

# Interpreting quantitative and qualitative characteristics in comparative analyses

A. H. FITTER

*Department of Biology, University of York, York YO1 5DD, UK*

Westoby *et al.* (1995) believe that the application of phylogenetically 'correct' analyses of comparative data sets can obscure real adaptive patterns. Harvey & Nee (1995) hold that related species are not independent data points in such analyses. This is true, but it is also true that taxa in one clade will sometimes share a characteristic not possessed by taxa in another clade not because all members inherited it from a common ancestor but because it has arisen several times in the one clade. The challenge is to recognize these situations: sometimes a good phylogeny will help; but often one is not available.

An important prediction arises from Westoby *et al.*'s statement that it is unreasonable to give priority to phylogenetic constraints as an explanation for patterns in quantitative traits over long periods of time. This prediction is that quantitative traits should be the least constrained phylogenetically and hence should show less variation at high taxonomic strata in a hierarchical analysis.

I have therefore revisited the data in the Ecological Flora database (Fitter & Peat 1994) which we used to undertake comparative analyses of British angiosperms (Peat & Fitter 1994). For 10 quantitative characteristics,

an average of 12% of the variance occurred at the level of order or above. For 12 qualitative characteristics, 30% of the variance was at these levels.

This analysis gives some support to Westoby *et al.*'s argument, but it does not resolve the most important operational issue. How does the comparative analyst proceed when a potentially adaptive pattern of the distribution of a characteristic is confounded with a taxonomic pattern?

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## Phylogeny and ecology reconsidered

DAVID D. ACKERLY and MICHAEL J. DONOGHUE

*Department of Organismic and Evolutionary Biology, Harvard University, Cambridge MA 02138 USA*

The synthesis of phylogenetic and ecological approaches is surely a positive development in evolutionary ecology. The recent commentaries by Westoby *et al.* (1995) and Harvey *et al.* (1995), stimulated in part by Leishman *et al.*'s (1995) analysis of seed size variation in temperate floras, raise several basic issues in comparative biology. We agree with points in both papers, and disagree with others. In all research, the choice of methods and the relevance of different sources of information depends on the questions asked. Evolutionary processes underlie many ecological patterns and we believe that careful consideration of phylogenetic (and other historical) information will greatly enhance our understanding of these phenomena. The synthesis of phylogeny and ecology is still at an early stage and many exciting challenges lie ahead.

### Phylogeny is not a correction

Early attempts to utilize phylogenetic information in quantitative analyses of trait variation focused on parti-

tioning variance among taxonomic groups (e.g. Kochmer & Handel 1986; Mazer 1989; Stearns 1983) or levels of the taxonomic hierarchy (Bell 1989; Harvey & Clutton-Brock 1985), or partitioning phylogenetic vs. specific variance in a trait (Cheverud *et al.* 1985). The goal of these analyses was to 'factor out' or 'account for' the portion of variance attributable to 'phylogeny' or 'phylogenetic constraint', in order to isolate that portion of the variation that might reflect ecological or selective processes. The Westoby *et al.* critique focused on this type of comparative method, which they called 'phylogenetic correction' (PC). To the extent that taxonomies actually reflect phylogenetic history, such analyses do allow partial consideration of evolutionary relationships. However, methods that focus on partitioning variance among taxa at a particular rank (e.g. genus, family) do not take advantage of phylogenetic relationships above or below that level. In any case, methods based on the hierarchical nesting of higher taxa impart an objectivity to taxonomic ranks that does not, in fact, exist (Doyle & Donoghue 1993), and com-

parative methods have developed considerably in recent years, with a shift away from taxonomic ranks and an increasing emphasis directly on phylogenetic trees.

