

# On misinterpreting the ‘phylogenetic correction’

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## Introduction

The last 10 years have seen important advances in methodology for taking phylogeny into account when analysing a comparative dataset. This commentary is about a class of interpretive procedures associated with these new statistical methods. We will call the interpretive logic ‘phylogenetic correction’ (PC for short), because this phrase summarizes the approach. Our essential message, however, is that a PC procedure is not in fact a ‘correction’, an adjustment to remove errors. Rather, it is a conceptual decision to give priority to one interpretation over another. Accordingly, it is an error to believe that PC is a methodology that must routinely be applied in all comparative analyses.

The present Forum was proposed by the Editor during the review process for a paper about comparative ecology of seed mass (Leishman *et al.* 1995; see p. 517). Accordingly, examples will be drawn from the literature on seed mass, but the points made would be true of many species attributes.

By ‘comparative dataset’, we mean a table with present-day species as rows, and attributes as columns. Some columns describe phylogenetic relations among the species, and others describe present-day attributes affecting the ecology of each species. Ecological attributes may include both those recording the behaviour of species in the field, such as capacity to establish in small canopy gaps (Kelly & Purvis 1993), and those that would be manifested even in glasshouse or garden, such as seeds per carpel (Hodgson & Mackey 1986). The analyses we are concerned with examine between-species variation in a focal ecological trait (here, seed mass), by investigating its correlation with other columns in the dataset.

## PHYLOGENETIC CORRECTION

Of the variation in a given trait (Fig. 1), some will be correlated with ecological attributes, some with phylogeny, and some will be uncorrelated with any other attributes in the dataset. There is almost always very substantial overlap between the portion of variation correlated with ecology and the portion correlated with phylogeny (Fig. 1; Mazer 1990; Peat & Fitter 1994; Lord *et al.*, in press). A phylogenetic correction first extracts variation in seed mass that is correlated with phylogeny. This can be done in various ways (Harvey & Mace 1982; Felsenstein 1985;

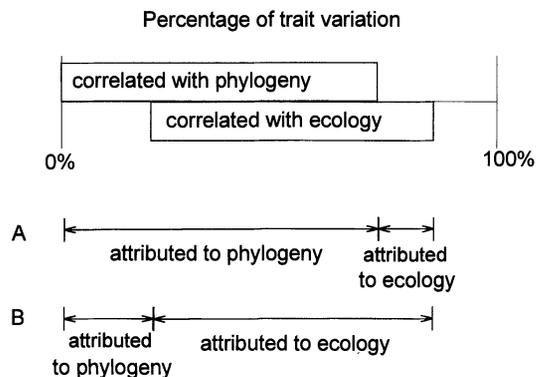


Fig. 1 Schematic illustrating percentages of variation between species in a trait such as seed mass correlated with phylogeny and ecology, and the two extremes (A and B) of the spectrum of possible attributions of variation. Extreme A is phylogenetic correction (PC).

Burt 1989; Grafen 1989; Mazer 1990; Harvey & Pagel 1991; Frumhoff & Reeve 1994; and many others), but the exact statistical method is not important for the purpose of this commentary. Only after variation correlated with phylogeny has been extracted, is residual ‘corrected’ variation analysed for its relationship to present-day ecology. PC therefore allocates the maximum possible variation in a trait to phylogeny, considering only the residual as potentially attributable to ecology (A in Fig. 1). PC is usually represented as statistically conservative, in the sense that it adopts a minimum estimate for the number of independent phylogenetic divergences for the trait. Actually, the allocation of trait-variation under PC corresponds to one extreme of the possible attributions of variation among different correlates. The other extreme (B in Fig. 1) would be to attribute the maximum possible variation to ecological correlates, leaving attributable to phylogeny only whatever residual could not be related to present-day ecology.

