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Conservation evaluation and phylogenetic diversity

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Protecting biological diversity with limited resources may require placing conservation priorities on different taxa. A system of priorities that reflects the value of taxonomic diversity can be achieved by setting priorities such that the subset of taxa that is protected has maximum underlying feature diversity. Such feature diversity of taxon subsets is difficult to estimate directly, but can be predicted by the cladistic/phylogenetic relationships among the taxa. In this study, a simple measure of phylogenetic diversity is defined based on cladistic information. The measure of phylogenetic diversity, PD, is contrasted with a measure of taxic diversity recently developed by Vane-Wright *et al.* (*Biol. Conserv.*, **55**, 1991). In re-examining reserve-selection scenarios based on a phylogeny of bumble bees (Apidae), PD produces quite different priorities for species conservation, relative to taxic diversity. The potential application of PD at levels below that of the species is then illustrated using a mtDNA phylogeny for populations of crested newts *Triturus cristatus*. Calculation of PD for different population subsets shows that protection of populations at either of two extremes of the geographic range of the group can significantly increase the phylogenetic diversity that is protected.

INTRODUCTION

The goal of conserving biological diversity will not be met without addressing the gap that exists between basic conceptual representations of biological diversity and the actual requirements for practical, working definitions of biological diversity for conservation evaluation. One difficulty in working with biological diversity in practice is that the accepted units of diversity (usually species) may be hard to identify and their geographic distribution hard to estimate (the 'assessment' problem, McNeely *et al.*, 1990). Another difficulty is that limited resources for conservation may impose practical limitations on the conservation of these units of diversity (the 'resources' problem, McNeely *et al.*, 1990).

Research on biological diversity has begun to respond to these challenges. In response to the difficulties of assessing biological diversity at the species level (both because of limits of taxonomic knowledge and problems in estimating the number of species in any particular place), other biological units or attributes have been identified that can be used in place of species. Units based on environmental types or community types mean that biological diversity is more generally represented by some measure of the number of different biological 'attributes' present (Pressey & Nicholls, 1989). Similarly, Noss (1990) recommends that the vague concept of biological diversity be replaced in practice by the use of a number of measurable *indicators* of biodiversity, defined at various levels of biological organisation (landscape, community, population, or genome).

The resources problem has prompted research relating to optimal strategies for conservation evaluation, including procedures for the design of nature reserves. For example, the minimum number of areas can be found which, as a set, meets the requirement that each species (or other attribute) is represented a fixed number of times (Margules *et al.*, 1988). When limited resources

mean that not all the species can be represented in the reserve system, the optimal set of areas will maximise the number of species or other attributes that are successfully included in the reserve system (for review see Margules, 1989; Margules *et al.*, 1991).

In the scenarios above, each of the species is implicitly of equal status. The inability to provide equal protection for all species suggests the need to assign priorities that may be used to determine which species deserve special attention on their own, or which subsets of species should be included in reserve systems. These priorities may be determined by the degree of threat to a species (IUCN, 1980; McNeely *et al.*, 1990) or through assessments of the relative 'value' of different species (IUCN, 1980). Such valuations can be based not only on economic (McNeely *et al.*, 1990) and ecological (Noss, 1990) utility, but also on measures of the 'uniqueness' (IUCN, 1980; Tisdell, 1990) or 'distinctiveness' (McNeely *et al.*, 1990) of the species, relative to biological classification.

Species that are taxonomically distinct will be expected to make a large contribution to some overall measure of diversity of any subset of the total set of species. This is apparent if species are replaced as the basic units (or attributes) of biological diversity by *features* of species. Taxonomically distinct species then contribute more to the diversity of a given subset because they contribute different 'features'.

Interpretation of taxonomic diversity or distinctiveness as indicative of feature diversity helps to clarify its link to conservation value. Diversity is seen as important as the raw material for adapting to change (McNeely *et al.*, 1990), and so provides what McNeely *et al.* (1990) and others call 'option value': a safety net of biological diversity for responding to unpredictable events or needs. The diversity of features represented by a subset of species provides option value in ensuring not only that one or more members of the subset can adapt to changing conditions, but also that society may be able to benefit (e.g. economically) from features of these species in response to future needs.

Because the features above are not explicitly enumerated, taxonomic diversity again raises the difficulty of assessing or measuring the attributes of interest, and suggests that some measurable indicator is needed. Vane-Wright *et al.* (1991) make the important claim that this level of diversity can be indicated in a general way by the cladistic (phylogenetic) relationships among the species, and have proposed quantitative methods for assigning preference weights to different species based on measures of taxonomic distinctness. However, one limitation of their methods, acknowledged by Vane-Wright *et al.*, is in their particular definition of the manner in which cladistic relationships are to provide useful indicators of the diversity of a given subset of species. The use of such information on hierarchical relationships as an indicator of diversity among species requires further study (May, 1990).

