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# On Words, Tests, and Applications: Reply to Faith et al.

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Q1

Faith et al. (2003) strongly criticize our paper (Posadas et al. 2001). Their criticisms are based on what they consider our “ill definitions” and “erroneous applications” of the words *complementarity*, *endemism*, and *biodiversity*. The objectives of our reply to Faith et al. are to demonstrate that their criticisms do not satisfy epistemological and methodological tenets and to compare some aspects of the methods used by Posadas et al. (2001) and Faith et al. (2003) when applied to a real case.

## On Words

*Complementarity* is defined as the “property of two (sets of) sites that occurs when some of the natural features in a site differ from the features in another site. When (sets of) sites are highly complementary, they contain (almost) nonoverlapping representation of natural features” (Cabeza & Moilanen 2001:246). Faith et al. do not take into account that “a natural feature in a site” could be the presence of a given taxon, so the number and composition of species is part of the complementarity between two sites. For complementarity, the feature to evaluate is differential composition as it relates to the natural attributes to be measured (presence of species, in our case). Faith et al. used another (and more restrictive) definition of complementarity as it relates to Faith’s phylogenetic diversity index. Faith et al.’s definition does not dismiss Jaccard complementarity. In the same way, Faith et al. also use endemism in the context of their phylogenetic diversity index. In its classical sense, *endemism* is a property of the area, valued as the number (or proportion) of species on a site not found in any other site. In this sense, it is not possible to apply the endemism concept to a set

of species, as Faith et al. claim. So, we use the terms *endemism* and *complementarity* as they are generally defined and *endemism*\* and *complementarity*\* to indicate values associated with the phylogenetic diversity index.

## On Tests

From an epistemological perspective, a valid comparison must be based on the same or commensurable (sensu Kuhn 1970; Feyerabend 1988) definitions. Faith et al. based their criticisms on the redefinition of *endemism* and *complementarity*. If one considers two different definitions—using different frameworks—a given approach could be appropriate according to one definition and inappropriate according to the second definition. Faith et al. show that *complementarity*\*, with the phylogenetic diversity index as the background, behaves better than standard complementarity. In this way Faith et al. advocate that their method is better than the one we used. They use a conventionalist approach in which they define a word and use it to “test” (indeed to compare) other methods. This approach only serves to show that their method agrees with their logic, and not, as they argue, to dismiss other methods based on a different framework.

Seeking to contrast and test our approach, Faith et al. applied the methods of Posadas et al. and their phylogenetic diversity approaches to a hypothetical data set (their Fig. 1). This comparison fails from an epistemological viewpoint: they made a biased comparison, not a test, because they disregarded the philosophical logic of a true test (Grant 2002). A comparison must use the same “units” and count the gain of such units when adding the same (or at least comparable) items to a set of objects to obtain contrastable results. Furthermore, Cabeza and Moilanen (2001:244) state that “the success of a reserve network depends on the initial conservation objectives and, hence, success *can and should* be measured in

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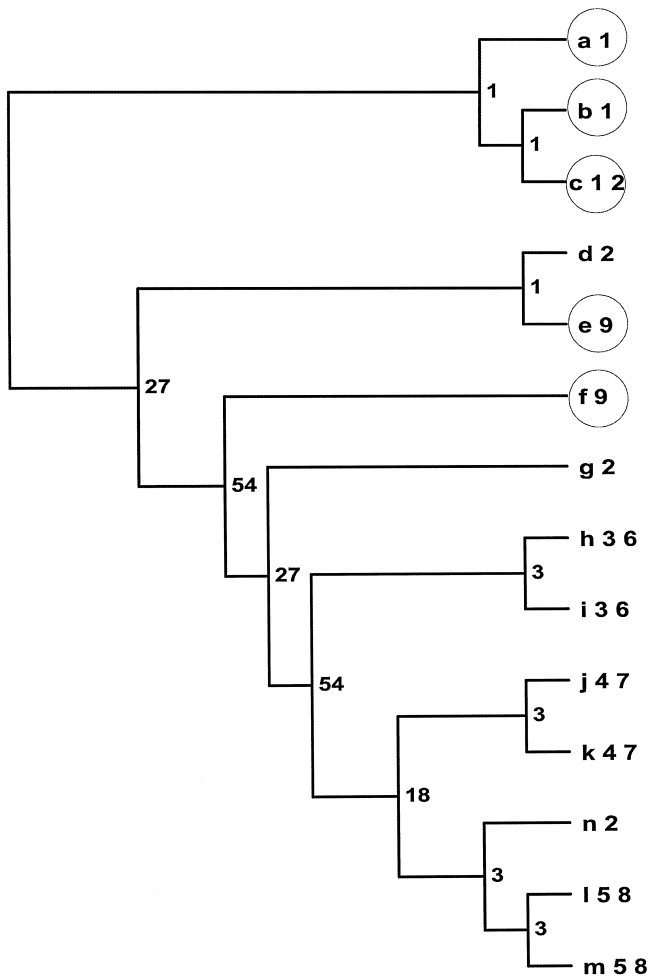


