



Nordic Society Oikos

Phylogenetic Approaches in Ecology

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Source: *Oikos*, Vol. 57, No. 1 (Feb., 1990), pp. 119-132

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

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MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Phylogenetic approaches in ecology

Hans-Erik Wanntorp, Daniel R. Brooks, Thomas Nilsson, Sören Nylin, Fredrik Ronquist, Stephen C. Stearns and Nina Wedell

Wanntorp, H.-E., Brooks, D. R., Nilsson, T., Nylin, S., Ronquist, F., Stearns, S. C. and Wedell, N. 1990. Phylogenetic approaches in ecology. – *Oikos* 57: 119–132.

This paper argues that many ecological studies could benefit greatly from a phylogenetic approach. For this purpose, cladistics is an appropriate method to reconstruct phylogeny. Case studies from seven research topics in ecology are reviewed. In all studies, historical explanations have played a central role, and mostly, cladograms have been used. Connections to statistical methods for estimating quantitative variation among taxa are discussed. A phylogenetic base would greatly strengthen both problem formulation and analysis. This is true for population studies as well as for all areas where adaptational explanations are invoked; single species studies as well as comparative studies or coevolution studies. Three cladistic procedures useful in ecological research are briefly described. Ecology and systematics have much to offer each other and it is a challenge to bring the two fields together.

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But a still more important consideration is that the chief part of the organisation of every living creature is due to inheritance; and consequently, though each being assuredly is well fitted for its place in nature, many structures have now no very close and direct relations to present habits of life. (Darwin 1859)

Introduction

In 1897, William Chamberlain, the President of the American Society of Geologists, spoke convincingly on the role of alternative explanation in science. By helping one to resist the temptation to confirm one's favourite hypothesis, the comparison of alternative explanations maintains objectivity, demonstrates error earlier in an investigation, and leads one closer to the truth

more quickly than would be possible with a single hypothesis (Chamberlain 1897).

Ecology and population biology have been dominated by explanations rooted in processes observable today. Evolution has often been seen as rapidly bringing populations into equilibrium with local conditions, an equilibrium in which the existence of certain genotypes and phenotypes is explained through their having been the best available. In community ecology, the historical

Accepted 13 September 1989

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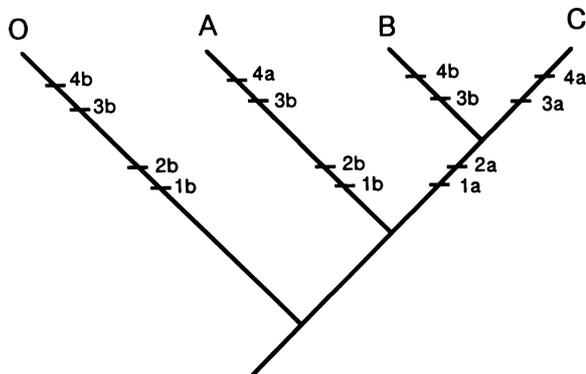


Fig. 1. Cladogram of three species, A, B and C. The traits 1b, 2b, 3b and 4b are interpreted as primitive because they occur also in the outgroup, O. 1a and 2a are common specializations uniting species B and C. 3a is a unique specialization in C. Trait 4a is homoplastic and has arisen independently in A and C as a convergence.

approach to hypothesis formation has been, until recently, equally negligible. Only in the biogeographical and geobotanical traditions has historical explanation continued to play a central role.

While ecology has been maturing as an experimental and theoretical science, cladistics has increased the rigor of historical explanations. This rigor has made the explanations based on phylogenies more reliable and more testable than they had previously been. At the same time, their own results have led ecologists to re-evaluate the role of adaptation, and they have begun to analyze comparative data with the aim of identifying historical constraints.

Community ecology and evolutionary ecology have been suffused with experimental and theoretical approaches in the last quarter century, and some of them have been making rapid progress on adaptationist assumptions. Because this progress has uncovered some patterns not readily explained by adaptation, attention has turned to techniques that can partition the effects of adaptation and constraint (reviewed by Pagel and Harvey 1988).

