PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Phylogenetic Pattern and the Quantification of Organismal Biodiversity

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Phil. Trans. R. Soc. Lond. B 1994 **345**, 45-58
doi: 10.1098/rstb.1994.0085

Phylogenetic pattern and the quantification of organismal biodiversity

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CONTENTS

SUMMARY

Biodiversity can be explored at a number of different levels and in principle may be separately quantified at each. Phylogenetic pattern has the potential to quantify and estimate biodiversity at the finest scale, that is, variation among species in features or attributes. This scale is an important one for conservation, as it should form the basis for prioritizing conservation efforts at the species level. Further, recent published objections to differentially weighting species are answered by defining option value at this feature-level. Unfortunately, there has been no consensus on exactly how phylogeny can be used to value species, possibly because proper consideration of the link between pattern and underlying features generally has been unresolved. 'Phylogenetic diversity' (PD) represents just one of several approaches that do consider diversity at the feature-level explicitly. These alternative approaches are discussed in the context of a general framework for using pattern to quantify diversity at a level below that of the original objects. The pattern framework highlights that estimation of biodiversity at a lower level using pattern will require decisions about the nature of the units of diversity, the kind of pattern to be used, the model relating unit items to pattern, and finally how this implies a pattern-based measure reflecting biodiversity. An alternative published model for relating features to a particular form of phylogenetic pattern is considered, and shown to make unwarranted assumptions. A possible alternative definition of the underlying units of diversity is examined, which may represent a different form of option value, also quantifiable using phylogeny. A possible alternative pattern to a phylogenetic tree for the prediction of feature diversity is also discussed. The appeal of these alternative approaches depends on the goals of conservation; in addition, justification for prioritizing or weighting requires that any practical approach avoid arbitrary, unwarranted, assumptions.

1. INTRODUCTION

This paper is concerned with the potential contribution of phylogeny to the general problem of quantifying and estimating organismal diversity ('biodiversity'). Although phylogenetics may contribute to the study of biodiversity and conservation in different ways (Eldredge 1993), the specific topic of this paper is the use of phylogenetic pattern to assign weights, values, or conservation priorities to taxa. This goal may not appear to be related to the quantification of biodiversity so much as to the conventional assignment of relative conservation value to the usual units of conservation, that is, species. However, the view advocated here is that

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Phil. Trans. R. Soc. Lond. B (1994) **345**, 45–58
Printed in Great Britain

phylogenetic information, as used to prioritize or weight species for conservation, will assign value only by quantifying biodiversity; further, this quantification is made at a level below that of species. This fundamental level of organismal variation corresponds to features or attributes of species (Faith 1992*a*). When biodiversity is defined at this level, the oft-stated conservation goal of 'protecting biodiversity' translates into protecting as much of this feature-diversity as possible; this has been equated with maximizing a form of option value in conservation (Faith 1992*a*; Weitzman 1992*a*). Option value defined at the level of features in turn has been used as a justification for differential weighting of species (Faith 1992*a*, 1994*a*).

This paper follows a recent profusion of papers (Faith 1993, 1994*a*,*b*; Williams & Humphries 1994, and references within these), all proposing some form of weighting of species using phylogeny (or taxonomy), although most of these proposals have not considered feature-diversity in any form (as discussed elsewhere in Faith 1992*b*, 1993, 1994*a*). Paradoxically, this paper also follows on a number of recent papers, discussed below, all arguing against weighting or valuing different species, particularly in the face of our indisputably poor knowledge about 'future' values for species. A first task for this paper is to argue that a value-system, properly based on the quantification of biodiversity at the lower level of features, largely avoids the difficulties raised by these critics of weighting.

At the same time, the argument here will not be that our inherently poor knowledge of biodiversity can be somehow circumvented – in fact, equating biodiversity with numbers of features – features that never can be counted in total (Faith 1992*a*,*b*), is perhaps an extreme case of limited knowledge. Because a 'complete' set of all features for a set of species will never be observed directly, inference of relative contributions of different species to overall feature-diversity will have to be made using some surrogate. Quantifying biodiversity at this level therefore is a difficult estimation problem. Phylogenetic pattern, and its potential predictive link with underlying features of species (Farris 1979; Faith 1992*a*,*b*) is explored as a possible solution to this estimation problem.

The second goal of this paper is to present a basic framework, outlined by Faith & Walker (1993), for using pattern to quantify biodiversity, which will highlight the requirements for using pattern as a surrogate (in principle at any level at which biodiversity is defined), and raise alternative formulations for how phylogenetic pattern might predict feature-diversity. I will also review one specific proposal, 'phylogenetic diversity' (PD, Faith 1992*a*), and show how it fits into this framework.

The main body of this paper considers some other alternative strategies, particularly those of Weitzman (1992*a*–*c*) and Polasky *et al.* (1993). These proposals share with phylogenetic diversity an explicit consideration of the link between pattern and underlying units of biodiversity. Consequently, their assumptions in this context can be evaluated. These alternative strategies for quantification and estimation raise the following issues:

1. If features are taken to be the units of biodiversity of interest, then what is the proper predictive model relating phylogenetic pattern to features?
2. Is there an alternative to features or attributes that should instead form the unit items of biodiversity, and can phylogeny then act as a surrogate for these?
3. Is the phylogenetic pattern the only pattern of choice for estimating biodiversity at the feature level?

The alternative strategies accompanying these issues reflect both variations in conservation goals and different assumptions about the nature of pattern and fundamental units of biodiversity. Consideration of assumptions particularly may exclude some proposed strategies; while our poor knowledge arguably does not absolutely exclude weighting or prioritizing, it does put a premium on doing this without making unwarranted assumptions.

2. OPTION VALUE AND THE QUESTION OF WEIGHTING

One explicit rationale for using phylogenetic pattern (or taxonomy as an approximation to phylogeny) to weight species has been based (Faith 1992*a*, 1994*a*; Weitzman 1992*a*) on a form of 'option value'. Although biodiversity might be defined at a number of different levels (e.g. ecosystems or species or features), option value as used here is interpreted as depending on quantification at the level of features; option value increases with the number of attributes or features of species that are protected (Faith 1992*a*). Option value in this sense is compatible with the general usage put forward by IUCN (1980) as 'a safety net of biological diversity for future generations'. Thus, the greater the number of different features represented by a protected subset of taxa, the greater the option value (Faith 1992*a*,*b*). An individual species of greater value is one contributing more novel features to a given subset, so increasing the overall biodiversity protected at this level.

At the base of the rationale for option value is some degree of ignorance about actual, realized values in the future. In response to this ignorance there is an attempt to keep options open, for realizing values of species in the future, by saving as much biodiversity as possible now. Such a goal would seem to be naturally applicable at the level of attributes of species. IUCN (1980) cites one form of valuation on species as based on taxonomic distinctiveness; presumably species valued in this way provide unique features or attributes that may be useful in the future. However, in spite of the intuitive appeal of weighting species in this way, option value at the level of features of species is arguably impractical; it raises a seemingly insurmountable new level of ignorance: variety at the feature level is to be maximized, but we are not even aware of all the unit items that make up biodiversity at this level. Thus, the practical difficulty in maximizing option value is that the unit items – features – cannot generally be counted. In fact, we cannot even name them all; the feature or attribute of great use to a future generation may well be one of which we are presently totally unaware. To make matters worse, there is no *a priori* way to narrow-down even the general kinds of features we are willing to consider.

Pattern at the species level can help overcome this problem if it is an effective predictor of biodiversity at the feature level. Phylogenetic pattern in particular should be able to predict relative numbers of different features in sets of taxa. The features accounted for in this way would be only constrained in scope by the requirement that they potentially are explained by phylogenetic relationships; that is, their distribution among species is accounted for by common ancestry (Faith 1992*a*,*b*, 1993). A species then contributes novel features if it represents a so-far unrepresented part of the evolutionary history of the group. This can form the basis for differentially weighting or valuing different species based on phylogenetic pattern (Faith 1992*a*, 1994*a*). The corresponding measure of 'phylogenetic diversity' is discussed in detail below.

This rationale for prioritizing or differentially weighting species unfortunately runs counter to a number of arguments in the conservation literature against species-weighting. Ironically, option value has been presented in these arguments both as leading to weighting and non-weighting of species.