More importantly, the aims of comparative biology extend far beyond partitioning variance in phenotypic traits. The primary objective is to infer patterns of evolutionary change in traits associated with diversification, and to use such information to test hypotheses regarding the causes and consequences of these changes (Donoghue 1989; Maddison & Maddison 1992). Such analyses, far from representing an alternative to ecological explanation, provide a rich source of information with which to test ecological hypotheses. For example, Westoby *et al.* correctly emphasize the potential importance of 'phylogenetic niche conservatism', in which an ancestral suite of traits is passed on to descendant species owing to its continued success in a particular environment. They argue that this process produces patterns of trait variation reflecting both phylogeny and ecology and that 'PC' will conceal the potential ecological processes involved. This process does appear to be widespread, but it must be recognized that its importance can only be identified by explicitly considering phylogenetic information, as in the subsequent analysis by Lord *et al.* (1995). It is phylogenetic analysis that reveals when a trait (or suite of traits) has been maintained throughout the diversification of a clade, and that maintenance, rather than change, is therefore the pattern that must be explained. Viewed in this way, phylogeny does not correct for anything. Everything has its history, and phylogenetic analyses help us to see one component of this history underlying present-day ecological patterns. They help us ask the right question (Wanntorp 1983).

### Phylogeny is not a constraint

We agree with Westoby *et al.* that phylogenetic comparative methods have tended to emphasize 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. 'Phylogenetic constraint' has sometimes been invoked as an explanation for the absence of change during evolution (e.g. Kochmer & Handel 1986). However, phylogenetic constraint is not a causal process in a mechanistic sense (cf. Edwards & Naeem 1993; McKittrick 1993). If we say that dandelions have yellow flowers 'because' the ancestor of dandelions had yellow flowers, we have only 'explained' the situation by implicitly invoking the spectrum of genetic and developmental processes that underlie biological inheritance and the generation of novelty (cf. Maynard Smith *et al.* 1985). It is these processes that should attract our attention as possible causes.

In the broadest terms, the absence of evolutionary change is due either to the absence of relevant genetic variation, or, if variation is present, to the action of stabi-

lizing selection. We agree with Westoby *et al.* that there is no reason to choose one of these explanations a priori, as their relative importance will depend on the particular trait, time scale, and taxa under consideration. The evolution of seed size may not, in fact, be constrained by a lack of genetic variation, so that present-day patterns may largely reflect selective forces. But what evidence should be used to make this judgement? We believe that knowledge of the nature of genetic variation observed within species is useful in this context. If present-day species exhibit significant, heritable variation within or among populations, then it is more likely that the differences (or similarities) observed among species reflect the action of selection (or genetic drift). On the other hand, an absence of variation in contemporary populations (e.g. the presence or absence of carpels in angiosperms) may reflect a similar absence in the past, which would have imposed a constraint on trait divergence among species.

Knowledge of the developmental basis of trait variation also provides insight regarding the potential for evolutionary change. Westoby *et al.* suggest that the herbaceous condition is not constrained by lack of variation, since small herbs have sometimes given rise to larger, woody plants on islands. While this is certainly true in some cases, it would be ill-advised to generalize too widely from such observations. In most angiosperm herbs cambial activity may simply be turned off or reduced, and small changes in regulatory genes may provide the necessary genetic variation for selection to favour woodiness. However, in monocot evolution the cambium has been lost altogether, so that mutations giving rise to woodiness are far less likely. Westoby *et al.* argued that the overlap in seed size among species belonging to different families 'falsifies the hypothesis that any unbreakable intrinsic phylogenetic constraint prevents all Scrophulariaceae from achieving the average seed mass of Rosaceae, or vice versa.' It is true that there is no evidence of 'unbreakable constraint', but there is equally little evidence that sufficient genetic variation has been present in every lineage throughout the history of these clades for selection to erase the signal of ancestral differences between these groups. And, it should be noted that the evidence invoked to falsify the hypothesis of constraint is phylogenetic (in this case that both Rosaceae and Scrophulariaceae are monophyletic groups), which again illustrates how phylogenetic information informs rather than distracts us from ecological hypotheses.

