uses counts of characters from a sample of character differences among organisms, and this is used for the branch lengths (23). Even though most characters are unsampled (74, 75), the empirical model assumes the sample to be unbiased (116, 117).

The clock model is popular among molecular biologists as the number of character changes along branches is related to duration (anagenesis). Clock models have been challenged (36, 98) because base substitutions can occur at different rates in highly constrained sequences (1, 2). In efforts to provide generalized models for all hierarchies, Faith (25) has also inferred equal branch lengths from taxonomic name hierarchies, which must be considered dubious given the arbitrariness of conventional taxonomic naming and ranking (117), but in the absence of other information, this is arguably better than nothing.

The cladogenetic model of character evolution is that favored by punctuated equilibrium theory (18) for character changes primarily associated with cladogenesis. In this model, characters important in conservation are those associated with nodes on trees. The debate about the relevance of cladogenetic models versus clock models has been equated to the debate about morphological versus molecular characters in systematics. Williams et al (116) suggest that different character suites are likely to follow different processes and models of change. This is what challenges the "universal" empirical model favored (at least implicitly) by Faith. Because different models will give different results from diversity measures, it focuses attention on choice of those characters and models most appropriate to perceived biodiversity value.

Although Faith (25) implies that only his methods (20–25) consider character diversity, we believe that all phylogenetic weighting methods devised to date make one standard assumption: that the underlying topology reflects character diversity. Williams et al (119, see also 112, 116) had already made the key point that choice of the underlying model is critical in terms of being able to justify the assumptions. The stated goal of protecting diversity has been equated by Weitzman (103–105) and Faith (20) with protecting as much character diversity (i.e. richness) as possible, and both maximum likelihood

approaches (103, 105) and parsimony methods (20) have been employed in efforts to maximize feature diversity.

In summary, of the methods described to date, those appropriate for assessing character diversity fulfil May's (57) request for a calculus of biodiversity. In discussing a range of measures, Williams et al (119) identified three criteria for measuring diversity of subsets of terminals on cladograms: taxon richness, higher taxon diversity, and dispersion across the classification (regularity).

However, higher taxon diversity and dispersion are incompatible. Clarification of diversity value as characters (20) and of how this can be related to taxonomy by evolutionary models (116) indicates that the distinction between higher taxon diversity and dispersion corresponds to measures of character richness and character combinations, respectively (see below). Thus, after selecting for an appropriate currency (characters) and a particular evolutionary model that will predict the distribution of characters over cladograms and trees, the remaining consideration is to decide whether greatest value resides within individual characters or in combinations of characters. However, before this issue is considered some discussion about characters as the currency of biodiversity is necessary.

VALUES, CURRENCIES, AND MEASURES OF BIODIVERSITY

Norton (69) suggests that because there can never be one truly objective measure of biodiversity, measures appropriate for restricted purposes are the only ones available. Measures of biological diversity, like all measures, imply a set of values (39, 61, 84, 114, 121), and the idea that genetic diversity is perceived by many biologists to be the basic currency of biological diversity seems to satisfy the widest range of interests (17). Although it is a reductionist argument (48), such a view implies that expressible genetic resources, however measured (116), are the important building blocks of the biosphere, and that all other levels within the hierarchy, even species (but also land classes and ecosystems), are the vessels containing, or surrogates representing, the basic currency (114).

Genetic resources can be assessed in myriad ways, raising the question of what constitutes an operational definition of diversity. It is clear that in the context of conservation biology, diversity is generally viewed as an anthropocentric value system. For example, IUCN/UNEP/WWF (44, 45, 61, 84) stresses that the preservation of genetic diversity in agriculture, forests, and fisheries is both a matter for future insurance and investment against environmental change. Consequently, option value can be an important justification for conservation because we are always working in ignorance or uncertainty about which characters will be valuable in the future. In the practical occupa-

tion of choosing *in situ* conservation areas there may be a general-purpose (if not universal) currency of diversity that can satisfy many sectoral interests, can be measured in particular groups of organisms or geographical areas, and can be integrated with the larger-scale subdivisions of the biosphere, including habitats, vegetation zones, and ecosystems.

Option Value

Although we consider that areas can be assessed by degrees of character difference and that this justifies the need for differential weighting of one area versus another, it is important to recognize that there are other opinions. While there remain disagreements on what warrants adequate representation, we will also disagree on which aspects of the taxonomic system should be used in measures of diversity. While arguments have been put forward for weighting, others have been proposed against it. To suggest that, because we lack knowledge of the future values of species, all species should be considered equally important (121) depends on where the fundamental currency of biodiversity is seen to lie (25).