Norton (1988) describes the economist's assignment of option value to species as involving the calculation of value for species 'of unknown worth'. Option value then is the value we should place on the possibility that a future discovery will make such a species useful. Norton quotes Fisher & Hanemann's (1985) characterization of option value as:

> 'the present benefit of holding open the possibility that a future discovery will make useful a species that we currently think useless. They would ask people how much they are willing to pay to retain the option of saving the species'.

Thus, an interpretation of option value is put forward here that appears to necessarily equate value with monetary amounts via a cost–benefit analysis. Norton argues that option value requires that we: (i) identify the species; (ii) guess what uses it might have, put some dollar value on those uses; and (iii) estimate the likelihood that such discoveries will occur at any future date. These unrealistic requirements form the basis for his rejection of this approach.

Ehrenfeld (1988) similarly argues that value in the sense of anticipated economic value is impossible to apply, and is a distraction from the root causes of decline in biodiversity. He takes the view that value 'is an intrinsic part of diversity' and does not depend on the properties or uses of the species in question.

The recommendation of no-weighting also has been justified by an argument that the basis of value is so general anyway that it is not possible to objectively assign weights. Tisdell (1990) sees the World Conservation Strategy's discussion of taxonomic weighting as relating to maintenance of options, but not limited to those of an economic nature. Based on this characterization, Tisdall supports a similar view to those calling for all species to be treated as equal.

Aylward (1992, p. 418) associates option value with 'the value placed on securing the future consumption of goods and services yielding direct and indirect value.' Direct value here is taken to relate to actual consumption of benefits, whereas indirect value includes benefits, for example, relating to maintenance of ecosystems. His option value nevertheless is seen as one component of total economic value. Elsewhere in the same report, Aylward & Gammage (1992, p. 425) express skepticism about our ability to assign economic importance to preserving options by maintaining biodiversity, and make the more general statement that 'biodiversity provides insurance against new needs that arise with changing conditions'.

Wilson (1992) contrasts an interpretation of value in which a cost-benefit analysis is to be carried out, with a strategy that views all species as 'an irreplaceable resource for humanity'. Option value here is portrayed as quite broad in its scope in being related to commodity, amenity and morality (Wilson 1992; Norton 1988).

Reid (1994) also implicitly takes a very general view of option value in his support for the basic idea of maintaining diversity so that humanity can adapt to change. He argues that most valuation systems are inherently subjective, and consequently does not put forward any arguments for differential weighting.

The views above may avoid the problem of quantification in a monetary sense, but also imply that any assignment of value is too risky and likely to be too subjective. The dichotomy then is that when option value is related to cost-benefit analysis one faces the pitfall of estimating actual value in the face of ignorance. When option value is related to a 'safe minimum standard', as proposed by Wilson (1992), this subjectivity is removed and all species are equal (although costs of protection may vary).

The discussion above shows a range of interpretations of option value, from one implying differential-weighting to one implying equal-weighting. The basic argument against weighting uses a rationale based on the proper response in face of ignorance about specific values in the future that can be of several different kinds. According to this view, it is absurd to suppose we know enough to differentially weight (as discussed by Tisdell 1990). Option value is the response to our inability to predict these specific values; it consequently views alternatives as of equal importance.

This would seem to exclude attempts to use taxonomic/phylogenetic information to weight species. However, the above arguments are clarified by re-examining the general rationale for option value. In its basic form it means that we have some 'items' whose value in the future cannot be known; consequently, this state of ignorance about future value directs us to avoid making unwarranted assumptions, to treat all these items as equal, and then to try to save as many of them as we can.

Thus, it is certainly possible within this framework to consider the items that may have value in the future as features of species, and not the species themselves. One reason that biodiversity is worth saving is that it may provide properties, characteristics or features that are of value to mankind. These units of diversity are properly all viewed, in our state of ignorance, as of equal weight. It follows that option value is increased to the extent that more of these features are protected.

This argument for equal-weighting of features leads to differential weighting at the higher level of species: we much prefer adding in a new species that offers many new features as compared with one that is so similar to an already-protected species that it offers few new features. Option value at this level means that differential weighting of species is inevitable. Thus, the arguments above, that ignorance means that we cannot afford to weight species, can be used to argue that we *must* weight species.

This leaves two plausible levels, species or features of species, at which option value may be calculated. It is useful, therefore, to re-emphasize that option value will, as interpreted here, require that we keep options open without making any unwarranted assumptions. The choice of the most effective level for concern about option value may then rest on which level best avoids unwarranted assumptions about future values of biodiversity. The assumption that all species are equal amounts to introducing possible unwarranted assumptions about features because it implies that they have different weights. In figure 1*a*, for example, equal-weighting would mean that, given species a, either species b or c could be chosen for protection; but this would imply that every one new feature b contributes is equal in potential value to ten contributed by c. Of course the prediction that c contributes more novel features is dependent on a model using the tree structure and branch lengths to infer feature-information. If the tree pattern and/or model is so poor that we can have little confidence in it, then it may be best to view the tree as in figure 1*b*, so avoiding unwarranted assumptions about the degree to which any two species can be expected to share features. When relative feature diversity is judged as not-quantifiable, we are left with option value defined at the level of species; species are therefore all equal as in figure 1*b*.

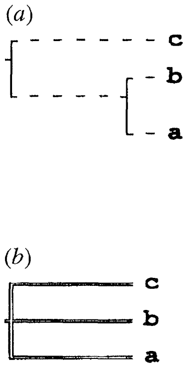

Figure 1. Hypothetical trees for species a, b, and c in which each dash mark along a branch represents an origin of a new feature. Species a is already protected and species b or c is to be given high priority for conservation. (*a*) Species a and b are closely related; (*b*) all three species are viewed as equidistant, as there is no reliable information about phylogenetic relationships.

This perspective also places demands on the species-level interpretation of option value. Species are hard to define, and policies that automatically treat these all as equal with regard to conservation efforts also can raise problems (e.g. O'Brien & Mayr 1991). Further, a definition of species within one taxonomic group may not mean much in another (Heywood 1994; Rojas 1992).

A challenge therefore exists for any proposed use of phylogeny or taxonomy to weight species for conservation. We need to examine carefully the proposed manner in which a given method attempts to predict biodiversity at the feature level; unwarranted assumptions about how pattern relates to features must be minimized. In practice, the challenge is to use phylogeny with the requirement that we accept it as a general predictor only if the prediction can be implemented in such a way that we avoid making arbitrary, unwarranted assumptions; otherwise, the task is open to the charge of present-day subjectivity.

3. PATTERNS AS SURROGATES FOR BIODIVERSITY

In this section, a general framework for using pattern to quantify biodiversity is explored (see also Faith & Walker 1993). I begin by looking at the quantification and estimation of biodiversity at the more familiar level in conservation where the concern is with choosing areas (for example for conservation reserves). Much of the recent progress in developing conservation evaluation procedures has been made in this context (Pressey *et al.* 1993), which also provides the definition of some basic terms and identifies concepts useful also at the feature-diversity level. The problem of prioritizing areas illustrates how pattern (specifically environmental pattern) can be used as a surrogate for biodiversity, in predicting the same components of biodiversity that would be used at the species level directly, notably complementarity (see below). This approach to using environmental pattern to quantify and estimate biodiversity can be generalized to cover other patterns as predictors of lower-level biodiversity. Following this general description, I consider how phylogenetic diversity fits into this framework.

(*a*) *Environmental diversity*

When the objects to be prioritized in conservation are areas (e.g. grid cells or 'polygons'), the biodiversity represented by a given subset of areas is equated with the number of species represented or sampled by the collection (see Margules *et al.* 1988;

Pressey *et al.* 1993). At this level, one scenario is that the species as the units of biodiversity are directly observed. A reserve system having all the species has maximum-possible diversity, and the diversity of any sub-optimal reserve system depends on how many of the species are represented. Thus, the value of an area as a candidate for addition to a reserve system depends, not on its individual species richness, but on its degree of 'complementarity': the number of *previously unrepresented* species that it contributes to the overall set (for review of complementarity, see Pressey *et al.* 1993). Complementarity at this level means that additional areas will generally contribute new species. The extent to which additional areas might contribute to representation of the majority of species therefore relies on the species 'turnover' among areas: that is, beta diversity (see, for example, Vane-Wright 1992).