In this study, a measure of cladistic or phylogenetic diversity is introduced that is an effective indicator of underlying feature diversity. Phylogenetic diversity will be viewed as based on cladistic relations among any set of taxa, not just species. Consideration here of other taxonomic levels follows work by Hopper and Coates (1990), who have referred to hierarchical relationships among *populations* in their discussion of conservation priorities at this level. The measure developed in the present study therefore was originally intended for application at the population rather than species level, but is applicable at the higher taxonomic levels of concern to Vane-Wright *et al.* Following the description of the measure, examples of its application are presented at both the population and species levels.

A MEASURE OF PHYLOGENETIC DIVERSITY

In order to introduce the rationale for the proposed measure suppose first that we do have the collection of features of conservation interest measured for the set of taxa (the general term 'taxa' will be used here rather than 'species'). It follows that alternative subsets of taxa, corresponding to those protected in alternative reserve designs, each could be directly evaluated as to their feature diversity (equal to the number of different features represented by the subset). For example, for the taxa and corresponding features shown in Table 1(a), the best subset of three taxa is {2, 8, 10}, in having 23 features. The best addition of a fourth taxon would be number 6, producing a subset representing 28 of the 36 features. Thus, a reserve system containing taxa 2, 6, 8 and 10 would, in having maximum feature diversity, be more representative of the total collection of features than would be any other reserve system having only four taxa.

Table 1. Hypothetical data (rows are taxa and columns are features; 1-state indicates presence of a feature)

(a) A collection of features with no homoplasy

0	00000000000000000000000000000000000
1	00111000100000000000000000000000000
2	00111000010000000100110000000101111
3	00111000010000000100110000000110000
4	00111000010000000100110000011000000
5	00111000010000000111000110000000000
6	00111000010000000111000101100000000
7	00111000010000000111001000000000000
8	00111000011111111000000000000000000
9	11000100000000000000000000000000000
10	11000011000000000000000000000000000

(b) A similar collection in which the last three features show convergence.

0	00000000000000000000000000000000000
1	00111000100000000000000000000000000
2	00111000010000100110000000101111
3	00111000010000100110000000110000
4	00111000010000100110000011000000
5	00111000010000111000011000000000
6	00111000010000111000010000000110
7	00111000010000111001000000000000
8	00111000011111000000000000000111
9	11000100000000000000000000000000000
10	11000011000000000000000000000000000

An extension of this same example shows how a cladogram of the taxa provides a prediction of the same result, without directly examining any features. The cladogram of these ten taxa (plus an ancestor, or 'outgroup', 0) is shown in Fig. 1(a). This cladogram accounts for the distribution of the features from Table 1(a) over these taxa, in that it groups together those taxa sharing a given feature. The cladogram is an estimate of the underlying phylogenetic tree for these taxa, so the pattern can be interpreted as showing the evolutionary derivation of these features. Here, each feature from Table 1 can be assumed to have arisen exactly once, in the common ancestor of the group. In cladistic terminology, each feature defines a monophyletic group of taxa. For example, feature 1 is shared by taxa 9 and 10, and the tick mark below the common ancestor of the monophyletic group formed by these two taxa represents the derivation of that feature (Fig. 1(a)). This example is somewhat idealised; in practice, some features may require more than one derivation, because a single cladogram topology cannot always form monophyletic groups defined by all the features. The significance of such cases of independent derivation of the same feature, implying extra tick marks or 'steps' on the cladogram, will be discussed below.

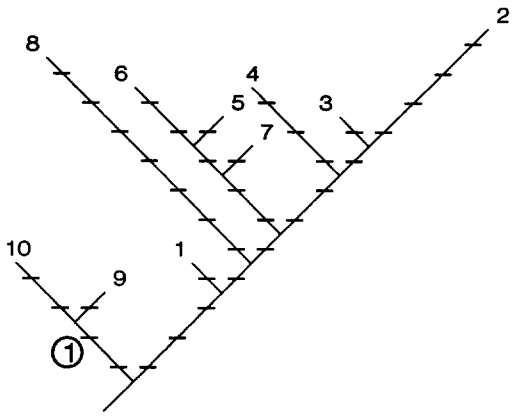

Fig. 1(a). A cladogram for the 10 taxa of Table 1 that accounts for the distribution of the Table 1(a) features over these taxa, in grouping together those taxa sharing a given feature. Each feature can be assumed to have arisen exactly once, in the common ancestor of the group. Feature 1 is shared by taxa 9 and 10, and the tick mark below the common ancestor-node of the monophyletic group formed by these two taxa represents the derivation of that feature. Other tick marks correspond to the derivation of other features.