The issue of whether we should weight or not has been clarified by using the taxonomic hierarchy to evaluate species through "option value" (20, 25, 103, 104). Option value (39, 106) reflects the willingness of a risk averse society to pay a premium, on top of the value itself, to guarantee access to resources of uncertain future supply. Haneman (40) suggests that option value has two interpretations: It may be akin to a risk premium arising from uncertainty as to future potential value should a protected area be preserved. Or, it may refer to the irreversibility of destruction and to the need for information. According to McNeely (60), in conservation: "option value is a means of assigning a value to risk aversion in the face of uncertainty." Norton (68) rejects the use of option value and argues that it means identifying species, guessing what uses they might have, and estimating the likelihood that discoveries about them will be made at a future date. In a simple sense, anticipated future-use value of species is considered impossible to apply (16). Those making other non-weighting arguments have been similarly sceptical about attempting to assign current value to species (6), arguing that taxonomic weighting refers to maintenance of future options (97). Wilson (121) favors equal weighting because all species are indeed "irreplaceable resources to humanity," in terms of commodity, amenity, and also morality (25, 68, 121). Reid (83), however, identifies option value of biodiversity with maximizing human capacity to adapt to changing ecological conditions, which in turn requires maximizing the rest of life's capacity to adapt to change. The key to this suggestion is that if we accept that option value reflects capacity to respond to environmental change, we cannot operate at the level of species but should

instead focus on biodiversity value at the fundamental level at which the objects for future use reside: expressible and heritable characters (114).

Equating option value with characters satisfies the requirement of IUCN (44), insofar as protecting subsets of taxa with as many features as possible would be the best safety net for keeping options open for future generations. As Faith (20, 21, 25) points out, characters can be seen as the fundamental "currency" with option value to the future. As Williams (114) puts it, biodiversity conservation must then focus on maximizing the amount of currency (counted as the number of different characters) to be held within the conservation bank (the set of secure species, ecosystems, or areas). If characters are seen as the basic unit of currency with equal weights applied to them (because of uncertainty), the vessels in which they occur (individuals, species, ecosystems, or areas) naturally may have different values because they contribute different numbers or combinations of complementary or novel characters.

Character Richness

If diversity value is interpreted to mean that it is the separate characters that are useful, as is the case for making pharmaceuticals or imparting disease-resistance, then the biodiversity measure that can identify the subset of organisms with the greatest number of character states would be chosen. Character richness for subsets of organisms can be maximized on metric trees with branch lengths scaled to character changes, by choosing a set of organisms within the floras or faunas of the areas under consideration linked by the maximum spanning subtree length (20, 21, 27, 112, 113). Ultrametric trees with clock-like character changes show maximum diversity in those areas that are richest in earliest diverging taxa. Williams et al (119) produced a measure for this when branch length data were lacking. Spanning-subtree length is also a consistent approach (20, 21, 27), but the branch lengths implied by ultrametric trees must be added (114).

Character Combinations

Within ecosystems, organisms are integrated by functional relationships. These may depend on combinations of characters. Thus an alternative interpretation of option value would be to assess the richness of different combinations of characters. To do this it is necessary to search for subsets of organisms that are most evenly spaced or distributed over the topology of the phylogenetic tree. This regular pattern will represent taxa at all levels within the hierarchy and therefore the largest number of diagnostic character combinations for subsets of a given size (112, 118).

Williams et al (112, 118, 119) devised the cladistic dispersion measure, which favors sets of organisms with the largest and most even distribution of nodes between them. The logical basis of this criterion is that the more evenly

spread choices maximize the degree to which subtrees represent the overall shape of the classification, and thereby the most dispersed subtrees are more representative of the variety of subgroups with their different character combinations (112). However, this measure has no clearly justified balance between regularity, numbers of organisms, and subtree length (21, 119).