The critical problem in choosing areas is that one wants a set of areas that maximizes *overall* biodiversity, not just that for a particular group of species that have been surveyed. Unfortunately, any one group of taxa may not be an effective indicator of the overall patterns for all organisms in the region of study (Ryti 1992). An alternative is to use environmental data as a surrogate for prioritizing areas; the rationale is that an area which is different, based on measured environmental variables, from a given set of areas is likely also to be complementary to the set in contributing many organisms that are not already represented.

This informal rationale for using environmental data as a surrogate can be quantified by expressing the environmental information for areas as a pattern and using a model relating this pattern to underlying species diversity. The natural model is the basic one from ordination in community ecology (Gauch 1982; Faith *et al.* 1987). This basic model assumes only that species will on average have general unimodal responses to environmental gradients; for presence-absence data, this means that the sites having a given species would be expected to form a 'clump' in the space (idealized as a circle or disc in the two dimensional case). It can be demonstrated (D. P. Faith, unpublished data) that under this simple model, the number of species sampled will be maximized if subsets of sites are selected so as to maximize a measure of 'environmental diversity' (ED; Faith & Walker 1993), defined on the environmental pattern as follows:

> 'The *environmental redundancy* of a subset of sites (sites which can be viewed as lying in an environmental or ordination space) is given by the sum of the distances of all points (representation points) in the defined space to their nearest neighbour in the set. The *environmental diversity* is greater to the extent that this environmental redundancy is smaller.' (Faith & Walker 1993.)

Thus, the environmental space is well-represented by the subset of sites (or areas) if, on average, the distance from any point in the space to its nearest member site is small. High 'environmental diversity' implies (under the assumptions of the general model) that we will also have high biodiversity at the level of the original units, i.e. species.

The critical components of this measure are: (i) the pattern and corresponding model showing how unit items are related to pattern; and (ii) an expression for how objects (here areas) must be chosen to maximize diversity at the unit level. For environmental diversity, the definition of the subset (say, of p sites) having greatest species diversity is an example of a 'p-median' criterion. In general, a p-median calculates the distances from 'demand points' to 'locality sites' (Handler & Rozman 1985; Love *et al.* 1988). This criterion is discussed below in the context of phylogenetic pattern.

(*b*) *A general framework for pattern diversity*

The use of environmental pattern as a surrogate for biodiversity at the level of species demonstrates how pattern can be used in principle as a biodiversity surrogate at any level, as long as certain conditions are met. In any specific application, the following general terms must be defined:

1. *Basic units*: the unit items defining biodiversity at the level of choice; the number of these equal-value items sampled is a measure of biodiversity, and equivalently, option value.
2. *Objects*: the things that must be prioritized or weighted for conservation; because objects differ in their component unit items, subsets of objects will represent different, estimable, relative amounts of biodiversity.
3. *Pattern*: some summary of relationships among the objects.
4. *Pattern model*: a model showing how a pattern of the objects should provide information about the diversity of sets of objects at the level of the underlying unit items.
5. *Pattern diversity*: a measure of diversity at the unit level, with values assignable to sets of objects based only on the pattern.
6. *Complementarity* (or 'pattern complementarity'): the degree to which an object or set contributes unrepresented unit items to an existing set; pattern-complementarity is the increment in pattern diversity when an object is added to an existing set.

In summary, biodiversity in its general form can be defined based on the (in principle) counting up of unit items, implying that sets of objects can be assigned option value depending on how many unit items they are expected to contain as a set. The value of a new object depends on its degree of complementarity, that is, the degree to which it offers new unit items. This depends on variation among the objects, or 'turnover' at the unit level. This framework can be extended to take into account pattern among the objects. Here a model is needed together with a definition of 'pattern diversity' that predicts the relative biodiversity at the unit level of different subsets of the objects.

This framework provides some general guidelines for using pattern at the species level. For species level biodiversity and environmental surrogates, it has helped to reveal the weakness of an alternative pattern approach based on clusters of environmental types (Faith & Walker 1993).

(*c*) ***Phylogenetic diversity***

There have been several proposals for measures using phylogenetic and/or taxonomic information to weight species for conservation evaluation. Most of these have not explicitly attempted to quantify diversity at the lower level of features or attributes of species. Exceptions include Faith (1992*a*,*b*) and Weitzman (1992*a*,*c*), where option value is defined at the level of variation among species in underlying features. A species or set of species has value to the extent that it is expected to contribute more novel features. This perspective makes it clear that the goal of maximizing option value by taxonomic weighting is equivalent to trying to maximize the sampled biodiversity at the level of features (Faith 1994*a*). Thus, maximizing feature-diversity is an exactly parallel problem to searching for a network of areas with maximum number of species.

The feature-diversity problem therefore can be placed in the same pattern-framework; the unit items are defined as features, the objects are taxa (generally species, but see Faith (1992*a*, 1993)), and the pattern will be some estimate of phylogeny. The model relating pattern to unit features is not as straightforward to define. One simple model that can relate phylogenetic pattern to the features has been derived from cladistic theory (Faith 1992*a*,*b*). It is based on the standard cladistic assumption that shared features among species are explainable (accounted for) by shared ancestry; this assumption is the basis for the parsimony criterion of cladistics, which estimates a phylogeny by searching for the tree implying the smallest number of changes, effectively maximizing the degree to which the tree explains shared features through common ancestry (see, for example, Farris 1979). The model therefore simply assumes that features arise and persist in all descendents. Further, an assumption is made that not only the branching pattern of the phylogeny, but also 'branch lengths' – estimates of relative amounts of change in different branches – can be used to assess feature diversity. The relative branch lengths may come from previous cladistic analyses of these taxa, from amounts of divergence estimated from existing classification, or from accepted models about modes of evolution; for example, regarding relative rates of change in different branches (Faith 1992*a*,*b*, 1993, 1994*a*,*b*). For any estimation, the relative branch length is assumed to predict the relative number of novel features that have arisen in a given line of descent (Faith 1992*b*).

This model implies that the relative number of features represented by a particular subset of species is given by the total length of the branches spanned on the tree by the set:

> The *phylogenetic diversity* (PD) of a subset of taxa is given by the sum of the lengths of the branches found along the path along the tree connecting all taxa in the subset (see Faith 1992*a*).

The phylogenetic pattern for the taxonomic group in question therefore provides a prediction of underlying feature-diversity patterns; a subset of taxa that spans a greater portion of the tree consequently is more diverse in this sense.

This definition provides the 'pattern complementarity' referred to above. If no other close relatives of a species are already protected (e.g. in an existing set of nature reserves), then the species will add more to the total represented path length along the tree, and so add more to the overall (protected) feature-diversity. Complementarity at the level of features arises because additional species can be expected to contribute new features; this phylogenetic turnover in features ('phi diversity') then plays the same role as the familiar beta diversity referred to above in the context assessing different areas.

The measure of complementarity can be calculated using only pairwise distances between species (Faith 1992*a*). For example, for the hypothetical tree in figure 2, the increase in phylogenetic diversity when species x is added to a set consisting of species i, and j is given by:

$$C = 0.5\,(d(\mathrm{x},\mathrm{i}) + d(\mathrm{x},\mathrm{j}) - d(\mathrm{i},\mathrm{j}))$$

Here, '$d(\mathrm{i},\mathrm{j})$', for example, is a measure of the number of feature mismatches between species i and j. C measures the length of the path from taxon x to the portion of the tree already represented by the given set of species i and j (i.e. the distance from x to point p). This length, in indicating changes from one feature into another, is expected to reflect the number of additional features gained with the addition of x to the set $\{\mathrm{i},\mathrm{j}\}$. Note that length '$d(\mathrm{i},\mathrm{p})$' (the length from i to point p) can be, for example, much longer than length $d(\mathrm{j},\mathrm{p})$; there is no expectation in general of equal rates of change in different branches.

The following hypothetical feature data, for this same tree, illustrate how phylogenetic diversity, via this formula, counts up underlying features:

	1	2	3	4	5	6	7	8	9	10	11	12
o	a	a	a	a	a	a	a	a	a	a	a	a
i	a	a	b	b	b	a	a	a	a	a	a	a
j	a	a	b	b	a	b	b	a	a	a	a	a
x	a	a	a	a	a	a	a	b	b	b	b	b

Here, a feature or attribute has changed into another feature on 12 occasions. The outgroup or sister taxon, o, has features arbitrarily labelled 'a'. The 'b' feature is, in cladistic terms, 'derived' rather than 'primitive'

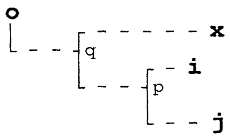

Figure 2. A hypothetical tree for three species x, i, and j plus outgroup species, o. p designates the ancestor to i and j and q the ancestor to x, i, and j. Each dash along a branch designates the origin of a new feature.

