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Environmental diversity (ED) as surrogate information for species-level biodiversity

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This paper is a response to an earlier Forum paper (Araújo et al. 2001) that posed the question, “would environmental diversity be a good surrogate for species diversity?” This issue of surrogacy is critical to biodiversity conservation planning, where representative networks of protected areas are to be identified using surrogate information as a substitute for complete species inventories over all areas (for review see Margules and Pressey 2000).

Araújo et al. used an extensive European data-base for vertebrate and plant species (indicating distributions of 3063 species over a total of 2089 areas) to examine whether representation of environmental variation (referred to as “ED”) could effectively represent species level diversity. The count of the number species represented when selecting optimal sets of areas under an ED criterion did not match that achieved when the species data were used directly to find representative sets of areas. Further, the level of species representation using ED often was not significantly different from the level obtained by selecting the same number of areas randomly. The study concluded that there was “only weak support for the idea that representative samples of environmental-space are also representative of species diversity”, and that “ED should be used only when its surrogacy value has been empirically demonstrated.”

Here, I will discuss alternative, positive, perspectives on the potential for ED to provide surrogate information for biodiversity. First, I will suggest that Araújo et al.’s results for ED actually are very encouraging. Their ED-based recovery of species diversity may have underestimated potential true recovery in this context, and, in any case, compares well to published evaluations of species-based surrogates. Second, I will suggest that the ED framework helps shift the surrogates problem from the perspective of environmental versus species data to

a broader perspective concerning how to make best-possible combined use of all available information.

“ED” and “environmental diversity”

Discussion of the role of “environmental diversity” as surrogate information requires clarification of that term. Initially, Araújo et al. used “environmental diversity” and the abbreviation “ED” to refer to any measure of environmental diversity employed as an environmentally-based surrogate (p. 103). However, in the main body of their paper, a specific “ED” procedure was applied that is based on a form of p-median optimization (for review of p-median applications, see Church 2002). This procedure therefore links directly to the p-median strategy for measuring environmental diversity that Faith and Walker (1996a, b and references within) developed and referred to as “ED”.

Faith and Walker’s ED approach was designed for conservation priority-setting through estimates of complementarity (the marginal gain in biodiversity when an area is added to a protected set) and of relative species-richness of sets of areas. ED typically is based on a pattern-representation of the areas in a region, called an ordination (Gauch 1982). That ordination pattern might be derived from environmental descriptions, from species data, or from a combination of these.

Robust ordination models assume that species have general unimodal “responses” in ordination space (e.g. Gauch 1982); high abundance of any given species is concentrated in some portion of environmental space. Based on this model, larger distances between areas in the space imply greater species composition differences. Further, a subset of the areas will have greater species diversity if the subset spans (represents) the space well

(Faith and Walker 1996a). The complementarity of an area added to a subset is large if it could fill a “gap”, such that the new subset would better span the space.

The ED method links such a representation of environmental space to the general “p-median” problem from operations research (e.g. Tansel et al. 1983). A p-median criterion seeks to minimise the distance from each “demand point” to its nearest selected “location”. For example, using the p-median, the best set of p fire station locations is the one minimising average travel distance to the houses (demand points) in the region. Replacing that map with an ordination space, the “locations” are to be selected from among the region’s candidate geographic areas, and the “demand points” are distributed uniformly throughout the ordination space that is to be represented. Thus, the environmental/ordination space is viewed as well-represented by a subset of areas if it produces a small sum, over all demand points in the space, of the distance from each point to its nearest selected area. That sum indicates the amount of diversity “forgone” by a selected set of (protected) areas. Under a simple model assuming unimodal species responses to environmental gradients, the number of species sampled will be maximised if and only if the set of areas is selected using this p-median criterion (Faith and Walker 1996a). While the basic model for ED assumes uniform unimodal responses, the p-median can be modified to take into account model-variations concerning differences in species richness and distributions of species “range sizes” in different parts of the space (Faith and Walker 1996a).

Two alternative forms of p-median underlying ED can be distinguished. The “continuous p-median” form of ED (Faith and Walker 1996a) refers to that case where the demand points are hypothetical points distributed uniformly throughout the continuous environmental space. The “discrete p-median” form of ED (Faith and Walker 1996a) simply defines each of the candidate areas as a “demand point”. Thus, in the discrete case, the demand points may well be clumped in ordination space. This clumping may reflect missing environmental factors that would have better distinguished among the areas, or may simply reflect the geographic frequency of environmentally-similar areas. Selection of areas using the discrete p-median form of ED therefore may not represent the environmental/ordination space uniformly.