Taxonomic dispersion has subsequently been developed by Faith & Walker (25, 27, 29), who have drawn from a family of p -median procedures used in operations research (53, 95) to locate objects in regular patterns on networks (such as a metric tree). The general model represents different combinations of characters as "discs" of differing diameter along the branches of metric trees (21, 27). If particular unique combinations of characters come and go over time, any point on the tree may be the center of distribution for a variety of character state combinations. The distance that can be travelled along the tree while still finding that combination defines the combination radius. All points are equally likely to be centers for a combination, and combinations can have any radius with equal probability. When searching for hyperdiverse sets of terminals, their continuous p -median measure maximizes representation of all historical character combinations by maximizing intersection of all discs anywhere on the tree with the selected terminals, and by minimizing the sum or average distances from all points on the tree to their nearest selected terminal among the p -set of terminals. The discrete p -median measure maximizes extant character combinations by maximizing intersection of discs centered on unselected terminals with the selected terminals, by minimizing the sum or average distances from all unselected terminals on a tree to the nearest selected terminal. Williams (114) suggests that the discrete version theoretically may be more appropriate in the context of conservation, because this seeks to maximize the representation of only those character combinations that actually exist as modern species (terminals on a tree).

Surrogacy

Representing character richness and character combinations has all the signs of providing a neat theoretical solution, but problems of application remain. Practical use of taxonomic measures recognizes that all characters of organisms can never be counted directly, which means that surrogate approaches are inevitable (28, 114). It is possible to recognize a scale of surrogacy within which suitable indirect measures reflecting character richness and character combinations can be chosen. The use of surrogates can exploit a predictive relationship between the surrogate variable and the target variable to reduce costs, but in all cases the surrogate must be demonstrated to predict diversity (51, 70).

In the absence of ideal knowledge of all characters, taxonomic diversity measures of the kind described above are capable of estimating option value

for all groups of organisms and sectoral interests, such as crop cultivars, from phylogenetic information. This has been done for Old World fruit bats by Mickleburgh et al (62), and for more than 30 other groups of plants, mammals, and invertebrates of global, regional, and local interest (118).

In some ways, the original weighting debate is turning full circle as, for large numbers of taxa at least, species richness is now seen to be a good surrogate for character richness. As Williams (114) points out, for this to fail would require that more species-rich faunas and floras become progressively taxonomically clumped as the number of taxa sampled increases. This result provides a stronger theoretical basis for using species-richness in diversity value measurement.

To ensure adequate representation from as wide a sample of organisms as possible, data sets for different species groups have been combined, and this has become an issue because incongruent patterns of species distribution are known at global (35, 115), national (72, 79, 80, 101), and local scales (85). Currently, various ways of combining data sets are being explored, for example, by summation of data sets (101) in a manner akin to the "total evidence" approach in systematics (15, 46). The predictive relationship depends on the notion that included diversity is indicative of total diversity, although it is unclear under what conditions predictor relationships for pattern by summation are better than when using one particular component group. There have been a number of claims from sectoral studies that well-chosen indicator groups are predictors of overall diversity [e.g. mycalesine satyrid butterflies as predictors of other groups in Madagascar (49, 50)]. These are only expected to work if there is a high level of nestedness (14, 73) or orderedness (85) in the distributions of the different species groups within each analysis.

Williams (114) has mentioned that, in principle, indicator groups could be selected and used in combination with a taxonomic diversity measure, but it remains to be seen whether adding taxonomic weight to species richness of one indicator group is a better predictor of total character richness than is species richness of the indicator group on its own. Kremen & Lees (personal communication) are trying to test this directly in Madagascar, using mycalesines as the target indicator taxon, through comparison with species richness for a number of other groups. Williams (114) predicts that such patterns might be predicted when there are strong repeating patterns in genealogy and space that could be explained by a vicariant model of biogeography (66), although it is quite possible that dispersals could obscure such patterns.

Any higher taxon, in theory, can be a surrogate for species. On one hand, this greatly reduces dependence on extrapolation between groups of the indicator approach, while on the other, it avoids some pitfalls of environmental surrogates. Williams (114) indicates that the idea behind such an approach is that mapping 1000 genera or families represents more of diversity than map-

ping 1000 species and may incur little or no extra data-gathering cost. Gaston & Williams (34, see also 115, 118) have used higher taxon richness as a surrogate for species richness, but when taxa are monophyletic, it may be possible to use higher taxa as surrogates for character richness using the tree-based measures (112).