(an alternative way to view these changes is that 'a' represents absence of the feature and 'b' its presence). The phylogeny or cladogram in figure 2 has branch lengths drawn to reflect these changes, and shows the minimum number of feature changes for this data set.

When x is to be added to the set defined by i and j, application of the formula for C yields:

$$C = 0.5\,(d(\mathrm{x},\mathrm{i}) + d(\mathrm{x},\mathrm{j}) - d(\mathrm{i},\mathrm{j})),$$
$$= 0.5\,(8 + 9 - 3),$$
$$= 7.$$

This is explained by examination of the raw data set. The set $\{\mathrm{i},\mathrm{j}\}$ has a base of 12 features plus three additional features (from changes 5, 6, and 7), while the addition of species x contributes seven more features (from occasions 3, 4 and 9–12).

Frequently, the taxa outside the group of direct interest may be assumed already to be 'protected'. If o is in the initial set, the initial diversity is now $12+5$, and the contribution of x changes to an amount equal to the length of branch $\mathrm{x}-\mathrm{q}$, that is, 5:

$$C = 0.5\,(d(\mathrm{x},\mathrm{o}) + d(\mathrm{x},\mathrm{j}) - d(\mathrm{o},\mathrm{j})),$$
$$= 0.5\,(7 + 9 - 6),$$
$$= 5.$$

C also can be viewed as estimating the reduction in diversity with the loss of species x from a set consisting of o, x, i, and j; the loss in diversity of five units is as if the branch leading to x has been 'pruned' from the spanning tree at point q.

A further example illustrates how the phylogenetic pattern may provide better predictions of general feature diversity patterns than would any one observed set of features. Figure 3 shows a phylogenetic tree for species a–f, and the origin of five features, 1–5. These features fit the tree perfectly (each new feature appears once and does not disappear); nevertheless this set of observed characters is not as informative about general feature diversity patterns as is the complete phylogeny. Here, the phylogeny, but not the observed set of features, indicates that, if species a or c can be added to a protected list, species c would be expected to contribute more novel features to the set. This example also highlights the degree to which the assumptions of the model relating pattern to features is critical.

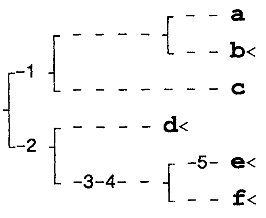

Figure 3. A phylogenetic tree for species a–f. Species marked with '<' are already protected and another species can be chosen. The numbers show the origin of five features, 1–5. These features are not informative about the expected greater gain in new features with the addition of species c to the set.

4. ALTERNATIVE MODELS FOR RELATING THE UNITS TO THE PATTERN

Weitzman (1992*a,c*) proposed a pattern-based measure of diversity based on an explicit model relating features to a form of phylogenetic pattern. His approach assumes that the value of a species should reflect the number of features it might contribute to a protected set. This approach to species weighting, based on a rationale in which option value is maximized by maximizing number of represented features, is similar in spirit to phylogenetic diversity. However, within the pattern-framework, it differs in two important ways from PD, both relating to the choice of assumptions about pattern and unit items. First, although phylogeny is used as the working pattern, Weitzman proposed a novel method for deriving an estimate of phylogeny from given distance data. Second, he then adopted a different model for describing the relationship of features to this tree pattern.

Weitzman attempted to avoid making unwarranted assumptions in deriving his general diversity measure, but the assumptions implicit in his approach can be shown to lead to a method, quite distinct from PD, that is unlikely to provide effective estimates of feature diversity. Yet superficially his approach appears similar to PD in its claimed properties, which include apparent use of a minimum-length tree, equating the number of features with the length of the tree spanned by a taxon set, and viewing the feature-diversity lost as equal to the length of the corresponding branch, as if it were 'snapped off'.

The above claims are clarified by examining the mathematical properties listed by Weitzman (1992*a*) as essential to any measure of diversity, and forming the foundation of his approach; following his notation, the diversity of a set of species, S, is $V(\mathrm{S})$ and the distance matrix is represented by d:

1. The natural distance from an object to a set (e.g. '$d(\mathrm{i,S})$') is given by the distance to its nearest neighbour:

$$d(\mathrm{j},\mathrm{Q}) = \text{minimum } d(\mathrm{j},\mathrm{i}) \text{ over all i in set Q}.$$

2. '$V(\mathrm{S}+\mathrm{i})$', the new diversity value after adding species i to set S, is greater than or equal to $V(\mathrm{S}) + d(\mathrm{i},\mathrm{S})$.

3. There exists an object 'j' within any set S such that $V(\mathrm{S}) = d(\mathrm{j},\mathrm{S}-\mathrm{j}) + V(\mathrm{S}-\mathrm{j})$, where '$\mathrm{S}-\mathrm{i}$' designates set S minus species i.

The above definition of the 'distance' of a species to a set is central to Weitzman's approach. This assumption has some intuitive appeal: the degree to which an object is distinct from a set is taken to be indicated by how far away its nearest neighbour is (see Faith & Norris 1989). Unfortunately, this definition is proposed by Weitzman without justification, and characterized only as a 'standard definition' (Weitzman 1992*a*, p. 367). It is certainly a reasonable definition under the PD model above – but only in the special case where the rate of evolution (the rate at which new features arise) is *constant* over all branches (that is, the set of pairwise distances between species are 'ultrametric').

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

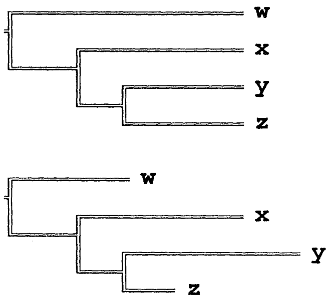

Figure 4. (*a*) Tree for species w, x, y, and z in which the rate of change is equal in all branches. The distance from z to its nearest neighbour, y, indicates the relative number of features gained with addition of z. (*b*) Tree for species w, x, y, and z in which the rate of change varies among branches. The distance from z to its nearest neighbour, y, does not indicate the relative number of features gained with addition of z.

For ultrametric distances, it is clear how the overall diversity, equal to the total length of the tree, can be built up from diversity of subsets and distances of species to the subsets using the formula from property 3 above:

$$V(\mathrm{S}) = V(\mathrm{S}-\mathrm{i}) + d(\mathrm{i}, \mathrm{S}-\mathrm{i}).$$

In figure 4*a*, the distance from *z* to the set of other species can be represented by the length of the branch to the rest of the tree, and this is exactly one-half its distance to its nearest neighbour, y. However, now examine the more general case in which rates of change are not assumed all equal. In Figure 4*b*, a different distance provides the best description of the distance of z to the set of other species, in better reflecting underlying features. The number of additional features is not related to the distance to a nearest neighbour at all, but instead depends on the amount of divergence along its new branch. In this situation, the 'distance' of a species to a set can only be given by the formula above for *C*, which is of course just the complementarity value under the PD model.

Weitzman (1992*a*) realized that his initial distances among species might not be ultrametric in general, and sought to relax this in-built assumption arising from the use of his particular definition of the distance of a species to a set. Using properties 2 and 3 listed above, he altered the formula for the general case to:

$$V(\mathrm{S}) = \text{maximum}, \quad \text{over all i, of } \{V(\mathrm{S}-\mathrm{i}) + d(\mathrm{i}, \mathrm{S}-\mathrm{i})\}.$$

Thus, the distances are, as Weitzman (1992*a*) described it, used to produce 'as if' ultrametric distances.