Figure 1. Hypothetical example used by Faith et al (2003 [this issue]) to compare both methods. Letters indicate taxa, and numbers indicate the areas they inhabit. Circles indicate the taxa protected given the two first priorities resulting from the application of the method of Posadas et al. Values at the nodes indicate the number of possible ancestral-areas reconstructions found by applying dispersal and vicariance analysis (DIVA). The biogeographic scenario resulting from this example is highly unlikely.

different ways” [emphasis added]. In our case we are ranking areas, not designing reserve networks, but the statement nevertheless remains valid.

Our conservation objectives differ from that of Faith et al. To make it clear, we use the same terms used by Faith et al. in the following statement: “In general, basic biodiversity ‘units’ of some kind are the items we want to count up. ‘Objects’ (containing various units) form sets, and we evaluate the biodiversity gain from adding a specified object to an existing set.” Although for the phylogenetic diversity index “units are features and characters, objects are species” and the focus of interest is “the gain in features when adding one or more species to a set of

species,” for the Posadas et al. protocol, the main desirable characteristic of a “unit” is to be a taxonomically rare taxon, and secondarily to be an endemic taxon. “Objects” are areas, and the focus is on the gain in rare or endemic taxa (units) when one or more areas (objects) are added to a set of areas. Furthermore, Faith et al. wrote that “. . . a ‘pattern’ of some kind defines relationships among the objects, enabling predictions of gains at the unit level.” If for both methods the pattern is phylogeny, Posadas et al. also considered the biogeographic pattern.

A problem with Faith et al.’s comparison arises from the example itself: the distribution of species they hypothesized is conflictive. In their example (Fig. 1), two species (e and f) were not assigned to any of the eight areas considered. If these two species were assigned to a hypothetical area 9, the results for the Posadas et al. protocol would be different (Table 1 in Faith et al. and Table 1 in this paper). The maximum value of  $W_e$  still corresponds to area 1, and the complementarity values are not affected. But now, according to the Posadas et al. protocol, the second priority will be given to area 9, which presents the highest  $W_e$  score among those areas with a maximum complementarity value related to the first area selected. In such a scenario, one can observe in the hypothetical cladogram (Fig. 1) that the set formed by areas 1 + 9 allows protection of the basal clade of the whole cladogram and a sample of the basal taxa within the second clade. Also, areas 1 + 9 allow conservation of five taxonomically rare taxa, four of which are endemic to

Table 1. Posadas et al.’s protocol for data from Fig. 1 of Faith et al. (2004 [this issue]).

Areas	$W_e^a$	Richness (%) <sup>b</sup>	Endemicity (%) <sup>b</sup>
1	8	3 (21.43)	2 (14.29)
2	7.14	4 (28.57)	3 (21.43)
3	1.33	2 (14.29)	0 (0.00)
4	1.14	2 (14.29)	0 (0.00)
5	1	2 (14.29)	0 (0.00)
6	1.33	2 (14.29)	0 (0.00)
7	1.14	2 (14.29)	0 (0.00)
8	1	2 (14.29)	0 (0.00)
9	5.33	2 (14.29)	2 (14.29)

Complementarity areas	1	2	3	4	5	6	7	8
2		0.833						
3	1	1						
4	1	1	1					
5	1	1	1	1				
6	1	1	0	1	1			
7	1	1	1	0	1	1		
8	1	1	1	1	0	1	1	
9	1	1	1	1	1	1	1	1

<sup>a</sup>The  $W_e$  is the  $W$  index of Vane-Wright et al. (1991) modified to include endemicity.

<sup>b</sup>Richness and endemicity values are in absolute numbers and percentage.

those areas. This result is in agreement with the requirements claimed by the Posadas et al. method.