### Challenges ahead

Curiously, perhaps, we think that the arguments above are not actually relevant to the decision whether to make use of phylogenetic information in comparative analyses. This decision depends on the questions that one poses, not on the answers one expects. Westoby *et al.* argue that '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 inci-

dence of attribute-constellations in different environments', and they imply that phylogenetic analyses are a diversion from the integrity and pursuit of this agenda. However, we doubt that there are many comparative ecologists whose interests stop at this level of description, without seeking deeper causal explanations. As Leishman *et al.* (1995) state at the outset of their discussion: 'patterns of association of seed size with other plant attributes provide an insight into the likely selection forces operating on seed size'. We agree. But if we are interested in inferring the potential selective forces shaping present-day trait variation, we will get a better answer if we know whether a trait under consideration evolves repeatedly among the species under study, or whether there were only a few evolutionary changes followed by diversification of lineages. Ecologists are comfortable invoking historical factors as explanations of present-day patterns, such as the influence of disturbance events and climate change on contemporary community composition. Phylogeny is another facet of history, one that is of particular importance in understanding the distribution and associations of traits among species. As such, it should be embraced, rather than rejected as an imposition or a distraction from the basic mission of comparative ecology.

Many new challenges do lie ahead in comparative ecological research, challenges that will necessarily draw on the expertise of ecologists and evolutionary biologists alike. Here we suggest several areas of particular importance in comparative plant ecology (also see recent reviews by Miles & Dunham 1993; Coddington 1994; Gittleman & Luh 1994; Pagel 1994).

1 Much research in comparative ecology addresses the adaptive significance of particular traits. These studies are sometimes based on samples of species from a single community or habitat (e.g. Armstrong & Westoby 1993), and when these data are analysed in a phylogenetic framework, comparisons among 'sister taxa' may involve species that are very distantly related (e.g. Kelly & Purvis 1993). These comparisons ignore information regarding more immediate relatives of each species, and provide little insight regarding the evolutionary origins of traits and trait associations. Caution must be used when testing hypotheses of adaptation using distantly related species (cf. Coddington 1992), and we recommend an increased focus on closely related taxa in the study of correlated evolution of plant functional traits (e.g. Garnier 1992).

2 On the other hand, research on questions at the community level, and on the comparative ecology of coexisting species, will also be significantly enriched by a phylogenetic perspective. For example, the distribution and associations of traits within a community reflect historical and ecological processes responsible for the contemporary species assemblage (e.g. species migrations, disturbance, competition), as well as the evolutionary processes underlying the trait constellation of each species (Brooks & McLennan 1994). Phylogeny may play an important role if some clades, with distinctive characteristics, are heavily represented in a community due to his-

torical factors. For example, Lord *et al.* (1995) demonstrate that the relative diversity of different families influences the distribution of seed size in temperate floras. However, few studies in plant ecology (e.g. Lechowicz 1984; Herrera 1992) have explicitly addressed phylogeny as one component of a broader historical analysis in order to explain the distribution of traits within a community. Further analyses and attention to new approaches to problems will be very valuable.

3 Finally, there are numerous drawbacks to the use of taxonomy as a source of phylogenetic information for comparative analyses (Harvey & Pagel 1991; Doyle & Donoghue 1993; Miles & Dunham 1993; Coddington 1994). Yet, comparative studies of angiosperms continue to rely heavily on traditional taxonomy and on the use of taxonomic ranks (e.g. Jordano 1995; Lord *et al.* 1995; Renner & Ricklefs 1995; Tiffney & Mazer 1995). It is true that information on plant phylogeny is currently far from complete, and detailed phylogenies for all groups are not yet available. Yet, this information is expanding very rapidly, and should be utilized whenever possible (e.g. Donoghue 1989); a little more 'tree-thinking' will go a long way. We hope that ecologists and phylogenetic biologists will collaborate to tackle these and related questions, as the answers will greatly enhance our understanding of the historical processes underlying the diversity of contemporary plant communities.

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

PAUL H. HARVEY, ANDREW F. READ\* and SEAN NEE

*Departments of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK and \*Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh EH9 3JT, UK*

### 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'?