This general formula also provided the basis for the estimate of the tree itself from the given distances. The calculation of the tree is a complex iterative approach, but the diversity measure can be understood by examining a simple three taxon case (figure 5). Suppose in this example that the given distances perfectly match those that could be measured along this tree (and are therefore equal to the number of feature mismatches for any two species, as assumed by Weitzman 1992*a*). Suppose further that length *a* (the length of the branches along the path from A to point p) is greater than *b*, which is greater than *c*. Then the distance, for example, between species A and B is $a + b$. Application of the general formula from above yields:

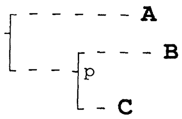

Figure 5. A tree for three species, A, B, and C. The distance along the tree from A to point p is *a*, from B to point p is *b*, and from C to point p is *c*. Weitzman's formula will assess the total diversity, *V*, represented by these three taxa by counting the intermediate length, *b*, twice.

$$\begin{aligned} V(\mathrm{s}) = k + \max\{ & b + c + \min(a+b, 8a+c), \\ & a + c + \min(a+b, b+c), \\ & a + b + \min(a+c, b+c). \end{aligned}$$

Here, the third element in this list is largest, and $V(\mathrm{s})$ therefore equals $k + a + 2b + c$; thus, this general three-species example shows that the intermediate length is always counted twice in calculating *V*. Therefore the diversity measure, *V*, in general not only cannot correspond to the length of the tree, but it introduces a seemingly arbitrary double-counting.

Further properties are revealed in the example in figure 6, in which the initial distances again reflect differences in numbers of features, and the lengths of the branches reflect the number of changes in features. The most-parsimonious tree (figure 6*a*) accounts for each new feature as having arisen once, along the tree topology shown. Given these corresponding distances between pairs of species, Weitzman's (1992*a*) algorithm produces the tree shown in figure 6*b*, demonstrating that the underlying assumption of ultrametricity, arising from the attempt to approximate 'as if' ultrametric distances even in the general case, is a poor basis for inference of phylogenetic pattern. Indeed, even if more and more data perfectly congruent with the true tree (figure 6a) were accumulated, the Weitzman algorithm would continue to return the wrong tree (figure 6b).

The corresponding diversity value using Weitzman's approach is also a poor reflection of the number of features in the set. While the PD value is 20 (found by counting up the dash marks along the branches in figure 6*a*), the *V* value is (where '*bd*', for example, is the distance between b and d):

$$\begin{aligned} V &= bd + ab + ac, \\ &= 7 + 10 + 15, \\ &= 32. \end{aligned}$$

These individual values that are summed correspond to the branching 'levels' derived from his approximation of ultrametric distances (figure 6*b*). In figure 6*c*, it is evident where these values come from, relative to actual path-length distances. *V* effectively counts parts of the path more than once. Again, there would

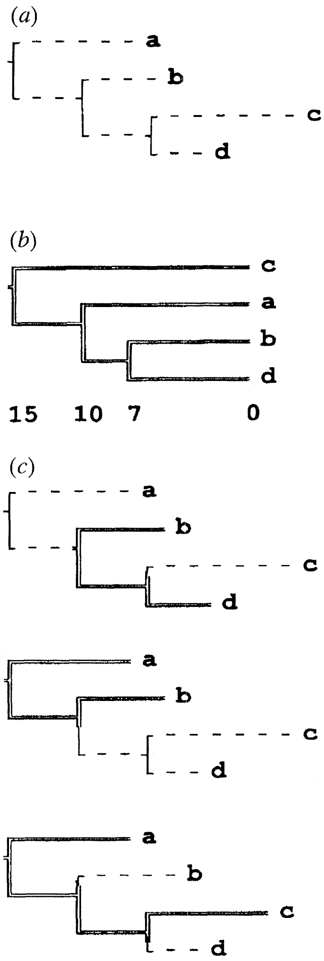

Figure 6. (*a*) A tree for species a, b, c, and d, in which each dash along a branch represents a new feature. (*b*) Application of Weitzman's method to the distances derived from the tree of figure 6*a* would produce the incorrect tree shown here. The numbers at the bottom show the scale for branch lengths in diversity units. (*c*) Redrawings of the correct tree showing the quantities corresponding to branch lengths that are added up using Weitzman's method to arrive at a value for *V*. The double counting of some branches means that *V* does not accurately reflect the number of features.

appear to be no justification for such multiple-counting.

Figure 7 demonstrates the consequent inability of *V* diversity to accurately reflect feature diversity differences. Again the distances are perfect path-length distances, reflecting numbers of features. Suppose that all species are currently protected, but that alternative conservation plans must exclude species b or c. The relative loss of *V* diversity is given by the relative magnitude of the diversity computed with the corresponding species removed. The diversity of the subset reflecting the loss of c $\{a, b, d\}$ is 19 (ad + the distance from b to $\{a, d\} = 12 + 7$), whereas that of $\{a, c, d\}$ (reflecting the loss of b) is 18 (ac + the distance from d to $\{a, c\} = 13 + 5$). Therefore it would appear that b is the more valuable species because its absence causes a greater reduction in diversity. However, the figure (and corresponding PD values) show that removal of c implies loss of three features for every one feature lost with removal of b. *V* does not properly reflect relative feature diversity patterns among species. Whereas PD yields an estimate of diversity equivalent to the 'loss' of its branch, this is not the case for the *V* measure.

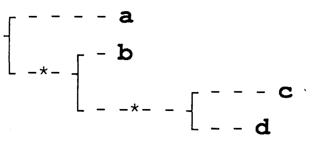

Figure 7. A tree for species a–d in which each dash mark represents a new feature. Alternative conservation plans must exclude species b or c. Using Weitzman's method, b is judged the more valuable species because its absence causes a greater reduction in diversity, *V*. However, the loss of c in fact implies loss of three features for every one feature lost with removal of b. Branches marked with '*' help to determine the degree to which b is isolated from the rest of the tree. For further information see text.

In conclusion, introduction of unwarranted assumptions, here related to equal rates of change over all branches, means that we can have little confidence in the prediction of feature-diversity patterns with Weitzman's method.

The failure of *V* to reflect feature diversity in the manner accomplished by PD has other implications. It is noteworthy that the length of the branch in the previous example leading to b could be 0, and an increment in *V* diversity would still be recorded, the magnitude of which would only depend on the location of the branch (e.g. how distant it was from other branches). Weitzman (personal communication) argues that b indeed might be preferred over c because b, in being isolated from other parts of the tree, is more likely to represent novel *combinations* of features.

This argument appears in another form in the justifications for the dispersion measures of Williams & Humphries (1994). In figure 7, their dispersion measure would select b if it was sufficiently isolated (branch lengths marked with '*' in figure 7 are long) so achieving an 'even' representation of the whole tree; this is intended to guarantee that 'subgroups with their different character combinations' (Williams & Humphries 1994, p. 277) are represented. The possibility that the unit items of diversity might be alternatively defined as 'combinations' of features is explored below. This will have implications for the choice of a pattern-unit model and resulting measure of diversity. The dispersion weighting method of Williams & Humphries, or the method of Weitzman, may be appropriate choices in that context.

5. ALTERNATIVE DEFINITIONS OF THE UNDERLYING UNITS DEFINING BIODIVERSITY

(*a*) *Combinations and p-median diversity*

If a conservation goal is to maximize the number of unique combinations of features sampled by a set of protected species, then careful examination of a model for how these combinations relate to the pattern is needed. Faith & Walker (1993; Horn *et al.* 1994) have proposed an alternative diversity measure, based on phylogenetic pattern, called 'p-median diversity'; this is intended as a candidate measure that might serve to maximize the number of sampled combinations of features. However, they did not present a model under which this measure might be justified.

The definition of p-median diversity is (as for the related definition of environmental diversity above) based on an optimization criterion from operations research work, where it is used for quite a different purpose (e.g. the location of facilities (e.g. fire stations) on road networks (see Tansel *et al.* 1983)). It is defined as follows.

> 'Given an estimate of a phylogenetic tree (or a classification drawn as a tree), the *p-median-diversity* of a subset of taxa is greater to the extent that, on average, the distance (path-length distance along the tree) from any point along the tree topology to its nearest-neighbour in the subset is small. Thus, the subset of size p that has greatest diversity is the one defining a continuous *p-median* of the tree, under the constraint that points in the subset must be terminal taxa and representation points are any points on the branches of the tree (the relative number of such points on a given branch is indicated by the corresponding branch length). The total of all nearest-neighbour distances is the complement of diversity or the *p-median-redundancy* of the subset.'(Faith & Walker 1993).

This criterion intuitively suggests that the chosen set must be evenly spaced over the tree. Faith & Walker (1993) list alternative definitions derived from other operations research; however, p-median diversity can be shown to best represent combinations of features. One simple model relating combinations to a phylogenetic tree is proposed here that appears to justify p-median diversity. In figure 8*a*, suppose that combinations of features can arise and disappear over evolutionary time, and that such combinations are equally likely to be centred on any point along the tree (longer branches will be interpreted as having more points and therefore more combinations along them); further, assume that the size of the 'radius' for a combination (how far along the branch it extends from its centre point) will be assumed to be equi-probable over all sizes.