## HEGEMONY OF PHYLOGENETIC CORRECTION

As an abstract principle, it is widely accepted that the procedure for analysing and interpreting comparative data must depend on the evolutionary models being compared (Felsenstein 1985; Grafen 1989; Harvey & Pagel 1991; Herrera 1992; and others), and by implication that no single approach can serve all purposes. In practice, though, the belief seems to have become very widespread that PC should be automatic and obligatory. Harvey & Pagel (1991) illustrate this disjunction between conceptual discussion and practical data analysis. To quote Williams (1992, p. 103), Harvey & Pagel in their Chapter 2 ‘make

it clear that similarities among closely related phylads can result from similarities in selection pressures and need not imply any kind of phylogenetic constraint', but (as Williams delicately puts it) 'the implications of this concession for their main argument are not developed'. In fact, the methods and examples that occupy the remainder of Harvey & Pagel's book consistently give priority to phylogenetic constraint as an explanation. Publications in leading journals now describe PC as 'modern comparative methods' (Rees 1993), with the connotation that PC is a technical improvement rather than a conceptual decision.

This misconception about PC seems to have become very widespread, and is encountered predictably during questions after seminars or during the review of manuscripts. Although PC first arose as an understandable reaction to naive versions of the 'adaptationist programme' (Gould & Lewontin 1979), fashions seem now to have swung to an opposite extreme, and we hope this Forum contribution may help to restore some reasonable balance.

#### PHYLOGENY AND ECOLOGY ARE NOT MUTUALLY EXCLUSIVE INTERPRETATIONS: PHYLOGENETIC NICHE CONSERVATISM

PC gives priority to phylogeny over ecology as a correlate of trait-variation, and in so doing implicitly treats the two as mutually exclusive interpretations. But in reality, a dominant mode of evolution generates patterns of trait variation that are *both* correlated with phylogeny and *also* maintained by the selective forces of present-day ecology. The process has been well appreciated since Darwin, was contrasted with phylogenetic constraint by Grafen (1989), and was called by Harvey & Pagel (1991) phylogenetic niche conservatism, the phrase we adopt here. It works as follows: the ancestor of a lineage possesses a constellation of traits, enabling it to succeed in a particular habitat and disturbance regime, through a particular life history and physiology. The lineage will therefore leave most descendants in similar niches. This niche conservatism in turn will tend to sustain a similar constellation of traits in descendants of the lineage.

Because of phylogenetic niche conservatism, it is a fallacy to suppose that only variation uncorrelated with phylogeny can be interpreted in terms of present-day ecology. The question whether the patterns are correlated with phylogeny or not, does not help one way or the other in deciding whether the patterns are being maintained by present-day ecological competence. Phylogeny and present-day ecology should be thought of as complementary interpretative accounts, not as mutually exclusive components of trait-variation (Grime & Hodgson 1987).

How do we know phylogenetic niche conservatism is important in the real world? Ecologists are familiar with it in the vegetation dynamics that ensue when a habitat is modified, for example by fertilizing a low-nutrient soil, or by climate zones moving polewards following the last glacial maximum. It might be hypothesized that the veg-

etation changes that ensue would be driven by directional selection on lineages already present at the site. But in reality, vegetation change is dominated by the arrival from elsewhere in the continent of other species, that are more competitive under the changed habitat conditions. Thus a large part of the effect of habitat change is to redistribute existing lineages geographically, rather than to modify their attributes.

On remote oceanic islands, taxa that are normally herbaceous have radiated into niches for woody, longer-lived, larger-seeded species (Carlquist 1974). This breakdown of phylogenetic niche conservatism, in a situation where niches for woody, larger-seeded plants are not pre-empted by other lineages, demonstrates that it has not been intrinsic constraint that has kept the lineage herbaceous and smaller-seeded in the continental situation. It would be better to speak of the lineage having a predisposition or tendency towards smaller seed size, rather than a constraint.