Given this cladogram (Fig. 1(a)), the same subset of four taxa, determined earlier as having maximum diversity, can be delimited by tracing a path along the cladogram that connects all four taxa (Fig. 1(b)). If the total number of tick marks is counted along this path, the total is found to be 28, matching the earlier result. This result suggests that the number of feature changes along such paths (the 'lengths' of the paths) in the cladogram is all the information needed for predicting feature diversity. To formalise this, two preliminary definitions are needed.

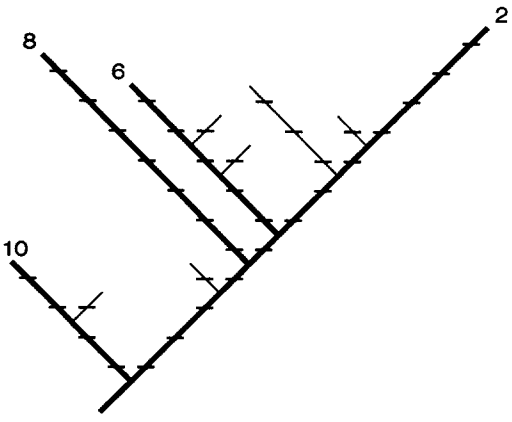

Fig. 1(b). The cladogram for the 10 taxa in which the path connecting the four taxa, 2, 6, 8, and 10, with maximum feature diversity is shown by the thickened lines. The number of tick marks traversed by this path is 28, corresponding to the number of different features found in this subset of four taxa.

Definition 1: A *branch* is a segment of a cladogram, lying between two *nodes*, and with no other nodes along it; the nodes can be terminal nodes or internal branching points.

Definition 2: Let **C** denote the cladogram for the complete set of N taxa, and *s* denote a subset of the taxa. The *minimum spanning path* for *s* is made up of the smallest assemblage of branches from **C** such that, for any two members of *s*, a path along **C** connecting the two can be found that uses only branches in the assemblage.

It follows from this definition that the minimum spanning path (Fig. 1(b)) for the four taxa {2, 6, 8, 10} is the same path as the one that was traced above. The minimum spanning path can be used to define a measure of phylogenetic diversity:

Definition 3: The *phylogenetic diversity* ('PD') of *s* is equal to the sum of the lengths of all those branches that are members of the corresponding minimum spanning path.

In Fig. 1(b), the PD of the subset of four taxa {2, 6, 8, 10} is simply the sum of the branch lengths in the minimum spanning path, or 28. In general, PD can be calculated for any subset of taxa on any cladogram, given some estimate of the relative branch lengths in the cladogram. This is an important property of phylogenetic diversity because it makes use of the cladogram as a predictive system (cf. the 'information content of the phylogenetic system' of Farris, 1979), without the necessity of examining feature data that may have been used to estimate the cladogram in the past, but are now unavailable.

The use of the cladogram, rather than any single feature collection, as an indicator of feature diversity is important for another reason. The cladogram can reveal features that do not define a monophyletic group, but rather are derived several times on the tree (having arisen independently or convergently). These features, if used for direct calculations of feature diversity, would provide misleading predictions about the general feature diversity for different taxon subsets. This is the case because the convergent features create misleading similarities among taxa, that are not predictive of similarities for other features.

As an example, suppose that an additional collection of features (Table 1(b)) is available for the taxa of Table 1(a). Interpreted relative to the cladogram (Fig. 1(a)), these features include three (the last three in the collection) that have arisen independently (convergently) in taxa 2, 6, and 8. The feature diversity calculated *directly* from these features (without reference to the cladogram) would imply that the subset of {4, 5, 8, 10} rather than {2, 6, 8, 10} is of greatest feature diversity. While this is true for the features in Table 1(b), it is a poor prediction of feature diversity in general.

Because the cladogram effectively records the individual derivations of convergent features, they are not misleading in the calculation of phylogenetic diversity. The features in Table 1(b), for example, still imply the same number of tick marks on the cladogram (Fig. 1(a)), further supporting the choice of {2, 6, 8, 10} as having maximum PD.

Greater phylogenetic diversity will, *on average*, imply greater feature diversity, as defined by any particular collection of features. However, this does mean that the diversity patterns for some features (namely those incongruent with the cladogram in implying extra steps) may be poorly predicted by phylogenetic diversity. This problem will be discussed further below.