Applications of ED have adopted the continuous p-median form of ED for this reason, and because: 1) the proof that p-median maximises number of species, under the unimodal response model, was restricted to the continuous case, and 2) an example analysis illustrated how the discrete, but not continuous, p-median would fail to maximise the number of species (Faith and Walker 1996a). The continuous p-median version of ED was applied in an early regional case study (Faith et al. 1996) and in a simulation study examining

surrogates (Faith and Walker 1996b). Current area-selection methods using costs trade-offs (Faith et al. 1996) and probabilities of persistence (Faith and Walker 1997) had their genesis in the context of the continuous p-median form of ED (Faith 1995). Additional conservation applications of the continuous p-median version of ED are found in (Faith 1996, 1997).

This distinction between continuous and discrete forms of ED will help in interpreting the apparent poor performance of ED in Araújo et al.’s study.

A positive perspective on Araújo et al.’s evaluation of “ED”

One of the key results in Araújo et al.’s evaluation of ED was the recovery/representation of 83% of database species (plants, birds mammals, and amphibians) in 211 areas selected by the ED criterion (ca 10% of all 2089 areas). This was slightly more than the 80% or greater recovery that could be achieved 5% of the time with random area selection. I interpret these species recovery results as quite favourable to the prospects for applications of ED based on environmental data. To develop this alternative perspective, I will examine Araújo et al.’s results based on: 1) their specific implementation of the ED method, 2) species sampling for the European data-base, 3) a comparison of ED’s performance in their study with the performance of species surrogates in other published studies, and 4) the role of randomizations in evaluating biodiversity surrogates.

1) Implementation of the ED method

Araújo et al.’s implementation of ED may have resulted in an under-estimation of the method’s potential recovery of European species diversity. Araújo et al. did not refer to the different forms of ED and the case studies indicating preferred use of the continuous form; nevertheless, it is apparent from Araújo et al.’s p-median formula (p. 104) that their application of ED was equivalent to the discrete, not continuous, form. Consequently, the “representative samples of environmental-space” that Araújo et al. correctly emphasized as fundamental to ED were lost to some degree by the clumped sampling of areas resulting from application of the discrete p-median (see their Fig. 2). ED theory predicts that species representation consequently might be reduced.

Araújo et al.’s use of only six environmental variables as input to ED may be another limitation of their implementation of ED, given that an effective surrogate for biodiversity may depend on environmental data that capture many different gradients (DeVellece et al. 1988, Faith and Walker 1996b). Further, in adopting

only the first two PCA axes derived from these six variables, Araújo et al. accounted for only 71% of observed environmental variation. Araújo et al. did suggest that using more dimensions from the PCA space might have improved ED results. But there is also a potential need for additional measured environmental variables as inputs to such an ordination analysis. Sarkar and colleagues (reported in Garson et al. 2002) found recovery of vertebrate species based on sets of areas selected using environmental data was ca 80% for individual classes of environmental data, but increased to 86% for combined use of all environmental data. The incorporation of only limited environmental variation into ED will limit the representation of species.

These arguments suggest that the level of species recovery in Araújo et al.'s tests (e.g. 83% of database species for 211 selected areas) may be a conservative estimate, relative to more effective implementations of ED.

2) Species sampling

In evaluating ED, not only environmental sampling but also species sampling can affect estimated species recovery. For the European database, some species inevitably would have been recorded at < 100% of all areas where they were truly present (e.g., Huntley et al. 1995 provides examples for European species where predicted distributions extend the recorded species-records). In contrast, the nominated environmental data was recorded/calculated for all areas. This creates a natural bias in measures of correspondence between the environmental data and species records. An area selected to capture environmental variation may not have all species recorded (among the set of 3063 species) that are actually present. The species recovery over these taxonomic groups consequently would be underestimated. While the sampling adequacy of species records no doubt varies widely among the 3063 species, these arguments suggest again that the calculated 83% recovery by ED is, to some unknown extent, an underestimate of the true recovery of diversity over these taxa.