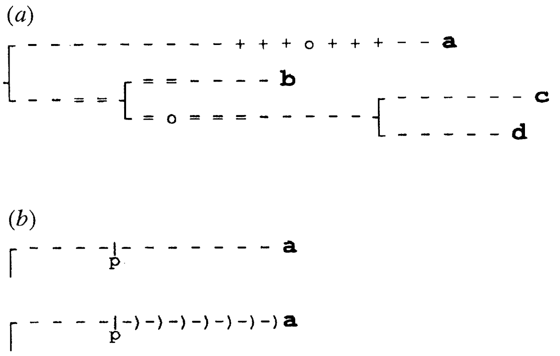

Figure 8. (*a*) A tree illustrating the model for combinations of features; + and = signify two different combinations. (*b*) A portion of a tree showing point p and its nearest neighbour species a; the ')' designate the edges of feature combinations, all centred at p.

This simple model leads directly to p-median diversity, as this measure predicts biodiversity at the level of combinations of features. This is demonstrated by proving the following proposition:

Proposition: If all points along branches of the tree are equally likely to be the centres for a feature combination, and the feature combinations can have any radius, *r*, with equal probability, then selecting a set of taxa using the p-median criterion will mean that the number of different feature combinations that is sampled by the set will be maximized.

Proof (see figure 8*b*): The p-median criterion implies that the best set of *n* objects (here species) will be the one that minimizes the average distance from a point to its nearest object from the set. Take any point, p, on the tree with its nearest neighbour, taxon a (from a set of *n* taxa). $d(\mathrm{p},\mathrm{a})$ is the distance along the branches from p to this nearest neighbour a. Any feature-combination centred on p, with a radius *r* that is greater than $d(\mathrm{p},\mathrm{a})$ will be represented by (contained in) taxon a. But all combinations with radius less than $d(\mathrm{p},\mathrm{t})$ will be missed by taxon a. Thus, $d(\mathrm{p},\mathrm{a})$ is a count of the relative number of combinations centred at p that are missed by the set of *n* taxa. Therefore over all points p on the tree, the total number of combinations missed is the sum, over all points p, of the $d(\mathrm{p},\mathrm{a}_\mathrm{p})$ values, where a_p is the nearest neighbour among the selected taxa for point p. This is the quantity that we wish to minimize, and this, by definition, is the same as the p-median criterion.

P-median diversity then maximizes the number of combinations (hence biodiversity as defined by these units), under the assumptions of this model. It is interesting that Weitzman's method does not appear

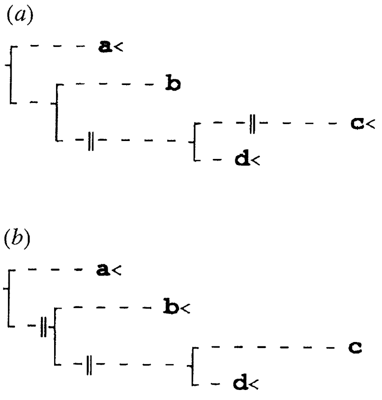

Figure 9. (*a*) A tree for four species a–d where each dash represents a point for p-median calculations. Species marked with '<' are protected, and the resulting neighbourhood for each protected species is indicated by the 'barriers' along the branches. This set of species yields a p-median value of 71. (*b*) For the same tree, species marked with '<' are protected, and the resulting neighbourhood for each protected species is indicated by the barriers. This set of species yields a p-median value of 67.

likely to maximize the number of combinations of features under this simple model. In figure 9, suppose that taxa a and d are protected, and taxon b or c is to be chosen. The calculation of p-median diversity yields a total sum of distances to nearest-neighbour taxa of 67 for the case in which b is chosen, and 71 for the case in which c is chosen; b would be preferred as it would imply the representation of a greater total number of different combinations (remembering that diversity is greater if the p-median is minimized). But application of the basic formula for Weitzman's V diversity shows that taxon c nevertheless would be preferred (total V for abd = 18; for acd = 22).

As might be expected, the model relating combinations to phylogeny, and the resulting p-median diversity, do not guarantee that the number of features in the original sense of PD is maximized. Again (figure 9), taxa a and d are taken as protected, and taxon b or c is to be chosen. The additional branch length gained in adding c is greater and so would be chosen by the PD criterion. In contrast, under the p-median criterion, b would be preferred even though it would be expected to contribute fewer new features.

(*b*) *Discrete p-median diversity*

Faith & Walker (1993) also refer to a simple version of p-median diversity (the discrete p-median) in which the points are restricted to the original objects (here species). Thus, the distance from any unprotected taxon to its nearest neighbour among the protected taxa is calculated and all these are summed up; this is equivalent to the p-median in the case where the points can only be taxa ('discrete p-median diversity').

The discrete version of p-median diversity is computationally simpler, as distances from species to other species need only be used. This appears to be equivalent to an approach suggested by Solow *et al.* (1993) for general distances; their approach would be equivalent to the discrete p-median diversity measure when the chosen distances were path-length distances on a phylogenetic tree.

Unfortunately, the discrete version has some undesirable properties. In figure 10, suppose that species from either of two positions might be chosen; in the first, species b is on its own; in the second, f plus five other species represent a set of closely related species. Species f would be chosen over species b under discrete p-median diversity, because this would greatly reduce the p-median sum; however, adding b would, under the combinations model, increase the number of new combinations sampled, as b is very isolated from the rest of the tree. Thus, the discrete p-median is incompatible with the model relating combinations to phylogenetic pattern.

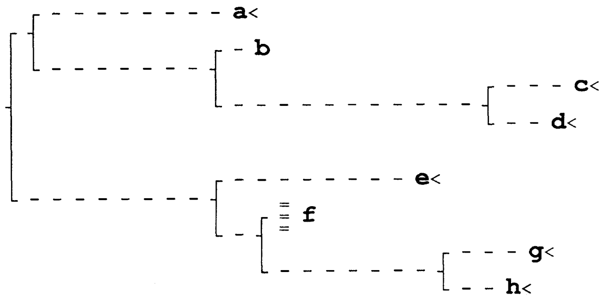

Figure 10. A tree in which dash marks represent new features, and '<' signifies a protected species. A species from either of two positions can be chosen; in the first, species b is on its own; in the second, species f plus five other species represent a set of closely related species.

(*c*) *A more general model*

Biodiversity below the species level has been alternatively interpreted above as counting features/attributes versus counting combinations of features. These different definitions of the unit items in turn have lead to different models describing the relationship of units to pattern. But given the lack of any clear rationale for saving 'combinations', these might be viewed as just another interpretation of the 'features' explained by phylogenetic pattern; thus, these two models also can be viewed as alternative models for the same unit-items: features or attributes. The p-median model applied to features implies that features continue to change along the tree; that is, they do not simply persist as assumed in the strictly cladistic model for phylogenetic diversity (PD). Perhaps this is the intuitive appeal of giving some value to species b in figure 7. It is on the end of a small branch, but is isolated from the rest of the tree; any feature found in the common ancestor of b and its sister group might well be found in b, but under the p-median model would be regarded as unlikely to persist over the evolutionary history represented by a possibly long branch length to c and d. Thus, b is of value according to this model because it is likely to contribute unique features. Its pattern complementarity is now different from its value under the PD model (see earlier discussion of figure 7).

This interpretation does reveal one weakness of the current p-median model. The p-median diversity measure would appear to take features into account without the need for many assumptions; the only assumption is that features are lost proportionally with length. But in reality this simple model makes some possibly unrealistic assumptions. As features, it is clear that the unit items – combinations or features – in figure 8*a*, in practice, must in each case originate at a certain point, but those features that have originated near the end of any branch are not all counted, because their 'centres' under the model would lie 'beyond' the terminal taxon (see 'Proof' above).

More realistic is a slightly modified model where the features are viewed as *originating* at a given point along a branch (rather than having a *centre* at some point along a branch) and then persisting for varying lengths; such that a doubling of distance away from a point means a doubling of the number of features (that had arisen at that point) which are now lost. It will be useful to contrast this not only with the previous model but also with that for PD. In the first (for PD), units arise with equal probability at different points, and then persist in all descendants (figure 11*a*).

