



## Further Remarks on the Role of Phylogeny in Comparative Ecology

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## Further remarks on the role of phylogeny in comparative ecology

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### Westoby *et al.* (1995b)

Rees (1995) provides a lucid and insightful summary of the principle scientific issues separating Westoby *et al.* (1995a) and Harvey *et al.* (1995), thereby covering most of the scientific issues in Westoby *et al.* (1995b). We therefore confine this discussion to some puzzling elements in Westoby *et al.* (1995b).

1 Westoby *et al.* (1995b) persist in their claim that modern comparative methods discard variation and quote Pagel (1992) in apparent support: this ‘class of methods subtracts from the species data points a component thought to represent similarity among species due to phylogenetic relatedness .... The remainder is used to test for adaptive relationships.’ But that statement was made as a prelude to dismissing such procedures. The next two sentences of Pagel (1992) continue: ‘The difficulty here is

that no one has ever given a good reason why differences among higher taxonomic groups should be treated as irrelevant to adaptive hypotheses...Felsenstein (1985) was the first to develop a method that...does not discard any of the variation in the data set.’ Pagel then proceeded to develop a method that does not discard variation. Since Pagel (1992) *explicitly* rejects methods that discard variation, why do Westoby *et al.* (1995b) quote him out of context so as to suggest the opposite?

2 We wrote that phylogenetic analyses ‘correct, to a large extent, for all other confounding variables’. Why do Westoby *et al.* (1995b) ignore the important qualification, ‘to a large extent’?

3 Harvey *et al.* (1995) took exception to the term ‘phylogenetic constraint’, so why do Westoby *et al.* (1995b) claim that we interpret particular ‘evidence as positive support for phylogenetic constraint’?

4 Westoby *et al.* (1995b) write 'Might it not be more natural to treat ecology and phylogeny as complementary, rather than mutually exclusive?' What does this *mean*? Evolution occurs in an ecological context, and ecological differences arise as a consequence of evolutionary processes. Those are the foundations of the comparative method as applied to ecology.

5 Contrary to Westoby *et al.*'s claim, we do not believe that everyone who asks 'What combinations of trait-values occur among present-day species, and how commonly ... has an underlying agenda to interpret evolutionary history'. But, we do believe that people asking those questions can neither be interpreting evolutionary history nor finding out why particular combinations of trait values occur.

#### Ackerly & Donoghue (1995)

Ackerly & Donoghue provide a useful expansion of points raised by Harvey *et al.* (1995), except on one substantive issue. They write: 'We agree with Westoby *et al.* that phylogenetic comparative methods have tended to emphasise trait changes in evolution, while treating the lack of change or the similarity among related species as a null expectation that requires no further explanation. Statistically, *the lack of variation is indeed usually treated as a null hypothesis*, and it is in this sense that phylogenetic methods may appear to give priority to phylogeny over ecology' (our italics). This is not the case: *the null hypothesis for the comparative methods under discussion is not lack of character variation but lack of character covariation*. Furthermore, branches of a tree where there is lack of character change usually contribute as many degrees of freedom to statistical tests as do branches where there is no change (Ridley 1983 is a notable exception). Consider some of the various comparative methods in use. Independent contrast methods for continuous variables use all the information in the tree and, if there was no difference in character states between a pair of sister nodes, there would be a point on the regression plot at the intercept of the axes which would contribute to the phylogenetic regression. Similarly, recent methods for the analysis of discrete variables, such as those of Maddison (1990), Harvey & Pagel (1991), and Pagel (1994) also use information from regions of the tree where there has been no change – although whether they should is a subject of debate (Read & Nee 1995; Nee *et al.* in press). Finally, the absence of change can contribute towards identifying significant associations when randomisation tests are used (specifically discussed in Harvey & Elgar 1989). Modern

comparative methods do not address the question of *why* the rate of character change is either low or high, and they cannot determine whether absence of change in a character results from either lack of environmental or genetic variation, or from stabilizing selection.

#### Fitter (1995)

Fitter (1995) asks how to distinguish independent evolutionary origins of a trait from common inheritance when a phylogeny is not available. The answer is that it is not possible.

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