CALCULATING PHYLOGENETIC DIVERSITY

In many cases, the simplicity of PD means that it readily can be calculated directly from the cladogram, by adding together the appropriate branch lengths, for a given subset of taxa. For large cladograms, for repeated calculations of PD for many different subsets of taxa from the same cladogram, for calculations for different cladograms corresponding to different groups of taxa, or for cases where PD calculations are used in combination with other reserve selection software, a simple computer-based algorithm will be useful.

The information required from a given cladogram for the calculation of PD can be summarised by a matrix of the pairwise distances between taxa, taken from the cladogram. The distance between two taxa a and b, $D_{a,b}$, is the sum of the lengths of the branches on the path between them.

The matrix of pairwise distances derived from the cladogram can be used for several basic calculations. If a subset of the taxa, *s*, is already represented, for example, in a reserve network, then it is possible to evaluate the gain, G, in PD implied by the addition of any other new taxon, x, to the subset:

$$G = \text{minimum, over all i, j in } s, \text{ of } 0{\cdot}5(D_{x,i} + D_{x,j} - D_{i,j}).$$

The rationale for this formula is clarified using the example of Fig. 2. The pairwise D values are represented by the arrows along the branches in the diagram. These branches show how the formula above provides a value equal to the gain in PD with the addition of x to the subset. Note that the value for the gain in phylogenetic diversity is based on complementarity (cf. Vane-Wright *et al.*, 1991), in that the contribution of a given taxon to PD will depend on which other taxa are already in the subset. In practice, the taxon providing the largest G value might be added to the subset of reserved taxa.

The same formula can be used to build up a subset of a required number of taxa from scratch. Here, the building process would begin by taking those two taxa that have maximum distance, D, apart and then consecutively adding the taxon to the subset that maximises G. Such calculations would be useful, for example, in incrementally building up a set of reserve areas such that phylogenetic diversity is maximised at each step.

Finally, the formula can be used to evaluate the PD of a pre-defined subset of taxa. This option will be useful, for example, when a given reserve system is to be evaluated relative to the overall phylogenetic diversity for a number of different groups of taxa. An estimate of the cladogram for each group of related taxa is used to calculate the PD value corresponding to the particular subset of these taxa found in the reserve system. These PD values for individual cladograms would then be summed together for an overall phylogenetic diversity score that could be compared to that for other nominated reserve systems. One requirement of this multiple-cladogram approach is that the branch lengths for the different cladograms be measured in comparable units. I will return to this strategy in the Discussion section below.

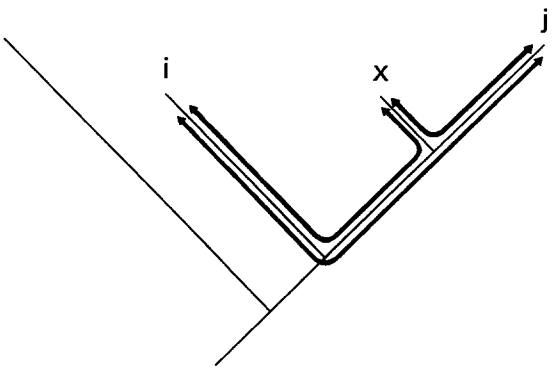

Fig. 2. A hypothetical cladogram of four taxa. Taxa i and j are already in the reserve system, and the potential contribution of taxon x is to evaluated. The thickened arrows correspond to the path-length distances $D_{x,i}$, $D_{x,j}$, and $D_{i,j}$. The amount that x adds to the total length of the minimum spanning path (the phylogenetic diversity, PD) can be calculated by adding together the lengths between x and i and x and j, subtracting the length between i and j, and dividing the result by 2. For further information see text.

It is noteworthy that informative distance values can be prepared even in the absence of exact estimates of branch lengths, as when the exact length of a terminal branch (corresponding to the number of uniquely derived features for the terminal taxon) is regarded as poorly known. Length estimates for terminal branches will often be poorly estimated in cladistic analyses because features unique to a single taxon are usually deleted from the analysis. In such cases, the branches may be assigned unit length, or lengths according to an assumption of equal rates of feature derivation in all lines of descent.

When all branch length information is unknown or ignored, the lengths can all be assigned unit length so that phylogenetic diversity then depends only on the branching pattern on the cladogram, The PD value, for any subset of taxa of size N, reduces to a simple function of the number of different nodes on the cladogram that lie along the corresponding minimum spanning path:

PD = (N – 1) + no. of internal nodes (branching points) on the minimum spanning path.

