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# Quantifying Biodiversity: a Phylogenetic Perspective

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## Introduction

Quantification of biodiversity presents a two-fold problem. First, there is the question of what exactly we should be counting. If that question is not difficult enough, it leads straight to the second practical question of how we can possibly accomplish such a count. At the species level, for example, even if we can decide what a species is (for discussion see Wheeler & Meier 2000), we must in practice use surrogate information to quantify relative numbers of species in different places.

These same issues recur when biodiversity is defined below the species level. Debates about taxonomic distinctiveness in biodiversity conservation (Vane-Wright et al. 1991; Faith 1992a; Williams et al. 1994), although initially concerned with quantification of biodiversity at the level of species, led to a recognition that what we would like to count when setting species priorities is biodiversity below the species level—broadly, “feature diversity” (Faith 1992a, 1992b; 1994a, 1994b; Williams et al. 1994). Furthermore, the rationale in such prioritization, conserving feature diversity to maximize “option value” (Faith 1992a, 1992b)—dictates that those “features” must include not only observed characters of organisms but also unobserved characters. Clearly, we cannot count all those features and so must turn to something like taxonomy and phylogenetic pattern to capture character diversification (Faith 1992a, 1992b; but also see Faith 1996).

Representation of “evolutionary history” (Faith 1994b), encompassing processes of cladogenesis and anagenesis, is assumed to provide representation of the feature diversity of organisms. Specifically, the phylogenetic diversity (PD) measure estimates the relative feature diversity of any nominated set of species by the sum of the lengths of all those phylogenetic branches spanned by the set (Faith 1992a, 1992b, 1994b). Although that method has subsequently been used in various biodiversity toolboxes (BioRap [Faith & Walker 1996] and Worldmap [Williams

1996]), there remains ongoing debate about the use of PD (Bininda-Emonds et al. 2000), including how we can best estimate branch lengths and whether prioritization of species by PD will yield results better than those of random selection (Nee & May 1997 [who call PD “evolutionary history”]; Russell et al. 1998).

Against this backdrop, Owens and Bennett’s (2000) recent paper, “Quantifying Biodiversity: a Phenotypic Perspective” makes some surprising assertions. The authors begin by acknowledging PD as “the best way to measure true phylogenetic distinctiveness” (p. 1015) and then claim that their new method, based on phylogenetic contrasts, is novel in attempting to capture the “processes” leading to “phenotypic diversification.” They also begin with the premise that biodiversity may be expressed in many different ways, such as “phylogeny, molecules, or phenotypic variation.” Thus, phylogenetic diversity is somehow separate from character diversity, and the fundamental process-based link between PD and character diversity is not acknowledged. Owens and Bennett appear to regard PD as vaguely about phylogenetic distinctiveness—simply providing a “ranking” for species rather than a quantification of the relative feature diversity of subsets of species.

Owens and Bennett also make the surprising claim that phylogenetic distinctiveness methods assume that “all phylogenetic divergences produce equal amounts of phenotypic change” (p. 1015). This might be interpreted as a reference strictly to the early approaches (Vane-Wright et al. 1991; Williams et al. 1994) that counted only the nodes of a cladogram to arrive at distinctiveness indices. But later, referring explicitly to PDs “maximum phylogenetic path length” based on branch lengths, Owens and Bennett restate their criticism of the approach: “it does not take into account the different amounts of evolutionary change that took place at different points of cladogenesis” (p. 1018). An immediate reaction, surely, is that this is exactly what branch lengths account for. Suppose we focus on the common ancestor to sister taxa, A and B. At the extreme, if the branch length is 0 leading to A and 100 units leading to B, then there has been no evolutionary change along the lineage leading to A, rela-

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tive to 100 units of change leading to B. Branch lengths indeed take into account the different amounts of evolutionary change that took place at different points of cladogenesis.