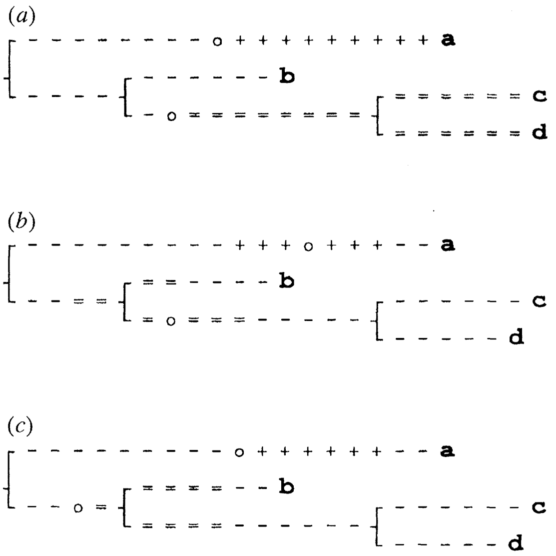

Figure 11. Three different models for the relationship of unit items (shown by '+' or '=') to phylogenetic pattern. For further information see text.

In the second, proposed above for combinations, any point is equally likely to be the centre of distribution of units with varying radii (figure 11*b*). In a third, modified model, the unit features originate with equal probability at different points, but do not persist in all descendants; rather they have an equal probability of persisting for any given evolutionary distance along the tree (figure 11*c*). Under this new model, quantifying biodiversity – the number of features represented by a given subset of taxa – now requires an explicit assumption regarding the number of features on average that originate for a given unit branch length versus how many are lost.

To see this, suppose that some fraction, F, of the features that have arisen at point p will be lost for each unit step in length (e.g. each dash mark in figure 11) away from some point, p, on the tree. Then how many features will be sampled by a given subset of taxa? First, as for PD, all those features arising on branches not having a descendant taxon contained in the set clearly cannot be represented. All other points along the tree can contribute features that may be represented by one of the member taxa. Therefore, we can first count up the total number of features estimated by the length of the represented spanning tree (as for PD), and then subtract the estimate of the number of features that would be lost on average before reaching the nearest terminal taxon. The diversity is therefore the usual PD value, minus the sum (over all points, p, found in this spanning tree) of: F times $(D_{\mathrm{p,i}})$, where $D_{\mathrm{p,i}}$ is the distance from p to its nearest *descendant* member taxon, i:

$$\text{PD} - \text{sum over p of } \{F(D_{\mathrm{p,i}})\}.$$

If F is taken to be 0 (i.e. any feature originating at a point is assumed to persist in all descendants), then this reduces to the usual phylogenetic diversity, PD. Alternatively, if F is so large that all features that arise are lost within one unit step, then all species are of equal status as there is no predictable redundancy among them. In the intermediate cases, the magnitude of F can affect which taxon is chosen for addition to a subset.

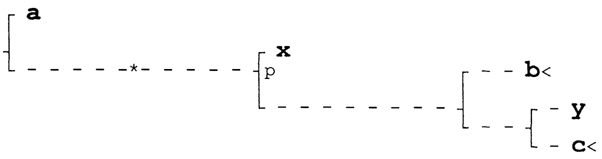

Figure 12. A tree for species a, x, b, y and c in which dash marks indicate units of branch length. b and c are protected and x or y can be selected. p is the immediate common ancestor of x and its sister group. the long branch marked '*' will imply the origin of many features which are more likely to be found in x than any of its sister-group species.

In figure 12, suppose that the species marked are protected and there is an opportunity to choose species x or y. If the value for F was greater than 0.01, it would be better to choose x, even though its additional branch length is shorter than that for y. The reason is that addition of x implies that, for each of the ten points along the branch (marked with '*') leading to the immediate common ancestor (p) of x and its sister group, ten unit steps in length are removed for the distance to nearest descendant, member species. As there are ten points, ten (points) times ten (steps) times 0.01 yields a value of 1, making up for the extra unit of branch length (and consequent new features) gained by choosing y.

6. ALTERNATIVES TO PHYLOGENETIC PATTERN

In two companion papers (Solow *et al.* 1993; Polasky *et al.* 1993), attempts have been made to provide measures of diversity at the level of features of organisms, but without relying on phylogenetic pattern (although other patterns are used). Solow *et al.* (1993) suggested that a tree model, in the role of a general model for predicting features of organisms, is too restrictive in its assumptions. Their argument against tree models unfortunately assumes, following Weitzman's work, that a tree representation is necessarily tied to a strict ultrametric model (see above). Nevertheless, their alternative proposal, and the further elaboration by Polasky *et al.* (1993), are worth examining, as they explicitly attempt to use patterns at the species level to predict diversity at the level of features. Ironically, both proposals face the same difficulties as found in Weitzman's (1992*a*–*c*) approach, in using a pattern and model implicitly based on unwarranted assumptions. However, the proposal by Polasky *et al.* (1993) is easily modified to overcome these difficulties, as shown below.

Solow *et al.* (1993) assumed that the observed information on species is a set of pairwise 'distances' (e.g. genetic distances) among them. They suggested that any measure of diversity based on such distances must satisfy three conditions:

1. If we have a subset of taxa then the diversity is equal or less than the original set.

2. If addition of a taxon adds 0 to diversity then its distance to its nearest neighbour in the set must have been 0.
3. If all pairwise distances between taxa are increased, then the diversity of any set can never decrease.

While the first and third criteria are straightforward, the second is misleading. As was illustrated above (figure 7), the increase for a species based on phylogenetic diversity can be essentially zero and nevertheless the species can be a relatively large distance from its nearest neighbour. This foreshadows the difficulties in using these properties to derive a general measure.

The diversity measure proposed by Solow *et al.* (1993) as satisfying these *a priori* conditions is simply the sum of the distances of all objects to their nearest neighbour in the set. This measure (Faith & Norris 1989) has been identified above in an earlier section of this paper as equivalent to the discrete p-median diversity, when this measure is applied to the general pairwise distances between species considered by Solow *et al.* (1993), and not just to those from a phylogenetic pattern. When the distances are those that would match the path-length distances from a phylogenetic tree, the problem already noted arises: there is a failure to predict feature diversity under plausible models for relationship of features to pattern. This suggests that the measure cannot be an effective general measure of diversity at the level of features.

Polasky *et al.* (1993) also begin with general distances between species as their basic observations, but use these under the more restrictive assumption that they will indicate an ordination ('spatial') pattern of the species. A model relating this pattern to species is adopted in which the features are assumed to form 'spheres' in this space. This pattern-model combination is similar to that for species in environmental space defined by Faith & Walker (1993), in which species (as the unit items of interest) could be expected to approximate to spheres; a measure of diversity based on the p-median then indicated biodiversity at this unit level. Polasky *et al.*'s (1993) proposed optimization of the number of sampled features, based on their sphere-model, is similar to the p-median criterion.

A difficulty with the approach proposed by Polasky *et al.* is that there is no justification for their expectation that features will form even approximate spheres for the species-pattern defined by their approach. They begin with general distance data, and derive an ordination of the species in such a way that a *linear* response of features to the space is assumed, rather than a unimodal or 'sphere-like' response (see above; Faith *et al.* 1987). Thus, there is a serious mismatch between the pattern and the model for how features are related to the pattern.

There is, however, a way to use an ordination model, and the same form of p-median diversity described above as 'environmental diversity', to indicate the relative number of features sampled by a subset of species. Here, an ordination is derived such that features will be expected to have unimodal responses (the resulting space is interpreted as an environmental or habitat space; Faith 1989). This is in fact an alternative pattern previously proposed as a candidate for predicting feature diversity (see Faith 1992*a*). Altering the Polasky *et al.* (1993) approach to use this pattern, in which features indeed can be expected to have unimodal ('sphere-like') responses, means that the pattern and model are then identical in form to that for the environmental diversity measure of Faith & Walker (1993; see above). The unit items of environmental diversity, species, are related to pattern in the same way as features are here. Thus, in principle, one can apply the same 'environmental diversity' measure to either species or site ordinations to achieve a measure of biodiversity at the lower level of the defined unit items.

7. CONCLUSIONS

The general framework discussed here for using pattern as a surrogate for lower-level biodiversity suggests that phylogenetic pattern can be well-justified for quantifying biodiversity only if the pattern and corresponding model relating unit-items to pattern avoid unwarranted assumptions. If assumptions that cannot be justified are made, then defining biodiversity and option value at the feature level is not a defensible alternative to simply viewing all species as having equal option value.