Thus, the best subset of N taxa is the one that spans the greatest number of nodes on the cladogram, and the best addition to a subset is the taxon adding the greatest number of nodes to the minimum spanning path.

These different methods of branch length assignment are illustrated for the bumble bee (Apidae) example discussed below.

A computer program 'PHYLOREP', written in Fortran 77, for PD calculations is available from the author.

EXAMPLES

Bumble bees of the *sibiricus* group

Vane-Wright *et al.* (1991) used a cladogram for species of bumble bees in the *sibiricus* group of *Bombus* Latreille (Williams, in press) to demonstrate their method of taxic diversity weighting. This sample was also used in the discussion by May (1990) to highlight differences between equal weighting to all species and taxic diversity weight-

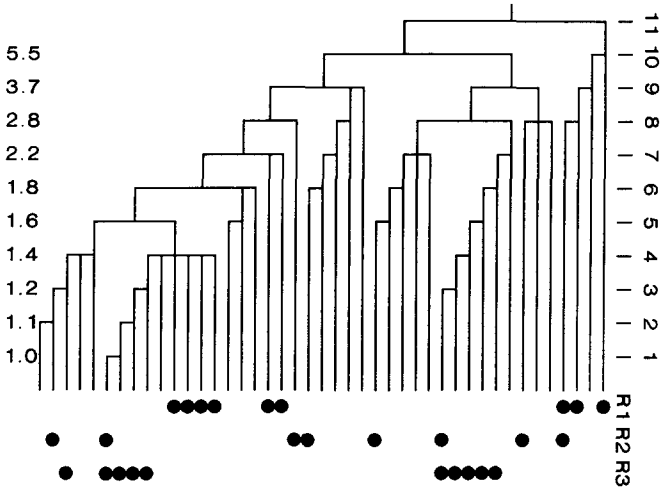

Fig. 3(a). The cladogram for bumble bee species, redrawn from Vane-Wright *et al.* (1991). The taxic diversity weights scale is shown at the left of the tree, and the scale for branch lengths is given at the right of the tree. At the bottom of the tree, the presence of a given species, for each of three hypothetical reserve areas (R1, R2, R3), is represented by a solid circle next to the corresponding terminal node on the tree.

ing. Re-examination of this example will serve to contrast the phylogenetic diversity and the taxic diversity approaches. The cladogram of these species (Fig. 6, Vane-Wright *et al.*, 1991) is redrawn in Fig. 3(a). The taxic diversity weight is found for any species by moving from its terminal node on the bottom, upwards along the tree, until the first branching point is reached; the level along the weights axis (left of Fig. 3(a)) at this node is the corresponding taxic diversity weight for the species.

Application of the phylogenetic diversity measure to this same cladogram requires some assessment of what branch length information is available from the tree. Note that the particular convention for drawing cladograms used by Vane-Wright *et al.* and in the redrawing of their tree here (e.g. compare Fig. 3(a) to Fig. 1(a)) may mean that the lengths of some branches are arbitrary; in particular, the terminal branches are by convention all extended to the same distance from the root of the tree (this is equivalent to assuming equal rates of feature derivation in all lines of descent). In the absence of alternative estimates of branch lengths, the relative lengths of the branches as originally drawn will be assumed to provide meaningful estimates of branch lengths for calculation of PD. The resulting scale for measuring relative branch lengths is found along the right of the tree (Fig. 3(a)).

At the bottom of the tree are three hypothetical reserve areas, R1, R2, and R3 (following the

Table 2. Values for phylogenetic diversity and for taxic diversity for each of the three reserve areas, R1, R2, and R3 from Fig. 3(a). Also shown is the number of species for each reserve network

	R1	R2	R3
Number of species	9	8	10
Phylogenetic diversity	66	71	50
Taxic diversity	21·1	15·1	12·7

labelling convention of Vane-Wright *et al.*, 1991). The solid circles on the diagram indicate the presence of the corresponding species in that area. The values assignable to each reserve area, based on PD or on taxic diversity, can be computed using this distribution information. The resulting values for each index are shown in Table 2. R1 has a much greater value (21·1) for total taxic diversity relative to R2 (15·1) and R3 (12·7) and so would be the preferred area for reservation by the taxic diversity criterion. This is the case in spite of the fact that R3 has one more species; a similar scenario was noted by May (1990).

