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Abstract: The present paper contains a principal discussion on the notion of historical bonds in ecology and evolution. A method is proposed, to the benefit of comparative life-history analysis, to make use of phylogenetic trees imposed on life history variation in order to unveil evolutionary events leading to adaptation in single and coupled characters.

Introduction

Interspecific comparison is one of the most powerful tools in the study of evolution (Darwin 1859, Mayr, 1966, Clutton-Brock & Harvey 1984, Brooks 1986). In this paper we discuss one of several comparative methods for the analysis of evolution of ecological characters. We use hypotheses on the phylogenetic relationship between taxa as a basis for the analysis. Such information may be inferred from phylogenetic trees achieved by cladistic analysis (Wiley 1981) or from other methods of analysis, but it is not within the scope of this paper to discuss different taxonomic methods. The outcome of a comparative analysis will partly be dependent on the choice of the taxonomic level (species, genus, family etc.) at which the comparisons are made. For the purpose discussed here, the species level is best suited as the unit of comparison. We here assume that a phylogenetic tree describes the "true" phylogeny of the species group studied. The phylogenetic tree should be derived independent of the ecological data set under study.

If an ecological character is shared by a group of species in a higher-level taxon, it is reasonable to assume that the ancestor of the group possessed the character. If this character is also unique at that level, it probably originated in the ancestral species. When considering explanations of the origin of adaptations it is thus essential to identify those extant species which are the descendants of the ancestor in which the character originated, and which thus share the character by descent. Our aim is to discuss an extended use of information of independent origin of ecological characters in the adaptive interpretation of these characters. Similar approaches have been advocated by Eriksson et al. (1983), Ridley (1983), Wanntorp (1983), Felsenstein (1985) and Coddington (1988). Felsenstein (1985) concluded that comparative analyses incorporating phylogenies are connected with immense technical problems. For instance one might need data on branch lengths in phylogenetic trees. Our aim in this paper is to suggest a simple method to make the inclusion of phylogenies into life-history analysis easily comprehensible. *

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We explicitly address two issues: Firstly, how to test hypotheses on the relationship between the environment and supposedly adaptive ecological variation. Secondly, how to identify possible constraints and compromises between ecological characters.

Ecological adaptation and environment

If we accept the hypothesis that an ecological character is an adaptation to a specific environmental situation, we expect a causal connection between that character and that environment. If we have a phylogenetic tree of the group of species under study, it is then possible to test whether such a connection exists. If the distribution of the character suggests that it has evolved independently several times within the group of species, and the environmental situation is distributed congruently (Figure 1a), the hypothesis that the character in question is adaptive in that environment is supported. A lack of congruence consequently falsifies the hypothesis and may give ideas for alternative hypotheses.

The same apparent connection between the character and the environment may occur even if the character has not evolved more than at one occasion (Figure 1b). In a phylogenetic sense this case represents only one connection between the character and the environment. This is because a character shared by all species in a monophyletic group most probably evolved in the ancestor to the group. It is important to realize that this situation gives no clear-cut information on the relationship between the character and the environment, since it is the repeated occurrence of a connection to the environment which is the criterion for support to the tested hypothesis.

The same characters can have different explanations at the species level in extant species depending on where they appear in the phylogenetic tree. They can also have different explanations although their origin is independent. We would prefer the most parsimonious explanation with as few evolutionary events as possible.

One important point needs mentioning: The investigated ecological characters should not be included in the data set that forms the base for the phylogenetic tree. If so, there is a risk of circularity in the conclusion. The inclusion of ecological characters in the data base might reshape the phylogenetic tree and enforce a reformulation of the adaptive hypotheses to be tested. In that case one ought to search for more information to solve the apparent conflict.

Constraints and compromises

Ecological life histories comprise complex combinations of "characters". One important topic in the study of life-history evolution is to infer what is a character, and what is a coherent complex of characters. If two characters appear together among several species, and the combination of them has evolved several times independently (figure 2a), this suggests some kind of "coupling" between the characters. The repeated independent origin of the coupling in turn suggests some causal relationships between the characters. If, on the other hand the two characters are shared by all members of a monophyletic group (figure 2b), in analogy to such a relationship to the environment, no inference on coupling can be made. The co-occurrence of the characters together may as well be incidental.