3) ED performance compared to that for species surrogates

The methodological and sampling perspectives presented in the previous sections indicate that ED's recovery for the European species data may be an under-estimate. Nevertheless, even this conservative recovery estimate compares favorably with the performance of species-based biodiversity surrogates in other studies.

Such a comparison of ED with species surrogates represents a shift in perspective from Araújo et al.'s study, which did not compare ED recovery to the use of species as surrogates. I consider the use of surrogate data, whether abiotic, biotic, or a combination of both, to be inevitable in conservation planning, because all species making up biodiversity will never be completely recorded over a set of areas. In accord with this perspective, published studies (see below) have examined taxonomic groups as surrogates in recovery tests in order to suggest what average recovery might be like for the many unobserved species making up total biodiversity.

An analysis of the European database might have contrasted ED recovery of any one target taxonomic group with the recovery of that target group by surrogates based on other taxonomic groups (e.g. comparing recovery of plant diversity based on ED sets to the recovery of plant diversity based on areas selected using birds). In the absence of these comparisons, it is informative to briefly consider the performance of species-based surrogates in other studies where surrogate-based sets of areas are evaluated in terms of recovery of one or more other taxonomic groups.

ED was compared to a species-based surrogate in an early example (Faith and Walker 1996b) of diversity-recovery tests based on surrogate-defined sets of areas. Based on simulated data, a species-based surrogate's recovery of other species was not as good as that of ED based on environmental data. Real-world case studies using species surrogates similarly are revealing in documenting species recovery comparable to the 83% for ED in Araújo et al.'s study. For example, Fleishman et al. (2001) found that "conservation of subsets of locations with relatively high numbers of umbrella species, generally would protect > 0.75 of each assemblage." That result was based on an indicator carefully selected for its indicator value. Pharo et al. (2000) found that a set of areas that reserved 90% of vascular plant species captured only 65% of bryophyte species and 87% of lichen species. Garson et al. (2002) found that < 40% of target species were represented in their minimum sets of areas based on species of birds. Andelman and Fagan (2000) found < 30% of target species were represented by the minimum sets of surrogate species. Even when 10% of total area was selected (comparable to the 211 out of 2089 areas in Araújo et al.'s study) by seeking multiple replicates of surrogate species, only ca 50% of target species were represented.

Some surrogates studies also have contrasted their results with those achieved for random sets of areas. A study by Howard et al. (1998) did not calculate upper 95% limits on random-sets recovery, but it was clear for plant species as surrogates that recovery of other species was less than mean random recovery. Other species surrogates in that study produced sets of areas with recovery levels that appear to be less than the 95% level

for random sets. In general, the recovery levels did not exceed ED's 83% level. For example, for sets covering 20% of total area, there was at best 80% recovery of target species.

Lund and Rahbek's (2002) recent study allows interesting comparisons with that of Araújo et al. They similarly examined species recovery based on sets encompassing 10% of all areas, derived in their study using species-based surrogates. About 5% of the time, recovery (of diversity of the other taxonomic groups) at least as good was found under random selection. Viewed as a null hypothesis test, there was no significant difference from random.

Lund and Rahbek noted the potential problem of sampling artifacts (see also Howard et al. 1998), and so restricted their analyses to only those cells in which all taxonomic groups were recorded (only 124 out of > 600 cells). Their surrogate-based recovery values nevertheless may be inflated; this restricted sample of cells reduces the selection-availability of cells that are attractive for one taxonomic group but are naturally poor representatives of other groups.

4) The role of randomisations in evaluation of surrogates

While ED performs about as well in recovery tests as species-based surrogates, both kinds of surrogates sometimes produce recovery of target species that is not significantly different from that of random sets. It is not clear from the published contrasts with random sets exactly what the interpretation of such randomizations is to be. A non-significant departure from random (failure to reject a null hypothesis) might be interpreted as reason to dismiss the surrogate strategy, arguing that one could simply select areas at random. This may not be a fair conclusion, because the non-significance on its own does not indicate how often random sets would better the surrogate. An analogy with the conventional use of null hypothesis testing to detect ecological impacts is useful. The idea of confidence limits on "effect sizes" can be extended to the surrogates context; a good surrogate will indicate a large "effect size". Imagine that repeated application of a biodiversity surrogate would provide recovery results distributed around some true mean recovery effect size. We can ask how large an average effect size, "e", attributed to the surrogate is warranted, given our observed recovery value of, say, 83% (for examples of similar post-test inference, see Mayo 1996 and Fig. 12.2 in Downes et al. 2002). Asserting any greater true effect size than e would not be warranted because it would make the actual observed recovery value appear quite improbable (say, probability < 0.05). Thus, a poor observed recovery does not warrant characterising the surrogate as having any large mean recovery. This post-test inference indi-

cates the possible advantage, relative to random selection, provided by a given surrogate.