The PD values for the three areas reveal a different pattern. R3 has the largest number of species, but because several of these are close sisters on the cladogram, R3 has the lowest PD score (50). While R2 has the smallest number of species, it nevertheless has the largest value for PD (71), because the species in this subset span (through their minimum spanning path) a large portion of the overall tree (Fig. 3(b)). This result leads to the prediction that, on average, the R2 subset would represent a larger amount of the underlying feature variation of the complete set of species. In contrast, the area with largest taxic diversity, R1,

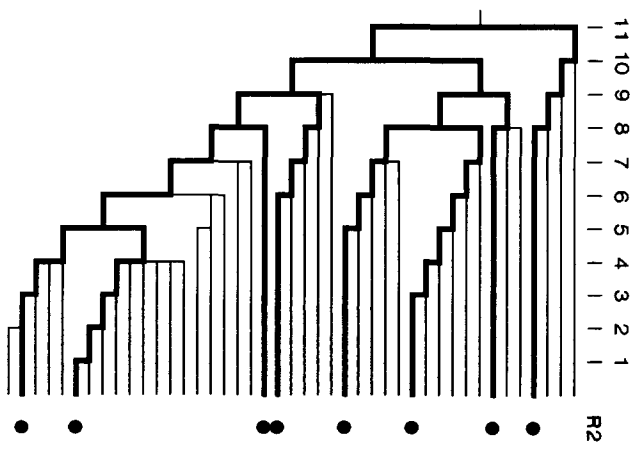

Fig. 3(b). The cladogram for bumble bee species, showing the minimum spanning path for the species found in R2. This reserve area shows highest phylogenetic diversity.

does not contain a subset of species that spans a large portion of the tree; consequently, the corresponding phylogenetic diversity for R1 (66) is low relative to that of R2.

Because the above example required some assumptions about the assignment of terminal branch lengths, alternative assignments of branch lengths were also examined. When all the terminal branches were simply set to unit length, it remained the case that R2 had greater PD than R1, though the difference between the two was now greater (38 versus 19). It turns out for this example that these are also the resulting PD values when branch lengths are ignored by setting all lengths to 1 (because all but the terminal branches had lengths of 1 already). Thus, the contrasting evaluation of R1 and R2 by taxic diversity versus PD is largely a product of the branching pattern, rather than branch length estimates.

More detailed comparison of PD with the taxic diversity strategy would result from calculating PD and taxic diversity values for actual distribution information for these species in alternative reserve areas. The PD and taxic diversity priorities assigned to different areas will be expected to differ, with the optimal area for PD providing a greater representation of feature diversity. One way to evaluate this prediction would be to calculate, for one or more sets of recorded features for these species, actual feature diversity values for the area chosen as optimal by the PD criterion versus the area chosen by taxic diversity.

Mitochondrial genomes of crested newts *Triturus cristatus*

This example demonstrates the application of PD to cladograms defined below the species level, where limited resources may require priorities as to which populations are included in a reserve system. Wallis and Arntzen (Fig. 4, 1989) derived a cladogram of mitochondrial DNA genomes for crested newts (*Triturus cristatus* superspecies), whose populations are broadly distributed over Europe (Wallis & Arntzen, Fig. 1, 1989). Each step along the cladogram (redrawn here as Fig. 4) represents a site change in the mitochondrial DNA. Wallis and Arntzen note the problems of conservation of genetic variation in this species group, and the potential for endangered populations in the future due to increased agricultural development. While genome types 1, 11, and 12 are represented by several populations, the genome types found only in the extreme southern and western areas of the range are only represented by one or two known populations (Table 1 and Fig. 2, Wallis & Arntzen, 1989). Wallis and Arntzen therefore argue that these peripheral populations deserve special conservation attention, in order to ensure conservation of genetic variation in this superspecies.

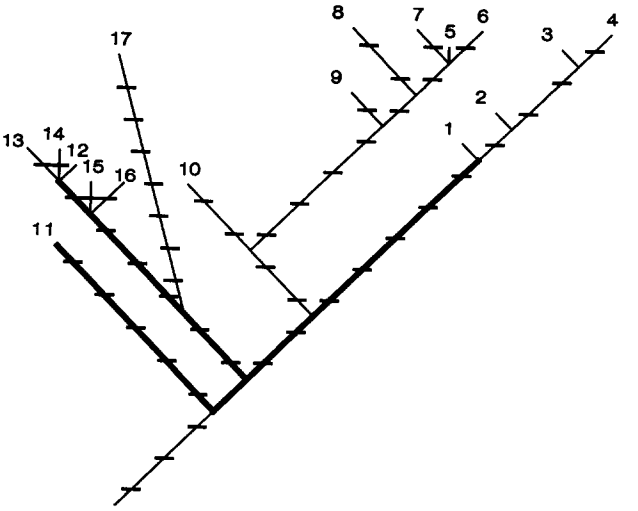

Fig. 4. A cladogram of mitochondrial DNA genomes for crested newts (*Triturus cristatus* superspecies), redrawn from Wallis and Arntzen (Fig. 1, 1989). Each step along the cladogram represents a site change in the mitochondrial DNA. The initial minimum spanning path for genomes 1, 11, and 12 is shown, with a length (PD) of 19. For further information see text.