The use of cladistics in comparative biology has become more widespread only during the last few years. Cladistics is a method of analysis, also known as phylogenetic systematics, that was first developed by the German entomologist Willi Hennig (Hennig 1950, 1966). Hennig devised it as an empirical method for discovering and justifying phylogenetic relationship. All species are mosaics of primitive and derived traits, and the phylogenetic relationships in a group of species can be deduced from the pattern of their shared derived traits. The method is thus based on (1) determining which traits are relatively primitive and which are relatively derived with respect to the group being studied and (2) grouping the various species according to their shared derived traits. The relatively primitive traits (called *ple-*

siomorphies) are identified by using outgroup comparison – any trait found in at least one member of the group being studied that is also found in species outside the group is most parsimoniously interpreted to have evolved prior to the origin of the common ancestor of the group, and is hence plesiomorphic. The corresponding traits not present in the outgroup are then relatively derived (*apomorphies*). Once a collection of apomorphies has been assembled for a group, cladistic analysis groups the species according to their shared apomorphies (*synapomorphies*) (Fig. 1). Due to parallel and convergent evolution, not all apomorphies will conform to a single pattern, however. Contemporary cladistics uses a variety of numerical methods and computer-assisted programs for discerning the pattern of synapomorphies that best fits the data at hand (Wiley 1981, Fink 1986, Platnick 1989). The pattern that results is a hypothesis of cladistic relationship, a cladogram, which can be interpreted as a phylogenetic tree to support historical explanations in biology. Cladograms are atemporal representations of relationship. They say nothing about the process of evolution. In contrast, phylogenetic trees are historical interpretations of cladograms. The relationship represented in one cladogram is compatible with more than one phylogeny (Nelson and Platnick 1981). Wiley (1981) is a useful handbook for those further interested in cladistic analysis.

Cladistics is, thus, a method that uses traits to investigate the systematic relationship of organisms. Comparative biology, on the other hand, uses cladograms to investigate the systematic or temporal distribution of traits. The idea of using the comparative approach to historical explanations in ecology was widespread in the 19th century and has continued as a central theme in the European geobotanical tradition and in comparative morphology (Riedl 1978, Lauder 1982). It has become increasingly prominent in ecology. The historical approach complements the current adaptationist approach to evolutionary ecology. The main difference is the use of indirect estimates of history and the emphasis on adaptation in evolutionary ecology and the use of direct estimates of history (through phylogenetic trees) and the emphasis on constraint in historical ecology. Historical ecology is best suited to asking questions about the origins and diversification of ecological phenomena, ranging from life history traits to community structure. As a form of comparative biology, it is a method for suggesting patterns and locating possible adaptations. It is a method for discovery and descriptive explanation but it can also, indirectly, discriminate among causal explanations (O'Hara 1988), e.g. through statements about the sequence of origination of traits.

This paper reviews case studies in which a historical approach has produced alternative explanations that have brought insight into ecological problems. The case studies illustrate methods and suggest connections to other quantitative techniques, such as nested analysis of variance developed below. Wider use of historical ex-

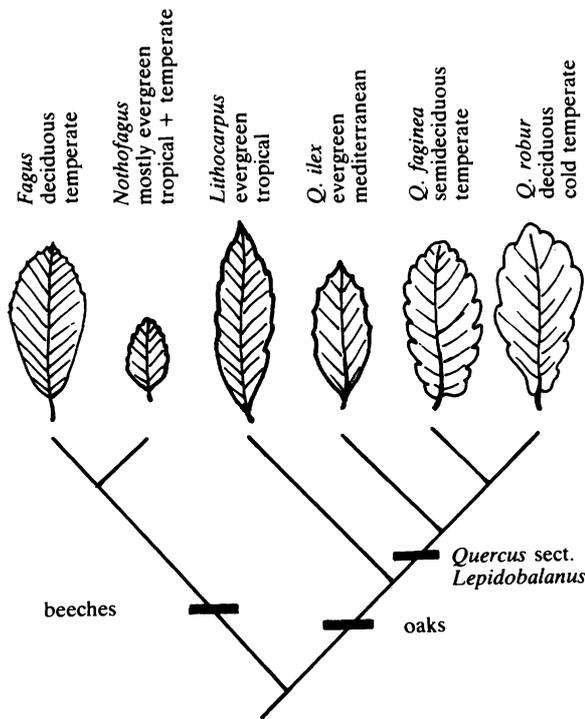


Fig. 2. Simplified cladogram of oaks showing that evergreenness is an ancestral trait within the genus *Quercus*. In European oak and some other species, deciduousness has evolved as a specialization to cold climates.

planation in ecology would enrich ecology and lead phylogenetic systematics into constructive engagement with a field in which it has much to offer.