Even when a hypothetical example could be useful to illustrate the properties of a given method, it could result in unlikely statements. For example, the biogeographic distributions hypothesized by Faith et al. in their example are highly unlikely, and therefore the resulting biogeographic scenario is also unlikely (for a detailed introduction to historical biogeography, see Crisci et al. 2003). The application of dispersal and vicariance analysis using DIVA 1.2 (Ronquist 1996) to Faith et al.'s hypothetical example results in 162 alternative, equally optimal reconstructions for the ancestral distribution at each node. Such a result indicates biogeographic incongruence (Fig. 1). This makes their example highly problematic because Faith himself postulates as follows: "However, it is clear that consideration of phylogenetic diversity values alone can be misleading, especially where there is no underlying history of vicariance or there are differences among areas in rates of evolution or lineage sorting that affect several of the species assayed" (Moritz & Faith 1998:426). That means that phylogenetic diversity results are only understandable in an appropriate biogeographic context.

There exist some additional problems with the definition of the phylogenetic diversity index. We will not discuss these problems in detail here, but only enumerate them: (1) when data sets (on which cladograms are based) are used to evaluate branch lengths, it is possible that two different data sets (e.g., morphological and molecular) will result in different estimates for the same branch; (2) when dealing with polytomous cladograms it is necessary to decide whether polytomies will be considered hard (multispeciation events) or soft (artifacts due to lack of data) (Coddington & Scharf 1994, 1996), and this decision determines how the information contained by the polytomy will be handled.

## On Applications

Faith et al. applied phylogenetic diversity to a real data set (their Fig. 2). They defined the area units "arbitrarily": a 25-km radius around a midpoint of the sample record. Such an area definition disregards the relevance of biogeographic information claimed by Faith himself and with which we agree (Moritz & Faith 1998). The definition of *area* and *area of endemism* is critical to biogeographical thinking (Henderson 1991; Platnick 1991; Morrone 1994; Szumick et al. 2002; Crisci et al. 2003). This is not a trivial criticism; a different area definition could give a different result.

If we set this criticism aside for a moment—because it is not relevant to comparing the methods in a particular example when considering their properties—and apply the Posadas et al. method to the real case studied by Faith et al. (Table 2), we should select area 4 as the first area to be

**Table 2.** Method of Posadas et al. applied to the real case of Faith et al. (their Fig. 2) (2004 [this issue]).

Areas	$W_e^a$	Richness (%) <sup>b</sup>	Endemicity (%) <sup>b</sup>	Endemicity/richness	
1	20.60	22 (34.92)	10 (15.87)	45.45	
2	16.22	26 (41.27)	5 (7.94)	19.23	
3	9.20	15 (23.81)	4 (6.35)	26.67	
4	22.55	26 (41.27)	8 (12.70)	30.77	
5	19.51	26 (41.27)	7 (11.11)	26.92	
<i>Complementarity areas</i>		1	2	3	4
2		0.667			
3		0.724	0.633		
4		0.857	0.762	0.861	
5		0.829	0.732	0.829	0.556

<sup>a</sup>The  $W_e$  is the  $W$  index of Vane-Wright et al. (1991) modified to include endemicity.

<sup>b</sup>Richness and endemicity values are in absolute numbers and percentage.

preserved. Then, given complementarity, the second area should be area 1 or 3. Because area 1 presents a higher value of  $W_e$  than area 3, we would prefer area 1. Table 3 summarizes the corresponding phylogenetic diversity values for each area and for each set of two areas. Areas 4 + 1 behave well not only for the Posadas et al. protocol, but also when endemicity\* is considered as well (Table 4). Only in these two areas is endemicity\* higher than endemicity (endemicity value for areas 5 + 1 is 17, whereas endemicity\* is 18; for areas 4 + 1 endemicity is 18, whereas endemicity\* is 20); we do not know whether this is an instrumental situation or a real "indicator" (Table 2 in Faith et al.). Additionally, areas 4 + 1 have the highest values of endemicity and richness (Table 2).

Faith et al. postulate that "Areas 1 and 5 form the best set of two areas for phylogenetic diversity [PD] representation (92 units)." If we select areas 1 + 5, we may have the highest phylogenetic diversity value (92 units), but we are not conserving as much as with areas 4 + 1 in terms of endemicity\*, either of taxonomic distinctness, endemicity, or richness (Table 2). However, the phylogenetic diversity value for 4 + 1 is as high as 91 phylogenetic diversity units (Table 3). So we must ask ourselves two questions: (1) Even when endemicity, taxonomic distinctness, or richness should not be considered in the context of the phylogenetic diversity index, as is not the aim of Faith's method, is a one-unit difference in the phylogenetic diversity index so significant that other factors, such as endemicity\*, can be disregarded? (2) Is the statement postulated by Faith et al. in the introduction—"any application of their proposed methods [the Posadas et al. protocol] could be detrimental to biodiversity conservation"—correct or even likely? The results summarized in Tables 2 and 3 reject Faith et al.'s statement because the Posadas et al. protocol allows one to select (as the first two