A further surrogate approach, environmental diversity, has been described by Faith & Walker (27, 28) as an expression of environmental pattern so that environmental variation can be seen as a continuum rather than being partitioned into clusters. Faith & Walker relate environmental variables to species distributions using a standard ecological continuum model. Thus, because they can estimate environmental space from environmental data directly or indirectly by using some indicator group, the corresponding surrogate-measure, "environmental diversity," makes best-possible use of either kind of data. They conclude that the "arbitrariness" of the attribute method can be replaced with a robust surrogate "pattern" approach that is flexible and avoids unwarranted assumptions (28). While this approach is very promising, and maybe the best available for many poorly sampled areas of the world, it too usually has to depend on very simple and unrealistic assumptions about even and regular species distributions in niche space, and assumptions that the distribution of species among areas is at or near equilibrium with governing environmental factors (114).

We consider that, compared with most other approaches, taxon-based surrogates retain identities of attributes (taxa) for each area unit under consideration. By retaining the identity of taxa across areas, and hence some knowledge of spatial turnover (118), faunas and floras within networks can be assessed efficiently using complementarity (100). Critically, this conclusion does not suggest that option value in terms of characters has to be scored using mathematically complex taxonomic measures, but option value supports the use of less direct approaches that have been identified within the usual three tiers of genes, species, and ecosystems. These range from direct counts of characters, to progressively more remote surrogates in species, higher taxa, ordinations of species assemblages, land forms, landscapes and ecosystems (114).

SUMMARY AND CONCLUSIONS

Biodiversity can be assessed from a wide range of viewpoints for conservation, but some basic principles are emerging that are common to many of the evaluation methods that have been proposed. Biodiversity value can be identified with option value and character richness (or combinations) and can be estimated using phylogenetic models or by using surrogates such as species-richness, assemblage-richness, or land-class richness. Combined with the ability to assess areas in terms of their complementarity (turnover) and degrees of

rarity (endemism), this approach provides the minimum framework for an appropriate system of relative measurement (99). To date, there are very few studies that accommodate all of these principles into one system, although the picture is changing.

A more general framework for the assessment of biodiversity must be able to use available information from a range of levels, and it is clear that some basic issues have yet to be resolved. However, for all of these methods it has been shown that there is an initial requirement to recognize attributes, whether genes, characters, species, higher taxa, or land classes. At the most fundamental level, characters can be considered as attributes with equal option value.

Secondly, these attributes have to be scored for geographical analyses at the appropriate spatial scales, from small pastoral units, to large standardised regional grid cells (81).

The third requirement is an estimate of the pattern as a summary of relationships among the attributes or parcels of attributes that need to be conserved. The thrust of this paper has been to review how phylogenetic pattern can be used to predict this underlying distribution of characters for biodiversity (20, 25, 100, 117, 119). In the case of grid cells as areas with species as parcels of character attributes, the phylogenetic relationships of the species provide the underlying pattern that can be used, in turn, to determine levels of biodiversity representation (e.g. character richness) and relative option value.

The fourth requirement is to provide a reliable model of how the pattern of conserved areas should provide information about diversity at the level of the attributes. Still being explored is the question of which model provides a robust explanation of how variation in the attributes is predicted by the pattern, and there remain some unresolved issues. For example, if unwarranted assumptions are made by one model for linking characters and option value to the phylogenetic pattern, then the resulting diversity scores may be even less defensible than when simply viewing all species as equal. Faith (25), for example, criticized Weitzman's (103) approach as being hard to justify because it requires assumptions of clock-like rates of evolution both for derivation of the pattern and for the model linking pattern to characters. We suspect that when empirical branch length data are not considered reliable, the cladogenetic model may prove to be more predictive than simple species richness or the clock model.