A related rationale for examining random sets is that non-significance might be interpreted as strong evidence that there is no predictive, surrogate, relationship. This perspective might lend support to Araújo et al.'s conclusion, in light of some non-significant departures from random, that "ED should be used only when its surrogacy value has been empirically demonstrated." I agree with Araújo et al. that surrogates strategies need to be investigated, but wish to introduce a different perspective on the interpretation of such non-significance. From this perspective, we are concerned with testing an hypothesis that surrogate strategy "x" is an effective surrogate for biodiversity in the context of conservation planning. It follows that a degree of recovery of the diversity of test taxa, by a set of areas selected using "x", can be viewed as one form of positive "evidence" for that hypothesis. If evidence that good is assessed as improbable by other, alternative, explanations (e.g. an explanation that says that the set of areas could just as well have been selected randomly), then that evidence provides corroboration for the hypothesis (Popper 1983; see also Faith 1999). On the other hand, if the positive evidence appears to be not so improbable (e.g. 5% or more of the time we could get the observed recovery even with random sets of areas), then there is little corroboration of the hypothesis from that particular evidence.

Such corroboration assessment of the evidence for surrogates can take different forms. Randomizations are just one strategy to try to "explain away" apparent good evidence. For example, one of the studies cited above illustrates how recognition of sampling bias could identify high recovery values as probable even for a weak surrogate. Another example of explaining away evidence is through a determination that the test set of taxa is biased in some way (say, having some dependence on the surrogate data that is absent in general for other components of biodiversity).

In this context, the form of the evidence itself is an issue. Early surrogates studies examined surrogates prediction of test-species richness of individual areas. However, this supposed evidence was seen to have little bearing on the success of the surrogate in biodiversity planning (see Faith and Walker 1996b). Thus, prediction-of-richness as evidence could be explained away as sometimes arising even for ineffective surrogates.

Evidence (e.g. recovery value) that has not been "questioned" in this way (and survived the questioning) cannot corroborate an hypothesis of surrogacy. But a surrogate that so far has produced only evidence that has been explained away cannot be labeled a useless surrogate. It does not mean that we have evidence against the surrogacy hypothesis. Low corroboration based on the current evidence, as found for ED and species-based surrogates, does not warrant a conclusion

of no surrogacy value. Other evidence may corroborate that same surrogacy hypothesis.

This perspective is important given that a failure to gain corroboration can arise simply through evidence derived from weak data or weak implementation of the surrogate method. For example, underestimating the variation for any surrogate (e.g. using only 10 butterfly species out of a total of 100 species as surrogate information) will tend to make the corresponding recovery results appear more like those for purely random sets of areas.

Environmental data provide a recent, real, example. In a study of Panamanian biodiversity patterns (Duivenvoorden et al. 2002), there was weak evidence of environmental surrogacy (only 41% of species turnover was explained by environment). However, improved analysis of the same data explained 84.4% of species turnover, and associated significance testing of this new evidence providing corroboration of this surrogacy value (Faith and Ferrier 2002). That corroboration of environmental surrogacy countered the general conclusion (Duivenvoorden et al. 2002) that environmental data had little value for predicting biodiversity patterns in the tropics.

From this perspective, poorly-corroborated environmental and biotic surrogates may have to be used even as we seek further evidence for their evaluation. This perspective on evaluating surrogates therefore directs our efforts in two ways. We try to avoid accepting at face value evidence for a surrogacy hypothesis that, if properly questioned, could be explained away. But also we must try to avoid only putting forward, and explaining away, weak evidence. We must try to find strong evidence for the surrogate when this is available. The hypothesis that (e.g.) butterflies are a good surrogate in practice for biodiversity may gain no corroboration if the only evidence put forward were based on even very good prediction of species-richness of areas.

