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Why ecologists need to be phylogenetically challenged

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Why species?

Westoby *et al.* (1995) define a comparative dataset as 'a table with present-day species as rows and attributes as columns'. Why species? Why not individuals? At first glance, individuals would be a much better choice, since one would then have an enormous dataset. The reason why not is that we are generally not interested simply in description. For example, the empirical generalisation that large seeded species are more likely to establish in small gaps is only interesting if one entertains the idea that seed size is relevant to where a plant can establish. Deciding to enter species in the comparative dataset instead of individuals is based on the recognition that individuals do not provide independent items of information for the evaluation of a hypothesis. Similarly, species do not provide independent information: related species share, for example, many ecological factors in addition to those under study. Until Westoby *et al.* provide a persuasive argument that species values are independent, then their railing against PC is no more audible than the squeaking of a mouse in a hurricane. PC is a constructive attempt to extract information from non-experimental data which is riddled with non-independence (Nee *et al.*, in press).

Revealing the truth

When the entirely analogous problems of pseudo-replication were uncovered in ecology (Hurlbert 1984), many beloved 'conclusions' became suspect. But there is no doubt that more rigour gives a deeper insight into the natural world. Similarly, PC will inevitably but correctly conclude in many cases that comparative evidence alone is insufficient for the evaluation of a hypothesis. However, a phylogenetic lens can reveal features of the world that would otherwise be invisible. Take an example. When we examined population density and body size in birds we, like others, found a negative relationship across all species (Nee *et al.* 1991). But when we took a phylogenetic perspective, we discovered positive relationships within taxa! Ecologists had recorded bird abundances for centuries without suspecting positive relationships with body size. We suggested an explanation for this novel finding which has been supported by subsequent work using experimentally manipulated populations (Cotgreave 1994).

Confounding variables

The phylogenetic representation of a data set may not only reveal unsuspected patterns, but it also provides a way of dealing with confounding variables. Again the problem of inference comes to the fore. Closely related species are similar morphologically, behaviourally, developmentally and ecologically. If we are examining variation in a trait, such as seed size, across species and we wish to infer anything about the reasons for differences in seed size, we are faced with the fact that more closely related species will be more similar in seed size and in other variables that are both relevant and irrelevant to the reasons for the origin and maintenance of species differences in seed size. Westoby *et al.* fail to appreciate that phylogenetic niche conservatism means that adaptations to different components of the niche (for plants this might be soil type, temperature tolerance, seed size, life history characteristics, anti-herbivore defence mechanisms, and so on) will be correlated; rational inference about the importance of any one of them is only possible within a phylogenetic framework. Analyses which compare independent evolutionary differences in seed size automatically correct, to a large extent, for all other confounding variables (both known and unknown) which are not directly associated with evolutionary differences in seed size. Westoby *et al.* should realise that the best modern comparative analyses, such as those performed by independent contrasts, utilise all the relevant information available – the tests are not conservative.

Riddled with errors

We now progress through some other errors in the article.

- *Only after variation correlated with phylogeny has been extracted, is residual 'corrected' variation analysed and later PC gives priority to phylogeny over ecology as a correlate of trait variation.* Wrong. Most recent comparative methods, such as contrast analyses, merely partition the variance so that degrees of freedom are biologically meaningful. Over a decade ago, some authors, particularly those using phylogenetic subtraction and phylogenetic autocorrelation methods, may have removed a phylogenetic component and discarded it as nonadaptive before residual analysis. Harvey & Pagel (1991, p. 137) warned against doing this. Contrast analysis for two variables produces plots in which all the variation in the data set in one variable is graphed against all the variation in the data set in the other variable; there is no extraction of

'variation correlated with phylogeny', whatever that may mean.

- *As Williams gently puts it, similarities need not imply phylogenetic constraint.* Of course not. But whatever the reason related species are similar (for example, because they experience a huge number of similar ecological factors) the character state of a species is not independent of the state of related species. Hence pseudoreplication results unless the analysis of species values uses a phylogenetic framework.

- *Harvey and Pagel's book consistently gives priority to phylogenetic constraint as an explanation ... PC gives priority to phylogeny over ecology as a correlate of trait variation.* The expression 'phylogenetic constraint' is not used in the book, and at no point is phylogeny given priority over anything. However, a sound basis for inference is given priority over analyses based on pseudoreplication.

- *PC first arose as an understandable reaction to naive versions of the 'adaptationist programme' (Gould & Lewontin 1979).* Phylogeny was taken into account long before Gould and Lewontin's onslaught. It seems quite natural for research biologists to incorporate such reasoning into cross-taxonomic comparisons. For example, Darwin (see Ridley 1992), Salisbury (1942), and even Clutton-Brock & Harvey (1977) independently realised that species could not be used as independent points in an ecological analysis.

- *Interpretation, not statistics, is the crucial step.* This is a value judgement: how do you test your interpretation without statistics?

- *Research agenda of comparative ecology.* Westoby *et al.* are presenting a goal but attempting to block off the major route for achieving it.

- *Redefinition of 'adaptation'.* The definition used by Harvey & Pagel (1991) is in accord with general usage in evolutionary biology. If authors use the same words to mean different things, confusion arises; adaptation is such a word. The points made in the first three paragraphs of this reply hold whether one is attempting to make inference about the origin of a trait difference or its maintenance.

- *Recommendations for evolutionary ecologists ... quantify each of the three components of variation.* For-

tunately, comparative biologists have progressed beyond such procrustean procedures.

Conclusion

There are various reasons why closely related species might be similar as is made explicit by Harvey & Pagel (1991). Phylogenetic niche conservatism is one such reason. The problem of rational inference from non-independent data remains however the similarity arises. That two related species share a character state does not provide two pieces of independent evidence that a particular ecological attribute is responsible: the species share many other attributes as well.

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