Coupled characters may result from a large number of genetic and ontogenetic

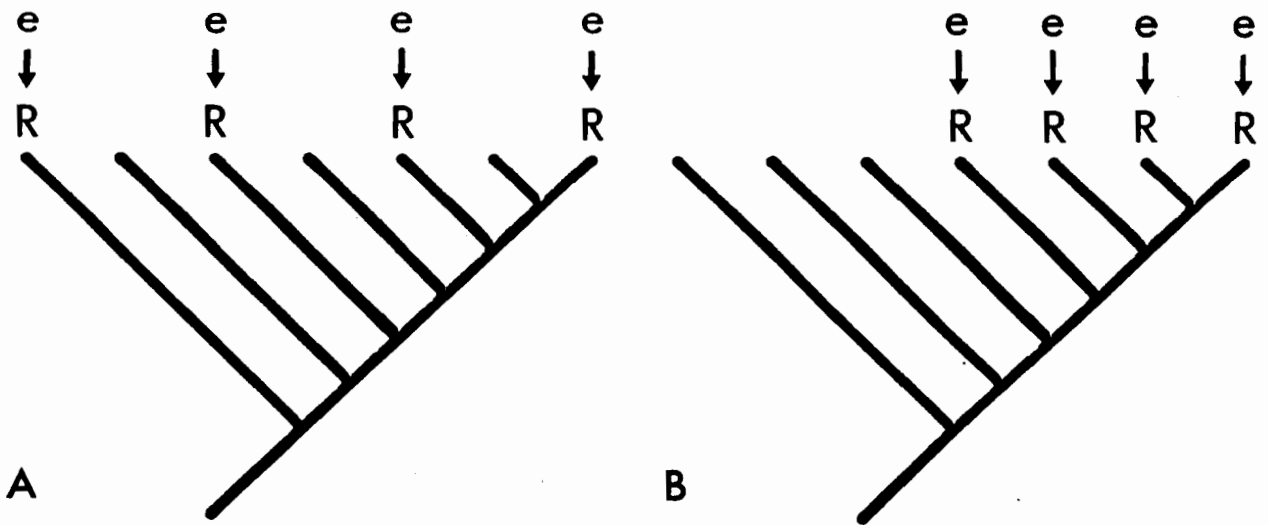


Figure 1. Distributions of a character (R) and an environmental situation (e) in a phylogenetic tree. A: The character and the environment are distributed congruently. The connection has evolved four times independently. B: The connection has evolved only once. See text for further explanation.

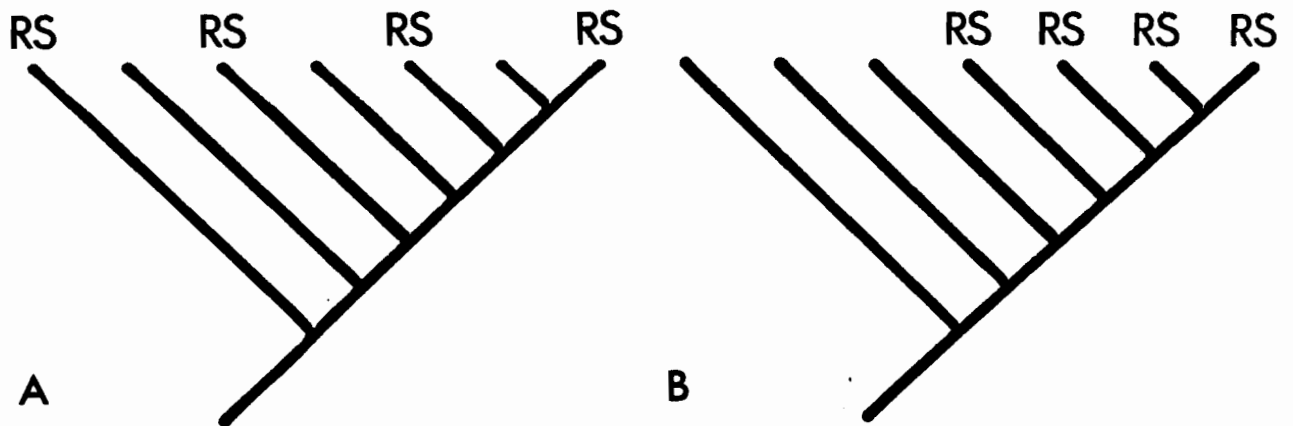


Figure 2. Distributions of two characters R and S in a phylogenetic tree. The two characters always occur together. A: The characters have evolved three times independently. B: The characters have evolved only once. See text for further explanation.

mechanisms. However, in life-history analysis it is meaningful at least to distinguish between "design constrained characters" and "compromises". One important kind of design constrained characters are those which in the extant species enhance fitness, but were not built by natural selection for their current roles. Such characters have been termed exaptations (Gould & Vrba 1982). One plausible example of this is the evolution of fragmentation in the clonal plant Potentilla anserina L. (Eriksson 1987). This feature is a consequence of the evolution of rooting on procumbent stems made up by annually withering above-ground shoots. The annual withering is ancestral in the group, and combined with a subsequent evolution of rooting above-ground shoots, the clones fragment into physiologically independent ramets. Once evolved, this feature may enhance fitness by reducing the mortality risk of clones in this species (Eriksson 1988).