For the sake of argument, we will take an adaptationist approach throughout this paper, accepting that whenever a new trait arises, it does so as the result of natural selection. We will consider phylogeny and history, not as providing alternatives to adaptation, but as a means of ordering the adaptationist explanations. The discussion whether specific traits should be interpreted as adaptations at all, falls without the scope of this review.

We will adhere rigorously to the principle of parsimony – not because the concept of parsimony is applicable to evolution or any process of nature, but because it is a necessary tool in our attempts at explaining those processes. Thus, change always requires an explanation, while inertia does not. To explain absence of change a priori as evidence that some agent (such as natural selection) is at work would indeed be an unnecessary multiplication of theories.

Examples of the phylogenetic approach

Identifying adaptations – Leaf retention in oaks

The European oak is well known for its habit of retaining its leaves far into the winter. This is especially noticeable in young specimens and makes them conspicuous in the deciduous woodland they inhabit. Several stories have been proposed to explain leaf retention as an adaptation (e.g., Otto and Nilsson 1981, Nilsson 1983).

Wanntorp (1983) showed how cladistic methodology can be used to identify traits as candidates for actualistic adaptive explanation and to rule out non-candidates: In broad perspective, temperate deciduous woodlands can be seen as an extreme habitat for oaks. Most of the hundreds of oak species inhabit regions with Mediterranean or tropical climates. All oaks of warmer climates are evergreen, and close relatives of the European oak are semi-evergreen (Fig. 2). Leaf retention is ancestral in oaks and needs no special explanation in European oak. Among recent oaks, deciduousness is the derived condition that needs an adaptational explanation.

Most traits in any organism are ancestral, a legacy of its history. The inheritance of the trait from ancestors should always be considered as the evolutionary null-hypothesis. Only the traits, demonstrated to be novel in the phylogeny – the *autapomorphies* – should be chosen as candidates for explanations that invoke actual environmental conditions.

Wanntorp concluded: “Already when formulating theories on which the traits are that one might investigate, one should have at least some idea about relationship. Otherwise one might, as in the oak example, discuss the vestigial ancestral condition (leaf retention) when the opposite (deciduousness) is the specialization in the actual species.”

A similar approach was applied to the origin of the orb web in spiders by Coddington (1986). Intricate orb webs were traditionally thought to be a convergent adaptation, derived in different spider groups from cob web types. Coddington, however, demonstrated orb webs to be an ancestral trait for a large group of spiders and the “simpler” cob webs to be derived from this condition. Like in the oak example, the sequence is reversed, and with it the need for adaptive explanation. The orb web is still a candidate for adaptive explanation, but at a much more general level. Like in the oak example, the strength of the phylogenetic approach is evident already at the level of problem formulation. There are few examples in the literature, but Greene (1986) fruitfully used this approach for identifying and studying possible adaptations in monitor lizards (Varanidae).

Behavioural ecology – Sex in sticklebacks

Sticklebacks and their relatives (Family Gasterosteidae) have played a leading role in behavioural and ecological