**Table 3. Phylogenetic diversity values and complementarity\* recalculated for Fig. 2 of Faith et al. (2004 [this issue]).**

	A	B	C	D	E	F <sup>b</sup>	G	H	I	J	Total
<b>Areas</b>											
1	6	4	5	7	5	3	3	9	11	8	61
2	8	3	3	5	7	5	6	7	14	9	67
3	8	3	4	5	0	5	4	7	4	5	45
4	8	5	3	2	6	6	3	11	13	8	65
5	9	8	3	5	4	6	6	7	11	8	67
<b>Set of areas</b>											
1+2	8	5	5	7	8	5	8	9	15	13	83
1+3	8	5	6	8	5	5	6	9	11	10	73
1+4	9	8	7	7	8	7	4	13	15	13	91
1+5	10	9	7	8	7	7	8	9	14	13	92
2+3	8	3	5	7	7	5	7	7	14	10	73
2+4	10	7	5	5	8	8	8	12	16	11	90
2+5	11	9	5	6	8	8	7	7	15	11	87
3+4	10	7	6	5	6	8	6	12	13	9	82
3+5	11	9	6	7	4	8	7	7	11	9	79
4+5	9	9	4	5	6	6	8	12	14	9	82
<b>Complementarity* areas</b>											
				1			2		3		4
2				83							
3				73			73				
4				91			90		82		
5				92			87		79		82

<sup>a</sup>The calculus was made for individual areas 1 to 5 and for each set of two areas. Letters correspond to each of the phylogenies of Faith et al. (2004 [this issue]).

<sup>b</sup>Cladograms containing a polytomy.

priorities) areas with the highest endemism, taxonomic distinctness, complementarity, and endemism\*, losing only 1 phylogenetic diversity unit relative to the choice of Faith et al. In other words, if the Posadas et al. method is detrimental to biodiversity conservation, then the same is valid for the phylogenetic diversity index. We are conscious that this comparison is only appropriate at the example level. A sound and valid comparison must be made using a broader number of real data sets that include as many real situations as possible to determine whether there is a consistent incongruence between the two approaches.

As a final statement, Faith et al. say that they "... have demonstrated that, although Posadas et al. properly argued for an integration of 'phylogenetic diversity' with complementarity and endemism, only phylogenetic diversity [Faith's phylogenetic diversity index] achieves this in a way that allows our knowledge of evolutionary history to serve biodiversity conservation." We strongly disagree with this statement. First, they did not demonstrate that phylogenetic diversity, complementarity\*, and endemism\* behave better than taxonomic distinctness, endemism, or richness. They simply showed that the phylogenetic diversity index, complementarity\*, and endemism\* behave well in their own context as surrogates of the phylogenetic diversity definition, whereas

complementarity and endemism behave well in the context in which they were defined—as attributes of the areas and not as a feature of the species in the areas. Second, the hypothetical example they use is biogeographically unlikely, and biogeography is a required framework within which to discuss diversity. A sound comparison must be made using a broader perspective, and the comparison must be epistemologically and biogeographically anchored, to show where the discrepancies and similarities arise and to demonstrate the conditions of that behavior. Third, because Faith et al. believe that "only phylogenetic diversity" achieves biodiversity conservation in a way that our knowledge of its history is useful, it is necessary to know whether Faith's phylogenetic diversity index explains (or does not explain) more in terms of complementarity\* and endemism\* and in terms of taxonomic distinctness, richness, endemism, complementarity, and all other biodiversity features that could be reflected by evolutionary history.

It is obvious that we need a strong tool with which to evaluate biodiversity so that we can use its information in making conservation decisions. An integrative approach based on phylogenetic as well as biogeographic information must be the *desideratum*. The method we presented in Posadas et al. (2001) is a possible way to rank areas based on that kind of information. There are, and there will be, many analytical tools with which to evaluate areas, given the species and the information derived from their history. We need sound comparisons to evaluate the comparative behavior of these tools, along with solid epistemological tools to understand present diversity and the ways to preserve as much of it as possible.

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## **Queries**

**Q1** Author: Please spell out "UIS" in full.

**Q2** Author: Please spell out "UIS" in full.

**Q3** PE: Faith et al. will need pp. nos. put in at proofs.