The PD measure can be used to quantify this argument. If the protection of one or more of the more central populations is taken as assured, then one can ask what increase in phylogenetic diversity is gained by ensuring the protection of one or more of the southern and/or western populations. In Fig. 4, the initial minimum spanning path for genomes 1, 11, and 12 is shown, with a length (PD) of 19. The increase in PD in saving one of the western populations (representing one or more of genomes 5 through 9, Wallis & Arntzen, Fig. 2 and Table 1 1989) will vary from 7 to 10, and an increase in PD of nine results from saving site 48 in Turkey with genome types 15, 16, and 17. Thus, protecting populations from either of these areas can increase the phylogenetic diversity that is protected by 35% or more (Fig. 4).

DISCUSSION

Choice of conservation units

The use of phylogenetic information as proposed

here is an effective response to cases where limited resources imply that priorities must be placed on the conservation of different species (or other taxonomic units). However, the justification for phylogenetic diversity goes beyond considerations of limited resources. This strategy may also circumvent the sometimes arbitrary decisions about what taxonomic units are to be the basis for conservation efforts, in that it puts less emphasis on 'counting up' taxonomic units (e.g. in reserve design), and more on representativeness of a cladistic hierarchy. The emphasis therefore is on preserving as much of this hierarchial variation as possible, no matter what the taxonomic units involved. Consequently, debates about what the natural units of choice should be (e.g. as in O'Brien & Mayr's (1991) emphasis on subspecies) or about how species are to be defined for conservation (see Wheeler, 1990) are perhaps less critical.

Nevertheless, using phylogenetic diversity does not escape the need for some decisions about taxonomic units for conservation. In the hypothetical example of Fig. 5, the addition of some taxonomic unit at the end of the branch that is highlighted will dramatically increase the value for PD. The taxonomic unit of choice could be at family (x), species (y) or subspecies (z) level. The final choice of the taxonomic unit for conservation efforts may depend in practice on other biological or management factors. For example, application of phylogenetic diversity criteria to the tuatara *Sphenodon* example (Daugherty *et al.*, 1990, discussed in Vane-Wright *et al.*, 1991) might suggest that only one of the two extant species needs to be protected if resources are limited. But the endangered status of these species may mean that conservation of the diversity represented by that branch leading to *Sphenodon* (the only surviving genus of one order of reptiles, Daugherty *et al.*, 1990) will only be assured by putting a high priority on the genus as a whole. In other cases, by contrast, a single subspecies might be an acceptable conservation unit. Thus, a conservation unit compatible with PD could be a group of sister species, a single species, or one or more subspecies. The point for emphasis is that the units of choice can be expected to vary, even within the application of PD to a given cladogram. The choice of conservation units is properly influenced both by diversity criteria and management considerations.

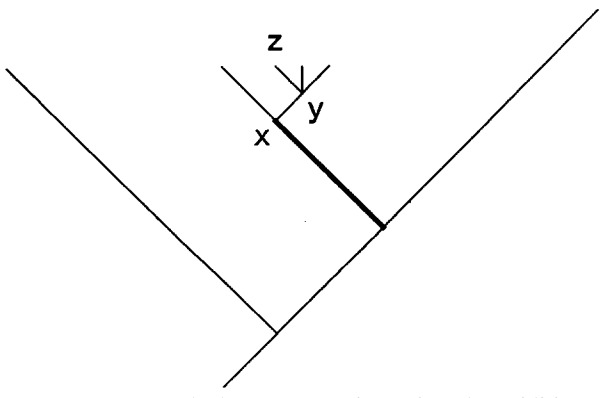

Fig. 5. A hypothetical cladogram in which the addition of some taxonomic unit at the end of the highlighted branch will dramatically increase the value for PD. The taxonomic unit of choice could be at family (x), species (y) or subspecies (z) level.