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Literature Cited

1. Albert VA, Backlund A, Bremer K. 1994. DNA characters and cladistics: the optimisation of functional history. In *Models in Phylogeny Reconstruction*, ed. RW Scotland, DJ Siebert, DM Williams, pp. 249–72. Oxford: Clarendon Press
2. Albert VA, Mishler BD, Chase MW. 1992. Character-state weighting for restriction site data in phylogenetic reconstruction, with an example from chloroplast DNA. In *Molecular Systematics of Plants*, ed. PS Soltis, DE Soltis, JJ Doyle, pp. 369–403. New York: Chapman & Hall
3. Altschul SF, Lipman DJ. 1990. Equal animals. *Nature* 348:493–94
4. Anderson D, Grove R. 1987. *Conservation in Africa*. Cambridge, UK: Cambridge Univ. Press
5. Austin MP, Margules CR. 1986. Assessing representativeness. In *Wildlife Conservation Evaluation*, ed. MB Usher, pp. 45–67. London: Chapman & Hall
6. Aylward B. 1992. Valuing the environment. In *Global Biodiversity*, ed. B Groombridge, pp. 407–25. London: Chapman & Hall
7. Bond WR. 1989. Describing and conserving biotic diversity. In *Biotic Diversity in Southern Africa: Concepts and Conservation*, ed. BJ Huntley, pp. 2–18. Cape Town: Oxford Univ. Press
8. Brooks DR, Mayden RL, McLennan DA. 1992. Phylogeny and biodiversity: conserving our evolutionary legacy. *TREE* 7:55–9
9. Brown JH. 1988. Species diversity. In *Analytical Biogeography*, ed. AA Myers, PS Giller, pp. 57–89. London: Chapman & Hall
10. Croizat L. 1958. *Panbiogeography*. Caracas: Publ. by the author
11. Croizat L. 1964. *Space, Time, Form: The Biological Synthesis*. Caracas: Publ. by the author
12. Crozier RH. 1992. Genetic diversity and the agony of choice. *Biol. Conserv.* 61: 11–15
13. Crozier RH, Kusmierski RM. 1995. Genetic distances and the setting of conservation priorities. *Conserv. Biol.* In press
14. Cutler A. 1991. Nested faunas and extinction in fragmented habitats. *Conserv. Biol.* 5:496–505
15. Donoghue M. 1995. Approaches to parsimony: "Consensus" or "total evidence." *Annu. Rev. Ecol. Syst.* 26: In press
16. Ehrenfeld D. 1988. Why put value on biodiversity? In *Biodiversity*, ed. EO Wilson, pp. 212–16. Washington, DC: Natl. Acad. Press
17. Ehrlich PR, Wilson EO. 1991. Biodiversity studies: science and policy. *Science* 253:758–61
18. Eldredge N, Gould SJ. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In *Models in Paleobiology*, ed. TJM Schopf, pp. 82–115. San Francisco: Freeman Cooper
19. Erwin TL. 1991. An evolutionary basis for conservation strategies. *Science* 253: 750–52
20. Faith DP. 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61:1–10
21. Faith DP. 1992. Systematics and conservation: on predicting the feature diversity of subsets of taxa. *Cladistics* 8:361–73
22. Faith DP. 1993. Biodiversity and systematics: the use and misuse of divergence information in assessing taxonomic diversity. *Pacific Conserv. Biol.* 1:53–57
23. Faith DP. 1994. Genetic diversity and taxonomic priorities for conservation. *Biol. Conserv.* 68:69–74