#### INTERPRETATION, NOT STATISTICS, IS THE CRUCIAL STEP

Of course, it can always be argued that any given partitioning of variation is in itself value-neutral, merely obtaining information about correlation-structure in the data. What is crucial in PC is the interpretive step that follows the data-analysis procedure: all seed mass variation that is correlated *both* with phylogeny and with ecology, is attributed to phylogeny and this attribution is seen as precluding an attribution to ecology. For example, Hodgson & Mackey (1986) concluded that their 'data provide compelling evidence that seed weight ... is constrained by ... factors in addition to those of present-day ecology, in particular by features of floral morphology and embryology'. Note that they used the word 'constrained', even though their own data showed clearly that some species from smaller-seeded families had been able to evolve large seeds, and vice versa. At times, variation found to be correlated with phylogeny has been dismissed as if it did not exist. Kelly & Purvis (1993) applied PC to a dataset compiled by Foster & Janson (1985) showing association between larger seed size and capacity to establish in smaller canopy gaps. Their reanalysis showed that this association between traits had evolved within only five of eight separate evolutionary divergences, a useful refinement of Foster & Janson's analysis. But their key conclusion 'this data set does not support the hypothesis that large-seeded species are more likely to establish in small gaps' was simply factually incorrect. Large-seeded species were indeed more likely to establish in small gaps, whether or not that pattern was also associated with phylogeny.

#### SPECIES AS INDEPENDENT ITEMS OF EVIDENCE

A common way to formulate the argument for PC is to say that related species are not independent data points. Actually this is not a simple statement of fact, but rather a claim with embedded assumptions about how long ago the evo-

lutionary process under consideration occurred. Suppose two species within a genus have similar seed mass and similar plant height. To say that they are non-independent as items of evidence for a connection between seed mass and plant height, carries with it the assumption that the question being asked is about evolutionary processes that occurred before the lineages diverged. The implied claim is that the independent maintenance of those trait values in two separate lineages up to the present did not involve forces of natural selection, or that if such forces were involved we choose to define them as not being 'causes' of the present-day trait values.

#### TRAITS, TIME-SCALES AND THE CREDIBILITY OF CONSTRAINT

When present-day trait similarity between species is attributed to past common ancestry rather than to continuing evolutionary processes, the hypothetical machinery connecting past cause to present outcome is that intrinsic properties of the lineage constrain change over time. PC gives logical priority to the hypothesis that such machinery exists, over the hypothesis that selective forces in the present favour similar outcomes to those in the past. In reality, the credibility of phylogenetic constraint or phylogenetic inertia must depend very much on the trait and on the time-scales in question. For a quantitative attribute such as seed mass, considered over the tens of millions of years separating genera or families, the constraint hypothesis amounts to saying that even over such periods of time, out of all the mutations that arose that affected seed mass, all of them without exception would at the same time have other effects through the genetic-developmental algorithm that were sufficiently deleterious to prevent any selection for seed mass change in the lineage. To us, this hypothesis actually seems so implausible that to give it credibility, one would need to bring forward strong evidence for a specific mechanism in the genetic-developmental algorithm that produced an unbreakable link between seed mass and some other trait under strong selection. But our point in relation to PC is not that constraint hypotheses should be rejected in general — they will be more plausible for discrete traits, and over shorter periods of time — only that there is no basis for giving them automatic priority over the hypothesis that present-day selective forces continue to favour the same trait-differences as were established by past selective forces.

In assessing correlations of a trait with phylogeny, it is helpful to look at distributions as well as means. Quantitative traits commonly show distributions like those for seed mass in Fig. 2 (data from Hodgson & Mackey 1986; similar data in Lord *et al.* in press). There is a significant difference between the families in mean log seed mass, which Hodgson & Mackey attributed to phylogenetic constraint. But the distributions show clearly that some species in the smaller-seeded Scrophulariaceae have been able to evolve larger seeds than the average for the larger-seeded Rosaceae, and conversely some species in Rosaceae have been able to evolve smaller seeds than the

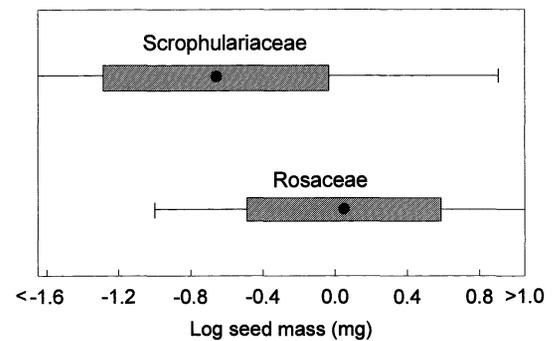


Fig. 2 Mean  $\pm$  SD and range of  $\log_{10}$  seed mass for selected smaller-seeded and larger-seeded families in the Sheffield herbaceous vegetation (data from Fig. 1 of Hodgson & Mackey 1986).

average for the smaller-seeded Scrophulariaceae. This kind of overlap between taxa clearly falsifies the hypothesis that any unbreakable intrinsic phylogenetic constraint prevents all Scrophulariaceae from achieving the average seed mass of Rosaceae, or vice versa (Lord *et al.* in press).