Difficulties with some proposed approaches to quantifying biodiversity, using phylogeny or other pattern, have been identified in this paper. Weitzman's approach is seen to be dependent on an restrictive assumption of equal rates of evolution in all branches, an assumption affecting both his derivation of pattern and his model linking pattern to features. The alternative proposal that the units be 'combinations' of features can be accommodated by an alternative model and diversity measure based on phylogenetic pattern, so that in principle phylogeny might predict biodiversity at this level. However, a difficulty is that the simple model for how these units relate to pattern is unrealistic in its behaviour at the ends of branches. A more general model overcoming these difficulties (and also applicable to features) has the limitation that it requires an additional assumption about relative amounts of gain and loss of features in branches. Finally, an alternative pattern, environmental space, does have a consistent model and resulting diversity measure, but has, at this stage, no clear rationale as to why it should be expected to provide a general prediction of feature-diversity for a given group of organisms.

Phylogenetic diversity (PD) remains the best candidate for quantifying biodiversity at the level of features of organisms. Its advantage over other approaches is that it uses a simple model based on few assumptions, and that this is the same model (that of cladistics) commonly used to derive estimates of phylogenetic pattern. Recent development of methods to evaluate the degree of confidence that we can have in estimated phylogenetic patterns (see Faith 1994*a*,*b*) may further support the view that option value can and should be defined at the level of features of organisms.

This paper was prepared while I was a guest at the Wissenschaftskolleg zu Berlin. I am most grateful for their support for this work. I thank my fellow biodiversity colleagues there, Dick Vane-Wright and Paul Williams, for many helpful discussions, and also thank G. Ranis and S. Mitchell at the Wissenschaftskolleg for exposing me to the fresh perspectives of other disciplines, particularly regarding the placing of values on species. Finally, I thank P. Walker and M. Horn for their valuable help in the development and evaluation of both phylogenetic and p-median diversity.

REFERENCES

Aylward, B. 1992 Valuing the environment. In *Global biodiversity: status of the Earth's living resources* (ed. B. Groombridge), pp. 407–425. London: Chapman and Hall.

Aylward, B. & Gammage, S. 1992 Preserving future options. In *Global biodiversity: status of the Earth's living resources* (ed. B. Groombridge), pp. 425–426. London: Chapman and Hall.

Ehrenfeld, D. 1988 Why put a value on biodiversity? In *Biodiversity* (ed. E. O. Wilson), pp. 212–216. Washington: National Academy Press.

Eldredge, N. (ed.) 1992 *Systematics, ecology, and the biodiversity crisis*. New York: Columbia University Press.

Faith, D.P. 1989 Homoplasy as pattern: multivariate analysis of morphological convergence in Amseriformes. *Cladistics* **5**, 235–258.

Faith, D.P. 1992*a* Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* **61**, 1–10.

Faith, D.P. 1992*b* Systematics and conservation: on predicting the feature diversity of subsets of taxa. *Cladistics* **8**, 361–373.

Faith, D.P. 1993 Biodiversity and systematics: the use and misuse of divergence information in assessing taxonomic diversity. *Pacific Conserv. Biol.* **1**, 53–57.

Faith, D.P. 1994*a* Phylogenetic diversity: a general framework for the prediction of feature diversity. In *Systematics and conservation evaluation* (ed. P. L. Forey, C. J. Humphries & R. I. Vane-Wright), pp. 251–268. Systematics Association Special Vol. No. 50. Oxford: Clarenden Press.

Faith, D.P. 1994*b* Genetic diversity and taxonomic priorities for conservation. *Biol. Conserv.* **68**, 69–74.

Faith, D.P. , Minchin, P. & Belbin, L. 1987 Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**, 57–68.

Faith, D.P. & Norris, R. 1989 Correlation of environmental variables with patterns of distribution and abundance of common and rare freshwater macroinvertebrates. *Biol. Conserv.* **50**, 77–98.

Faith, D.P. & Walker, P.A. 1993 *DIVERSITY: reference and user's guide*. Canberra: CSIRO Division of Wildlife and Ecology.

Farris, J.S. 1979 The information content of the phylogenetic system. *Syst. Zool.* **28**, 483–519.

Fisher, A.C. & Hanemann, W.M. 1985 *Option value and the extinction of species*. Berkeley, California: California Agricultural Experiment Station.

Gauch, H.G. 1982 *Multivariate analysis in community ecology*. Cambridge University Press.

Handler, G.Y. & Rozman, M. 1985 The continuous m-centre problem on a network. *Networks* **15** 191–204.

Heywood, V.H. 1994 The measurement of biodiversity and the politics of implementation. In *Systematics and conservation evaluation* (ed. P. L. Forey, C. J. Humphries & R. I. Vane-Wright), pp. 15–22. Systematics Association Special Vol. No. 50. Oxford: Clarenden Press.

Horn, M., Faith, D.P. & Walker, P. 1994 A new measure of taxonomic diversity, with procedures for measurement and optimisation. (Submitted.)

IUCN 1980 *World conservation strategy: living resource conservation for sustainable development*. Gland: IUCN-UNEP-WWF.

Love, R.F., Morris, J.G. & Wesolowsky, G.O. 1988 *Facilities location: models and methods*. New York: North-Holland.

Margules, C.R., Nicholls, A.O. & Pressey, R.L. 1988 Selecting networks of reserves to maximise biological diversity. *Biol. Conserv.* **43**, 63–76.

Norton, B. 1988 Commodity, amenity, and morality: the limits of quantification in valuing biodiversity. In *Biodiversity* (ed. E. O. Wilson), pp. 200–205. National Academy Press: Washington.

O'Brien, S.J. & Mayr, E. 1991 Bureaucratic mischief: recognising endangered species and subspecies. *Science, Wash.* **251**, 1187–1188.

Polasky, S., Solow, A. & Broadus, J. 1993 Searching for uncertain benefits and the conservation of biological diversity. *Env. Res. Econ.* **3**, 171–181.

Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I. & Williams, P.H. 1993 Beyond opportunism: key principles for systematic reserve selection. *Trends Ecol. Evol.* **8**, 124–128.

Reid, W.V. 1994 Setting objectives for conservation evaluation. In *Systematics and conservation evaluation* (ed. P. L. Forey, C. J. Humphries & R. I. Vane-Wright), pp. 1–13. Systematics Association Special Vol. No. 50. Oxford: Clarenden Press.

Rojas, M. 1992 The species problem and conservation: what are we protecting? *Conserv. Biol.* **6**, 170–178.

Ryti, R.T. 1992 Effect of the focal taxon on the selection of nature reserves. *Ecol. Applic.* **2**, 404–410.

Solow, A., Polasky, S. & Broadus, J. 1993 On the measurement of biological diversity. *J. envir. Econ. Manag.* **24**, 60–68.

Tansel, B.C., Francis, R.L. & Lowe, T.J. 1983 Location on networks: a survey. Part I: the p-center and p-median problems. *Management Sci.* **29**, 482–497.

Tisdell, C. 1990 Economics and the debate about preservation of species, crop varieties, and genetic diversity. *Ecol. Econ.* **2**, 77–90.

Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. 1991 What to protect – systematics and the agony of choice. *Biol. Conserv.* **55**, 235–254.

Vane-Wright, R.I., 1992 Systematics and diversity. In *Global biodiversity: status of the Earth's living resources* (ed. B. Groombridge), pp. 7–12. London: Chapman and Hall.

Weitzman, M.L. 1992*a* On diversity. *Q. Jl Econ.* **57**, 363–405.

Weitzman, M.L. 1992*b* What to preserve? An application of diversity theory to Crane conservation. *Q. Jl Econ.* **58**, 157–183.

Weitzman, M.L. 1992*c* *Diversity functions. Discussion paper number 1610*. Harvard University, Massachusetts: Harvard Institute of Economic Research.

Williams, P.H. & Humphries, C.J. 1994 Biodiversity, taxonomic relatedness, and endemism in conservation. In *Systematics and conservation evaluation* (ed. P. L. Forey, C. J. Humphries & R. I. Vane-Wright), pp. 269–287. Systematics Association Special Vol. No. 50. Oxford: Clarenden Press.

Wilson, E.O. 1992 *The diversity of life*. Massachusetts: Belknap Press.