24. Faith DP. 1994. Phylogenetic diversity: a general framework for the prediction of feature diversity. See Ref. 31, pp. 251-68
25. Faith DP. 1994. Phylogenetic pattern and the quantification of organismal biodiversity. *Phil. Trans. R. Soc. Lond. B* 345:45-58
26. Faith DP, Cawsey EM. *Phylorep, software for phylogenetic representativeness*. Publ. by authors
27. Faith DP, Walker PA. 1993. *Diversity Software Package and Reference and User's Guide*. Canberra: CSIRO, Div. Wildlife and Ecol.
28. Faith DP, Walker PA. 1995. Environmental diversity: how to make best possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiv. Conserv.* In press
29. Faith DP, Walker PA. 1995. Hotspots and fire-stations: on the use of biotic and environmental data to estimate the relative biodiversity of different sets of areas. *Biodiv. Lett.* In press
30. Fernholm B, Bremer K, Jornvall H. 1989. *The Hierarchy of Life; Molecules and Morphology in Phylogenetic Analysis*. Amsterdam, New York, Oxford: Excerpta Medica
31. Forey PL, Humphries CJ, Vane-Wright RI, eds. 1994. *Systematics and Conservation Evaluation*. Oxford: Clarendon
32. Gaston KJ. 1991. The magnitude of global insect species richness. *Conserv. Biol.* 5:283-96
33. Gaston KJ. 1994. *Rarity*. London: Chapman & Hall
34. Gaston KJ, Williams PH. 1993. Mapping the world's species—the higher taxon approach. *Biodiv. Lett.* 1:2-8
35. Gaston, KJ, Williams PH, Humphries CJ. Large scale patterns of diversity: spatial variation in family richness. *Proc. Roy. Soc. Series B* Submitted
36. Gillespie JH. 1991. *The Causes of Molecular Evolution*. Oxford: Oxford Univ. Press
37. Glowka L, Burhenne-Guilmin F, Sygne H, McNeely JA, Gündling L. 1994. *A Guide to the Convention on Biological Diversity*. Gland: IUCN
38. Grehan JR. 1993. Conservation biogeography and the biodiversity crisis: a global problem in space/time. *Biodiv. Lett.* 1:134-40
39. Groombridge B. 1992. *Global biodiversity: Status of the Earth's Living Resources*. London: Chapman & Hall
40. Haneman, WM. 1989. Information and the concept of option value. *J. Environ. Econ.* 16:23-37.
41. Harper JL, Hawksworth DL. 1994. Biodiversity: measurement and estimation. *Phil. Trans. Roy. Soc. B* 345:5-12
42. Humphries CJ, Vane-Wright RI, Williams PH. 1991. Biodiversity reserves: setting new priorities for the conservation of wildlife. *Parks* 2:34-38
43. Humphries CJ, Williams PH. 1994. Cladograms and trees in biodiversity. In *Models in Phylogenetic Construction*, ed. RW Scotland, DM Siebert, D Williams, pp. 335-52. Oxford: Clarendon
44. IUCN, UNEP, WWF. 1980. *World Conservation Strategy, Living Resource Conservation for Sustainable Development*. Gland, Switzerland: IUCN, UNEP, WWF
45. IUCN, UNEP, WWF. 1991. *Caring for the Earth, a Strategy for Sustainable Living*. Gland: IUCN
46. Kluge AG. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among Epicrates (Boidae, Serpentes). *Syst. Zool.* 38:7-25
47. Krajewski C. 1991. Phylogeny and diversity. *Science* 254:918-19
48. Krajewski C. 1994. Phylogenetic measures of biodiversity: a comparison and critique. *Biol. Conserv.* 69:33-39
49. Kremen C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecol. Applicat.* 2:203-17
50. Kremen C. 1994. Biological inventory using target taxa: a case study of the butterflies of Madagascar. *Ecol. Applicat.* 4:407-22
51. Landres PB, Verner J, Thomas JW. 1988. Ecological uses of vertebrate indicator species: a critique. *Conserv. Biol.* 2:316-28
52. Latham RE, Ricklefs RE. 1993. Continental comparisons of temperate-zone tree species diversity. In *Species Diversity: Historical and Geographical Perspectives*, ed. RE Ricklefs, D Schluter, pp. 294-314. Chicago: Univ. Chicago Press
53. Love RF, Morris JG, Wesolowsky GO. 1988. *Facilities Location, Models and Methods*. London: North-Holland
54. Magurran AE. 1988. *Ecological Diversity and Its Measurement*. London: Croom Helm
55. Margules CR, Austin MP. 1994. Biological models for monitoring species decline: the construction and use of data bases. *Phil. Trans. R. Soc. Lond. Ser. B* 344:69-75 CK
56. May RM. 1981. Patterns in multispecies communities. In *Theoretical Ecology*, ed. RM May, pp. 197-227. Sunderland, MA: Sinauer Assoc.