Similarly, recovery of diversity from surrogate-defined optimal sets of areas (as in the many studies cited above) may not be the best form of evidence. One concern is that such computer-generated sets of areas don't relate well to actual success in practical planning. While the paradigm of systematic, computer-based, selection of sets of protected areas has attracted much academic interest for more than a decade (see Margules and Pressey 2000 for review), to my knowledge, there is not a single example in the real world of such a selected set actually being implemented as a protected area system. There may be little justification for using such computer-generated sets as evidence for practical surrogacy effectiveness.

A form of evidence better linked to real world applications may be a measure of the surrogate's success at predicting, in any context, the true biodiversity complementarity value of a given area (Faith and Walker 1996b). However, the success of such evidence may

depend on the interpretation of "complementarity". Howard et al. (1998) explicitly built on Faith and Walker's (1996b) call for surrogates that "predict complementarity", but they adopted a notion of "complementarity" equal to calculated compositional dissimilarity between pairs of areas (rather than the marginal biodiversity gain offered by one area relative to a set, as in Faith and Walker 1996b). This dissimilarity-based measure can be misleading as a basis for adding areas to sets in order to increase represented biodiversity (Faith and Walker 1996a), and so may not be a good basis for corroborable evidence for effective surrogates. In accord with this view, Lund and Rahbek (2002) concluded that evaluations of dissimilarity-based "complementarity" were not informative about surrogacy.

The past and the future in ED development and evaluation

I have discussed how ED and species-based surrogates may not have their surrogacy value easily "demonstrated" because even a good surrogate may not be corroborated from currently available evidence. I don't intend this as a negative perspective. Instead, I see this evaluation process as a constructive pathway for the development of better surrogates. The ED method is best seen in its originally intended role as a basis for improving surrogacy value from environmental and biotic data, rather than as one fixed approach (see Faith and Walker 1996a, b). It will be constructive to ask (using randomization or other approaches), which variations on ED allow inference of a better surrogacy "effect size"?

This positive perspective on the investigation of surrogacy is highlighted by the response to the earlier randomization tests on ED carried out in Australia. Araújo et al. stated that some early Australian studies using environmental surrogates "did not question whether this would represent biodiversity at a rate higher than expected by chance," but this should not leave the impression that this issue had been ignored in previous work. Those cited studies were preceded by Australian colleagues' work on just this question (Ferrier and Watson 1997; summarised also in Garson et al. 2002). Ferrier and Watson (1997) pioneered the randomization-based evaluation of surrogates in which sets of areas selected by a surrogate are compared, in terms of some optimality criterion (say, recovery of a target set of species), to sets of the same size selected at random. Their study was the first to report that ED based on environmental data may produce recovery values no better than those of random sets. However, this result has not led to a conclusion that ED not be used until its value is "demonstrated". In N.S.W.,

Australia, the same workers at National Parks and Wildlife Service (NPWS) now have selected >4000 biodiversity survey areas based on ED estimates of complementarity (Ferrier pers. comm.). More generally, NPWS has endorsed the essential use of abiotic data in practice for assessing representativeness of protected areas (Pressey et al. 2000).

The interesting consequence of those early evaluations of ED is the follow-up Australian research on environmental surrogates. The same workers who explored randomizations have since investigated how ED may help in the development of surrogacy strategies that effectively use both available environmental and species data (following Faith and Walker 1996a, b). As one candidate strategy (Ferrier et al. in press) environmental “distances” among selected areas are used to explain species turnover (summarised as pairwise dissimilarities among these areas). This special regression model then allows prediction of dissimilarities among all areas in a region, derivation of an ordination for the region, and application of ED for subsequent biodiversity planning (see Faith and Ferrier 2002 and references within). In this way, ED may provide better surrogate information from available biotic and abiotic data.

The surrogacy issue therefore is not about species data versus environmental data. I see ED, not as a way to use environmental data to replace species data, but as a possible pathway to the best use of species records from museum collections (Faith and Walker 1996a, b). How that is best accomplished remains a research question. This perspective contrasts with the question posed in the title of Araújo et al.’s study: “would environmental diversity be a good surrogate for species diversity?” I encourage others to also consider the question implied in the title of our original paper: how does ED help us make “best-possible use of surrogate data”?

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