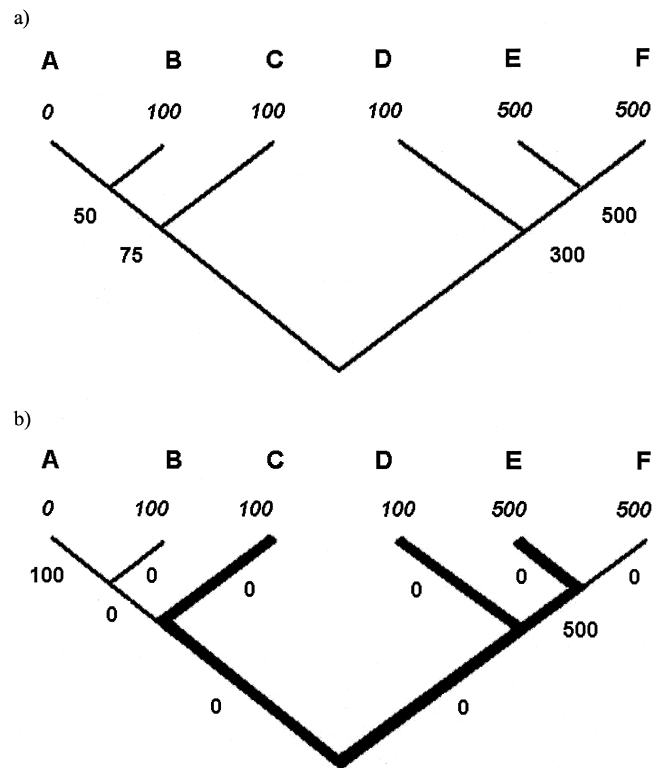
These misconceptions underlie Owens and Bennett's attempt to recreate some way to link phylogeny to character diversification. I argue that their resulting strategy is not useful for representing processes of diversification. One might expect, however, that any approach that tries to capture the processes leading to phenotypic diversity, at least in correct form, would point to something like PD. After documenting and correcting errors in Owens and Bennett's analyses, I show that this is the case.

### Calculations of "Phenotypic Diversification"

Owens and Bennett calculate phenotypic diversification scores for taxa and degrees of threat as inputs to proposed conservation priorities. Their diversification score for a taxon is calculated by first determining a "contrast" for each phylogenetic node based on character data recorded for all taxa (in their example, the single trait of clutch size). As an example (Fig. 1a), the phylogenetic node leading to taxa A and B has a contrast value of 100, calculated as the absolute value of the difference in values between the two descendent lineages. When one or both lineages arising from a node do not directly lead to a taxon but to another ancestral node, the contrast calculation uses a hierarchical average of character states of member taxa. For example, the contrast for the node leading to (A,B,C) (Fig. 1a) is the absolute value of the difference between the value of C (100) and the average of the values of A and B (50), or 50 units.

Representation of a contrast is said to exist if one or more member taxa are "present" for both of the lineages arising from the node in question. The total diversification score for a taxon, intended to reflect its representation contribution, is a weighted sum of contrasts (calculated according to Owens and Bennett's Table 1). For example, taxon F (Fig. 1a) would be credited with the E-F contrast, plus half the contrast of 400 units between D and (E,F), plus one-third the contrast between (A,B,C) and (D,E,F).

Owens and Bennett's example (their Table 2 & Fig. 2), for taxa defined by families of birds, raises problems. In their tree diagram (their Fig. 2), they wrongly claim that "the figures in circles are the estimated ancestral character states at each node"; these are contrast values. More worrisome is that it is impossible to reproduce their calculation results for diversification values. Some values (their Table 2) appear to credit a taxon like F in my example with only half, not all, of the contrast between E and F, contrary to their own formulae (their Table 1; my recalculated values are available on request).