By compromises we mean trade-offs between life-history traits such as the well known ones between life length and reproductive allocation, and between size and number of offspring (Stearns 1977).

The use of phylogenetic trees in life-history analyses may hence suggest cases of character coupling, providing a method to identify what is a character or what are complexes of characters.

Difficulties with the method

Clutton-Brock & Harvey (1984) consider a comparative technique based on phylogenetic trees such as described in this paper inappropriate as regards continuously variable characters. We disagree because of the generally arbitrary distinction between the qualitative and the quantitative aspects of a trait. For instance, in a strict mathematical sense the number of twigs in a birch tree is a discrete variable, but it may nevertheless be treated technically as continuously varying. Furthermore, the qualitative aspects of the quantitatively varying plant height stands clear: if hares are able to reach and eat plants only up to a certain height, to be eaten or not may be a qualitative matter.

In order to be included in a comparative analysis based on phylogenetic trees, the variation exhibited by a character must be divided into discrete classes. There are several means to perform this. For instance, one may use analysis of variance to depict appropriate levels of distinction between classes. Alternatively, the class limits can be chosen so that they correspond to discrete changes in ecological function. A continuously varying trait such as seed size might be divided into classes depending on the ranges of seed sizes consumed by certain seed predators. Preliminary studies of seed size, seed number, number of pollen, number of flowers, reproductive allocation etc. in the Asteraceae, the Scrophulariaceae and the Rosaceae have shown that continuous inter- and intraspecific variation can be satisfactorily subdivided into 2-3 (-4) natural classes by statistical analysis (Telenius, Angerbjörn & Eriksson unpublished).

Another possible limitation to the described method concerns the use of incomplete phylogenetic trees. It has been stated that unless the phylogenetic tree of the investigated group includes all of the species that exist in the group the method should lack predictive value (two anonymous reviewers). However, this objection is irrelevant since the decisive action is to identify independent evolutionary events, and that in principle can always be done. The lack of knowledge concerning the conditions that prevailed for extinct species can not invalidate explanations for life-history evolution in their extant relatives, and the inclusion in the comparative analysis of only a subset of the species in a monophyletic group is therefore sufficient for conclusions

regarding those species. Of course the result is strengthened the more detailed the phylogenetic knowledge is and the more and better characters that are included in the analysis.

Conclusions

We will now make use of two examples to emphasize the merits of the notion of phylogeny in life history analysis. The examples serve as illustrations and our comments should not be considered as criticism.

In the first of these Harvey and Clutton-Brock (1985) make an extensive overview of primate life-history variation. The authors invoke design constraints and linkage as determinants of much of the variation among primate species and subfamilies, but fail to take proper account of the independent origin of the investigated characters. Instead they try to identify and perform their analysis at the most equitable taxonomic level. In order to be able to make general statements they search for character variation that is "widely distributed across taxonomic sub-categories". They thereby even out interspecific differences and arrive at conclusions that are difficult to test.

In a study of adaptive variation in leaf shape among North American violets (*Viola* spp.), Givnish (1987) draws three general conclusions. Firstly, there seemed to be correlative variation between functional aspects of leaves and environment. Secondly, this correlation occurred repeatedly among several lineages of the genus *Viola*. Thirdly, information on chromosome numbers was used to make hypotheses on the sequence of invasion of violets into different habitats. Givnish did not explicitly include any statement on phylogenetic trees in this study. We suggest that such an inclusion would have improved the study by making it possible to evaluate the strength of the conclusions. In addition, the inclusion of a phylogenetic tree in the analysis would have revealed hidden relationships between different aspects of leaf shape and other features of the plants and their environment.

The method used by e. g. Harvey & Clutton-Brock (1985) is appropriate for analysing allometric associations and also other associations between quantitative ecological variables as well as phylogenetic aspects at family and subfamily levels. However, if we want to understand ecological patterns among specific extant species we must use the phylogenetic information that can give us the independent origin of the ecological characters.

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