57. May RM. 1990. Taxonomy as destiny. *Nature* 347:129-30
58. May RM. 1992. How many species inhabit the earth? *Sci. Am.* October:18-24
59. McNaughton SJ. 1994. Conservation goals and the configuration of biodiversity. See Ref. 31, pp. 41-62
60. McNeely JA. 1988. *Economics and Biological Diversity*. Gland: IUCN
61. McNeely JA, Miller KR, Reid WV, Mittermeier RA, Werner TB. 1990. *Conserving the World's Biodiversity*. Washington, DC: IUCN, WRI, CI, WWF and WB
62. Mickleburgh SP, Hutson AM, Racey PA. 1992. *Old World Fruit Bats, an Action Plan for Their Conservation*. Gland: IUCN
63. Myers AA, Giller PS. 1988. *Analytical biogeography; An Integrated Approach to the Study of Animal and Plant Distributions*. London & New York: Chapman & Hall
64. Myers N. 1979. *The Sinking Ark: A New Look at the Problem of Disappearing Species*. Oxford: Pergamon
65. Nelson G, Ladiges PY. 1990. Biodiversity and biogeography. *J. Biogeogr.* 17: 559-60
66. Nelson G, Platnick N. 1981. *Systematics and Biogeography: Cladistics and Vicariance*. New York: Columbia Univ. Press
67. Nixon KC, Wheeler QD. 1992. Measures of phylogenetic diversity. In *Extinction and Phylogeny*, ed. MJ Novacek, QD Wheeler, pp. 216-34. New York: Columbia Univ. Press
68. Norton BG. 1988. The constancy of Leopold's land ethic. *Conserv. Biol.* 2: 93-102
69. Norton BG. 1994. On what we should save: the role of culture in determining conservation targets. See Ref. 31 pp. 23-39
70. Noss RF. 1990. Indicators for monitoring biodiversity. *Conserv. Biol.* 4:355-64
71. Novacek MJ, Wheeler QD. 1992. Introduction: Extinct taxa: Accounting for 99.9...% of the Earth's biota. In *Extinction and Phylogeny*, ed. MJ Novacek, QD Wheeler, pp. 1-16. New York: Columbia Univ. Press
72. Oosterbroek P. 1994. Biodiversity of the Mediterranean region. See Ref. 31, pp 289-307
73. Patterson BD, Atmar W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagoes. *Biol. J. Linn. Soc.* 28:65-82
74. Patterson C. 1994. Null or minimal models. In *Models in Phylogeny Reconstruction*, ed. RW Scotland, DJ Siebert, DM Williams, pp. 173-92. Oxford: Clarendon
75. Patterson C, Williams DM, Humphries CI. 1993. Congruence between molecular and morphological phylogenies. *Annu. Rev. Ecol. Syst.* 24:153-88
76. Peet RK. 1974. The measurement of species diversity. *Annu. Rev. Ecol. Syst.* 5:285-307
77. Pielou EC. 1967. The use of information theory in the study of the diversity of biological populations. *Proc. 5th Berkeley Symposium on Mathematics and Statistical Probability* 4:163-77
78. Polasky S, Solow A, Broadus J. 1993. Searching for uncertain benefits and the conservation of biological diversity. *Environ. Res. Econ.* 3:171-81
79. Prendergast JR, Quinn RM, Lawton JH, Eversham BC, Gibbons DW. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365:335-37
80. Prendergast JR, Wood SN, Lawton JH, Eversham BC. 1993. Correcting for variation in recording effort in analyses of diversity hotspots. *Biodiv. Lett.* 1:39-53
81. Pressey RL, Possingham HP, Margules CR. 1995. Optimality in reserve selection algorithms: When does it matter and how much? *Biol. Conserv.* In press
82. Raup DM. 1988. Diversity crises in the geological past. In *Biodiversity*, ed. EO Wilson, pp. 51-57. Washington, DC: Natl. Acad. Sci. Press
83. Reid WV. 1994. Setting objectives for conservation planning. See Ref. 31, pp. 1-13
84. Reid W, Miller KR. 1989. *Keeping Options Alive: The Scientific Basis for Preserving Biodiversity*. Washington, DC: WRI
85. Ryti RT. 1992. Effect of focal taxon on the selection of nature reserves. *Ecol. Applic.* 2:404-10
86. Schulze E-D, Mooney HA. 1993. *Biodiversity and Ecosystem Function*. Berlin: Springer-Verlag
87. Sisk TD, Launer AE, Switky KR, Ehrlich PR. 1994. Identifying extinction threats: global analyses of the distribution of biodiversity and the expansion of the human enterprise. *BioScience* 44: 592-604
88. Smith EP, van Belle G. 1984. Nonparametric estimation of species richness. *Biometrics* 40:119-29
89. Smith FDM, May RM, Pellew R, Johnson TH, Walter KR. 1993. Estimating extinction rates. *Nature* 364:494-96
90. Smith FDM, May RM, Pellew R, Johnson YH, Walter KR. 1993. How