*Figure 1. A hypothetical example of diversification for families A through F with phenotypic values for taxa shown in italics. Families A and F have all member species threatened, whereas C, D, and E have no member species threatened. Family B is extinct. Either A or F will be given priority for protection. a) Values next to nodes are inferred average phenotypic values used in calculating contrasts. In an analysis using the method of Owens and Bennett, F has a diversification under threat score of  $0.0 + 0.5(500 - 100) + 0.333(300 - 75) = 275$ , and A has a diversification under threat score of  $100.0 + 0.5(100 - 50) + 0.333(300 - 75) = 200$ . Family F has highest priority yet represents no additional diversification given that E is well protected. b) An alternative strategy, compatible with phylogenetic diversity, views the diversification (shown by heavy lines) as represented without threat and compares the contributions that A versus F can make to representing additional diversification. Branch lengths representing inferred evolutionary steps for the phenotypic character are shown along branches. Family A is given high priority because it contributes 100 additional units, whereas F contributes 0.*

Based on their calculations of diversification scores, Owens and Bennett's results section presents a series of eight significance tests, focusing on apparent departures from randomness. The 10 families with highest diversification scores capture more diversification than if they had been selected at random. The implications of such

tests are unclear. For most any set of numbers assigned to 133 taxa, the 10 highest would be significant in this way.

A more revealing test might ask whether these diversification scores reveal significant signals in the data, suggesting recovery by this method of some key aspect of the diversification processes. A useful randomization with which to explore this would take the character values and randomly reassign them to taxa (Faith 1990). I applied this randomization to their example (their Table 2, in which the top three families, for example, captured 35.2% of total diversification), asking how often a randomized character set produced a total diversification for the top 3 out of 16 families that matched or bettered that percentage. For randomized sets, the top 3 families often (about 43% of the time) captured 35.2% or more of total diversification, suggesting no significant diversification signal in these data.

### Complementarity and the Representation of Contrasts

A better evaluation of such diversification scores might ask whether they provide a meaningful recovery of phenotypic diversification. Suppose we assume that representation of contrasts captures processes underlying phenotypic diversification. Unfortunately, Owens and Bennett's method does not provide a logical strategy for representing such contrasts. In my example (Fig. 1a), suppose that C, D, and E are secure, A and F are extinction-prone, and B is extinct. I ask whether protection of A or F best increases representation of contrasts. Taxon F's diversification score in part reflects a contribution of 200 units to the 400-unit contrast between D and (E,F). Taxon A contributes 100 units to the A-B contrast and contributes 25 units to the 50-unit contrast between C and (A,B). Both make the same contribution to the contrast between (A,B,C) and (D,E,F). Taxon F would receive higher priority than A in representing 75 more contrast units. But loss of family F would not alter any representation of contrasts at all. Owens and Bennett's assessment would assign high priority to a highly redundant taxon.

The example highlights the fact that Owens and Bennett's method does not employ complementarity, which is fundamental to setting biodiversity conservation priorities (e.g., for PD, Faith 1992a, 1992b). If we want to represent contrasts, the principle of complementarity suggests we tally up the number of represented contrasts for any nominated subset of the taxa and then record the loss or gain in contrasts representation for any one taxon, assuming its extinction or protection. Here, a contrast is represented when the minimum spanning path (Faith 1992a, 1992b) connecting taxa regarded as "present" includes both descendent lineages of the corresponding

node. We can also use probabilities of extinction in these calculations, as they are used with PD (Witting & Loeschke 1995).

Difficulties remain, however, in the application of complementarity to the problem of representing contrasts. Returning to the example (Fig. 1a), extinction ("absence") of B means that the A-B contrast of 100 character contrast is not represented, based on Owens and Bennett's representation requirement of the "presence" of both those taxa (or the presence of both descendent lineages in the spanning tree). Protecting A would only represent the contrast of 75 units, defined at the (A,B)-C node (Fig. 1a). Clearly, an alternative view suggested by the phylogeny is that protection ("presence") of both A and C does indeed capture the contrast between character values of 0 and 100. If the value 100 is the ancestral state to (A,B,C), as parsimony optimization of ancestral character states suggests (e.g., Kitching et al. 1998), then a change from 100 to 0 occurs along the lineage leading to A, and protection of A and C reflects that difference. Failure to represent the 100-unit contrast arises from Owens and Bennett's assignment of average character values at nodes and suggests that such a convention should be abandoned. Certainly, assigning average values to nodes paints an odd picture of the process of diversification. In Fig. 1a, averaging indicates many character-state changes on this phylogeny, including many reversals, whereas parsimony would suggest character changes as in Fig 1b.