#### RESEARCH AGENDA OF COMPARATIVE ECOLOGY

The research agenda of comparative plant ecology is to understand the spectrum of different ways of making a living, that is, the manner in which plant species attributes occur in combination with other attributes, and the incidence of attribute-constellations in different environments. We need to have confidence in the importance of this agenda, and not be diverted by questions and definitions from fields with different concerns (Grime 1993). There is no good reason to exclude phylogenetically correlated trait variation from consideration. The properties of present-day species are of interest to us in their own right, not only as a source of evidence about evolutionary history.

It will be recalled that in the years around 1980 the lively controversy over cladism had the effect of making evolutionists acutely sensitive to the distinction between shared derived characters and other shared characters, the reason being that only shared derived characters are informative for deducing the history of descent. A similar sharp distinction is upheld under PC, where the one mistake that must be avoided at all costs is to wrongly attribute a similarity between species to present-day natural selection. Connected with this, advocates of PC have included as part of their program a redefinition of 'adaptation' to refer only to the origin of a trait-difference, not to its maintenance (Gould & Vrba 1982; Harvey & Pagel 1991). To avoid being diverted by this manoeuvre, we have referred here to ecological rather than to adaptive interpretations of trait-variation. The point illustrates how a conceptual decision to focus on history rather than on the present, and to favour interpretation as constraint rather than as continuing selection, can manifest itself through semantics rather than through an overt statement of hypotheses (see Williams 1992 and Reeve & Sherman

1993 for balanced discussion of alternative usages of 'adaptation' and their implications.)

#### RECOMMENDATIONS FOR EVOLUTIONARY ECOLOGISTS

A comparative dataset provides correlative evidence. Inferences about causation can only be drawn through interpreting the correlation patterns in conjunction with other sources of evidence. Variation categorized as correlated with family membership only might in reality reflect a relationship through an ecological variable not included in the dataset, just as variation categorized as correlated with an ecological variable might in reality reflect a relationship through a family-specific morphological trait. No statistical procedure can substitute for serious thinking about alternative evolutionary scenarios and their credibility.

For describing the correlation structure in a comparative dataset we suggest two options. One is to test *a priori* hypotheses about pairs of variables without attempting to take account of cross-correlation with other variables. This is to adopt the view that because of phylogenetic niche conservatism, no useful purpose can be served by seeking to separate phylogenetic from ecological correlation. This has the virtue of being simple, but the disadvantage of depriving ourselves of information about the history of a trait association. The second option is to quantify each of the three components of variation, as in Fig. 1. Then variation correlated with phylogeny but not ecology (within the limitations of the variables offered as correlates by the dataset) quantifies the strength of association with traits that are phylogenetically conservative but are not explicitly included as measured variables in the dataset. Variation correlated with ecology but not phylogeny quantifies the extent to which covariation between the focal trait and ecology has emerged repeatedly within different lineages. Variation correlated with both phylogeny and ecology indicates the extent to which the focal variable is associated with a phylogenetically conservative suite of ecological traits.

#### SUMMARY CONCLUSIONS

In summary the effect of the phylogenetic correction procedure is (i) To treat phylogeny and ecology as mutually exclusive explanations of trait-variation (which they are not, because of the importance of phylogenetic niche conservatism), and (ii) To give priority to phylogeny, treating ecology as an explanation of last resort, to be adopted only to the extent that the alternative can be rejected. For quantitative traits considered over long periods of evolution, giving priority to a phylogenetic constraint hypothesis is unreasonable. If anything, the boot is on the other foot: phylogenetic constraint asserts that a trait has resisted selection over tens of millions of years, and very strong evidence should be required to support so implausible a proposition for a trait like seed mass.

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