The extension of phylogenetic diversity to levels below that of the species can present problems. Chambers and Bayless (1983) have reviewed methods for direct calculation of feature (or character) diversity at the population and subspecies levels, and note the problem of assuming that one character type (e.g. morphological) is more generally representative of overall feature variation. It is this representativeness problem that calls for the use of phylogenetic relationships among the units if these can be estimated. The key issue in such applications may be whether or not the assumption of a hierarchical, cladistic model for the relationships among such lower-level units is justified. This study has briefly explored the application of phylogenetic diversity at one lower taxonomic level (mtDNA genomes). The mtDNA *genomes* will be expected to have a cladistic relationship, but, as is the case for the crested newts (Faith & Cranston, 1991), the same data may not reflect a hierarchical relationship at the *organismal* (species or population) level.

Populations of a given taxon can be expected to be incompatible with PD calculations, because such populations may not display hierarchical/cladistic variation. However, variation among subspecies will arguably be cladistically structured (viewing subspecies as 'geographically defined aggregates of local populations', O'Brien & Mayr, 1991). O'Brien and Mayr argue that subspecies are appropriate conservation units because of their acquisition of unique characteristics and their potential to become unique new species. Such priorities for conserving subspecies mean that the method proposed here may be appropriate for the corresponding conservation evaluation problems at this level.

Limitations of cladograms

At any level of application, the predictive value of PD depends on having a cladogram that is a reli-

able estimate of the phylogenetic relationships among the taxa. Cladograms based on a small number of characters, or on characters that exhibit large amounts of homoplasy (convergences and reversals in the derivation of features), are probably less reliable, as indicated by recently developed statistical approaches for evaluating cladograms (Faith & Cranston, 1991, and references therein). This work particularly highlights the power of molecular data for resolving phylogenetic relationships, and these data may also provide effective estimates of branch lengths on the resulting cladograms. Thus, molecular data, while not necessarily representing features of direct conservation interest, can provide phylogenies that are predictive, through PD calculations, of more general feature diversity patterns.

Convergent similarities among taxa raise important issues in conservation evaluation, not only because they weaken cladistic inferences. Diversity patterns based on these features will be poorly predicted by the cladogram of the taxa. It follows that an optimal subset of taxa, based on PD values calculated from the cladogram, may not be representative of the range of features among the taxa that are derived convergently. In some conservation contexts, representation of convergent features is considered a reasonable goal, because these features correspond to different ecologically functional types (C. Margules, pers. comm.). In such cases alternative pattern representations of the taxa (robust ordinations, Faith, 1989) that account for feature variation due to convergence and/or function, and methods for representative sampling of such ordination spaces (Faith & Norris, 1989), may be a useful complement to phylogenetic diversity.

Prospects

While PD evaluations based on a single cladogram are sensitive to the quality of the branch-length and topology estimation, even partial estimates of cladograms may be useful when a number of different cladograms (for different groups of taxa) are used together in conservation evaluation. Such a strategy may be an effective basis for the evaluation of general (i.e. not taxon-specific) conservation priorities for different geographic areas. In this context, a given area will have high conservation value if it makes a large contribution to phylogenetic diversity, for each of a number of different groups of taxa.

While such an area would no doubt be valuable, is there any reason to expect that a single area can represent a large component of phylogenetic diversity for many different groups of taxa? One obvious scenario is that the area is so taxon-rich that it automatically represents a large portion of the phylogenetic diversity of any group. However, extreme taxon richness is not the only way in which an area can make a large contribution to phylogenetic diversity. An area could be of value because the taxa that it does have, in each group, tend to be complementary to those of other areas in providing representation of phylogenetic diversity. It appears that such an area, and the corresponding cladograms, would have to satisfy one or more of the following patterns:

(1) For each taxonomic group, the subset of taxa found in the area of interest arose because of a branching event in the corresponding cladogram. The branching event in each of the cladograms may have had a common cause corresponding to a vicariance event (Nelson & Platnick, 1981) associated with the separation of the area of interest from other areas. Thus, the historical origin of the area means that it may contain a phylogenetically distinct subset of taxa within each taxonomic group.

(2) Within each taxonomic group, there is a high degree of anagenesis (derivation of features within a line of descent) for those taxa found in the habitats peculiar to the area in question. Thus, adaptations that are a response to these habitat types imply that the taxa from this area, in each of the taxonomic groups, represent large numbers of uniquely derived features (reflected in longer branches on the corresponding cladograms).

The first of these explanations therefore depends on area-based congruence in cladogenesis (branching pattern) among different groups, while the second depends on area-based congruence in anagenesis among different groups (possibly accompanied by cladogenesis).

The identification of particular examples of such high-value areas, or the ability to predict where such areas may occur, would be of great practical use in conservation planning. A profitable line for future research therefore may be the pursuit of a better understanding of the reasons why some areas do (or do not) contribute strongly to phylogenetic diversity for many different groups of taxa.

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