An appealing alternative definition of contrasts would therefore imply that a "contrast" is represented on a phylogeny when there is an inferred change in one lineage but not the sister lineage, considering only lineages on the minimum spanning path connecting "present" taxa. For example, D plus E or F represents a 100 versus 500 contrast, and A plus B or C represents a 0 versus 100 contrast. That representation criterion turns out to be equivalent to counting up evolutionary changes along branches on the minimum spanning path (bold lines in Fig. 1b). Representation of contrasts therefore uses PD calculations. Any increase in the length of the spanning path by the addition of a branch length indicates that a "contrast" is represented, corresponding to the inferred character changes captured in that branch and not found in the sister branch. In general, for branch lengths based on many characters, the contrast representation is given by the path length and corresponds to PD. Furthermore, the PD criterion predicts that when we gain 100 units of character change (in our example, by protecting taxon A, not F) there is greater representation of feature diversity (Faith 1992a).

We now can compare the results when A versus F is protected (Fig. 1b). Branch lengths indicate the amount of character change. The loss of F does not indicate any loss in contrasts or total PD. Taxon A is given higher priority than F in contributing a greater representation of

PD and, equivalently, “contrasts” and character diversification.

## Biodiversity Indices and Goals of Biodiversity Conservation

Careful consideration of the representation of contrasts and “processes” of diversification reinforces the role of an existing measure, phylogenetic diversity, in linking phylogeny to processes of character diversification. Although the examples I examined were based, following Owens and Bennett, on a single character, PD is about many (often unmeasured) characters. The general link of PD to overall feature diversity stands in stark contrast to any research on “quantifying biodiversity” that examines a single character. It is ironic that, at the end of their paper, Owens and Bennett claim that “the major limitation to using methods such as the one we outline is that conservationists do not know which traits to put into the algorithms.” The very reason for using PD is that we do not know which traits will be of value in the future, so we are seeking to maximize representation among all of them.

Owens and Bennett’s paper better highlights a different “limitation” in applying methods related to distinctiveness. It provides another example of research on distinctiveness which reveals the gap between the ease of creating algorithms and indices and the difficulty of linking these to goals of biodiversity conservation. Harvey (1995) referred to much of the work following Vane-Wright et al.’s (1991) important paper on taxonomic distinctiveness as a “confused stagger through measurement space.” Some early methods, when corrected, have been shown to converge on PD (Faith 1994a). Contrasts have even been employed before in a method (Altschul & Lipman 1990; not cited by Owens and Bennett) that, if ever applied, would have given priority to low, not high, biodiversity (Faith 1993).

Conservation biology would be well served by better synthesis of the research on quantifying biodiversity. In the present context, such a synthesis might have included not only related papers on phylogeny and phenotypic diversity from the same journal (e.g., Linder 1995; Parnell 1995; Faith 1996) but also integration of important ideas from, say, Weitzman’s (1992) classic paper in which phenotypic variation in a phylogenetic context is addressed along with threats, costs, and complementarity.

Owens and Bennett’s concern with representing “process” does reflect the current literature (e.g., Margules & Pressey 2000), which calls for greater consideration of process in priority-setting methods. But that may not be a concern in the present context. In representing evolutionary processes of cladogenesis and anagenesis, an existing measure, phylogenetic diversity, already quantifies

Owens and Bennett’s assertion that “all taxa are not equal with respect to representing the evolutionary processes that lead to current phenotypic biodiversity.”

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