- much do we know about the current extinction rate? *TREE* 8:375–78
91. Solow AR, Broadus JM, Toning N. 1993. On the measurement of biological diversity. *J. Environ. Econ. Manage.* 24:60–68
 92. Stiasny MLJ, de Pinna MCC. 1994. Basal taxa and the role of cladistic patterns in the evaluation of conservation priorities: a view from freshwater. See Ref. 31, pp. 235–49
 93. Stork NE. 1995. How many species are there? *Biodiv. Conserv.* In press
 94. Stork NE. 1994. Inventories of biodiversity: more than a question of numbers. See Ref. 31, pp. 81–100
 95. Tansel BC, Francis RL, Lowe TJ. 1983. Location on networks: a survey. Part 1: the p-center and p-median problems. *Manage. Sci.* 29:482–97
 96. Taylor LR. 1978. Bates, Williams, Hutchinson—a variety of diversities. *Symp. R. Ent. Soc. Lond.* No 9:1–18
 97. Tisdell, 1990. Economics and the debate about the preservation of species, crop varieties, and genetic diversity. *Ecol. Econ.* 2:77–90.
 98. Usher MB. 1986. *Wildlife Conservation Evaluation*. London: Chapman & Hall
 99. Vane-Wright RI. 1994. Systematics and the conservation of biodiversity: global, national and local perspectives. In *Perspectives on Insect Conservation*, ed. KJ Gaston, TR New, MJ Samways, pp. 197–211. Andover, UK: Intercept
 100. Vane-Wright RI, Humphries CJ, Williams PH. 1991. What to protect? Systematics and the agony of choice. *Biol. Conserv.* 55:235–54
 101. Vane-Wright RI, Smith CR, Kitching IJ. 1994. Systematic assessment of taxic diversity by summation. See Ref. 31, pp. 309–26
 102. Walker BH. 1992. Biodiversity and ecological redundancy. *Conserv. Biol.* 6: 18–23
 103. Weitzman ML. 1992. On diversity. *Q. J. Econ.* 107:363–406
 104. Weitzman ML. 1992. Diversity functions. *Discussion paper number 1610*. Harvard University, MA: Harvard Inst. of Econ. Res.
 105. Weitzman ML. 1993. What to preserve? An application of diversity theory to crane preservation. *Q. J. Econ.* 108:157–83
 106. Weisbrod, BA. 1964. Collective-consumption services of individual-consumption goods. *Q. J. Econ.* 78: 471–77
 107. Western D. 1992. The biodiversity crisis: a challenge for biology. *Oikos* 63: 29–38
 108. Westman WE. 1990. Managing for biodiversity: unresolved science and policy questions. *BioScience* 40:26–33
 109. Whittaker RH. 1960. Vegetation of the Siskiyou mountains, Oregon and California. *Ecol. Monogr.* 30:279–338
 110. Whittaker RH. 1972. Evolution and the measurement of species diversity. *Taxon* 21:213–51
 111. Whittaker RH. 1975. *Communities and Ecosystems*. New York: Macmillan
 112. Williams PH. 1993. Choosing conservation areas: using taxonomy to measure more of biodiversity. In *Int. Symp. on Biodiversity and Conservation*, ed. T-Y Moon, pp. 194–227. Seoul: Korean Entomol. Inst.
 113. Williams PH. 1994. *Using Worldmap. Priority Areas for Biodiversity*. Version 3.0. London: The author
 114. Williams PH. 1995. Comparing character diversity using biological surrogates. In *Priority Areas Analysis: Systematic Methods for Conserving Biodiversity*, ed. CJ Humphries, CR Margules, RL Pressey, RI Vane-Wright. Oxford: Oxford Univ. Press In preparation
 115. Williams PH, Gaston KJ. 1994. Measuring more of biodiversity: Can higher-taxon richness predict wholesale species richness? *Biol. Conserv.* 67:211–17
 116. Williams PH, Gaston KJ, Humphries CJ. 1995. Do conservationists and molecular biologists value differences between organisms in the same way? *Biodiv. Lett.* 2:67–78
 117. Williams PH, Humphries CJ. 1994. Biodiversity, taxonomic relatedness, and endemism in conservation. See Ref. 31, pp. 269–87
 118. Williams PH, Humphries CJ, Gaston KJ. 1994. Centres of seed plant diversity: the family way. *Proc. R. Soc. Lond. Ser. B.* 256:67–70
 119. Williams PH, Humphries CJ, Vane-Wright RI. 1991. Measuring biodiversity: taxonomic relatedness for conservation priorities. *Aust. Syst. Bot.* 4: 665–9.
 120. Williams PH, Vane-Wright RI, Humphries CJ. 1993. Measuring biodiversity for choosing conservation areas. In *Hymenoptera and Biodiversity*, ed. J LaSalle, ID Gauld, pp. 309–8. Wallingford: CAB Int.
 121. Wilson EO. 1992. *The Diversity of Life*. London: Penguin
 122. WRI, IUCN, UNEP. 1992. *Global Diversity Strategy: Guidelines for Action to Save, Study and Use the Earth's Biotic Wealth Sustainably and Equitably*. New York: WRI