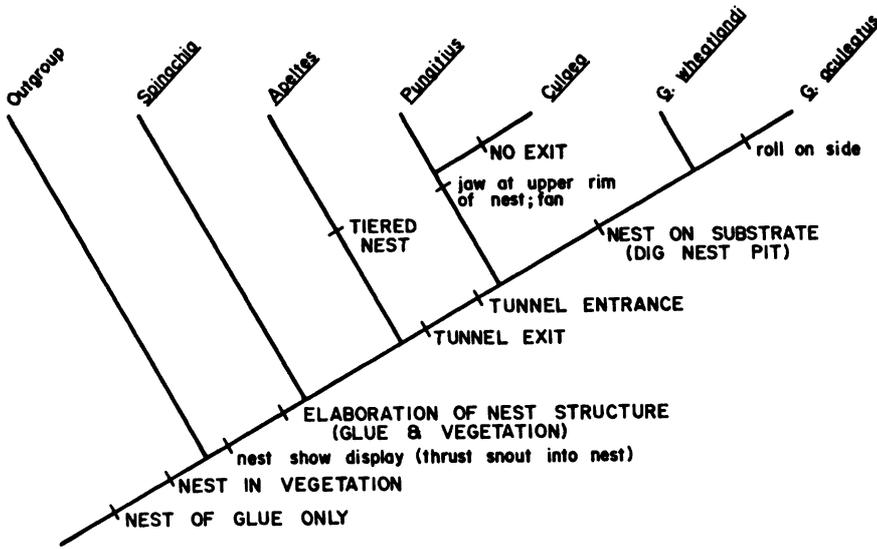


Fig. 3. Cladogram of sticklebacks (Gasterosteidae) based on behavioural and nest-building traits.

research for decades. One dominant paradigm in behavioural ecology asserts a tight connection between individual and social behaviour on the one hand, and environmental conditions on the other. Breeding systems, territorial defence, the opportunity for sexual selection, and many other aspects of behavioural biology are seen as resulting from selection imposed by actual conditions of the contemporary local environment.

In this context, a phylogenetic analysis carried out on sticklebacks by McLennan et al. (1988) is particularly intriguing. They constructed a stickleback cladogram from strictly behavioural traits using the PHYSYS program (Mickeyevich and Farris 1982). Their tree based on behavioural traits is closely concordant with trees based on morphological traits and has an even higher consistency index, indicating a high overall level of historical constraint and a low degree of evolutionary plasticity for the behavioural traits used to construct the tree (Fig. 3).

This result, coupled with the observation that a number of stickleback species are ecological generalists, ranging across a broad variety of environmental conditions and carrying the same behaviour patterns with them across that range, suggests that history and phylogeny have played a larger role in the determination of patterns of behaviour in sticklebacks than has adaptation to the actual local environments. Again we see here a constructive phylogenetic alternative that strongly suggests the need for a reappraisal of earlier adaptationist hypotheses.

Order of origin – Warning coloration and gregariousness in butterflies

It has long been thought that the development of aposematic, or warning, coloration required the involvement of kin selection (Fisher 1930, Turner 1971, Harvey et al.

1982). The idea was straightforward: the first mutants with warning coloration would be eaten, or damaged and killed, and only their siblings would benefit, for predators were thought to learn slowly and to kill their prey before determining their toxicity. Under this hypothesis, gregariousness had evolved first providing conditions in which aposematic coloration could then evolve through kin-selection.

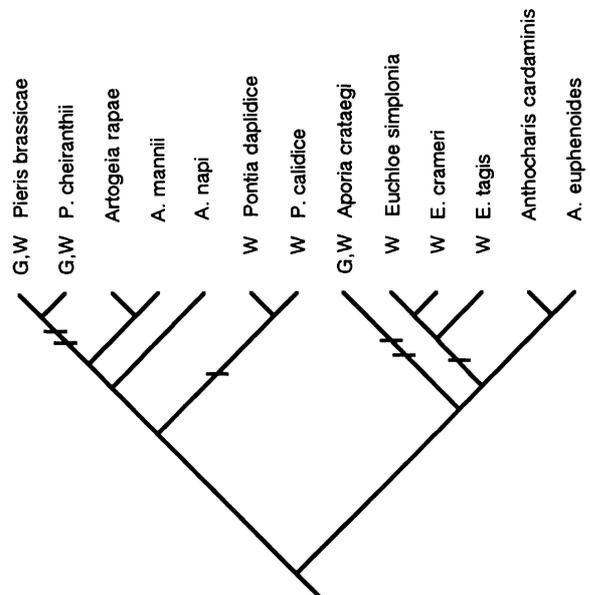


Fig. 4. Cladogram of some white butterflies (Pierinae). The occurrence of warning coloration (W) and gregariousness (G) are shown on top. The origin of these traits are shown as bars on the cladogram. (Outgroup comparison shows that cryptic and solitary larvae are ancestral.) In no case can gregariousness be demonstrated to arise before warning coloration.

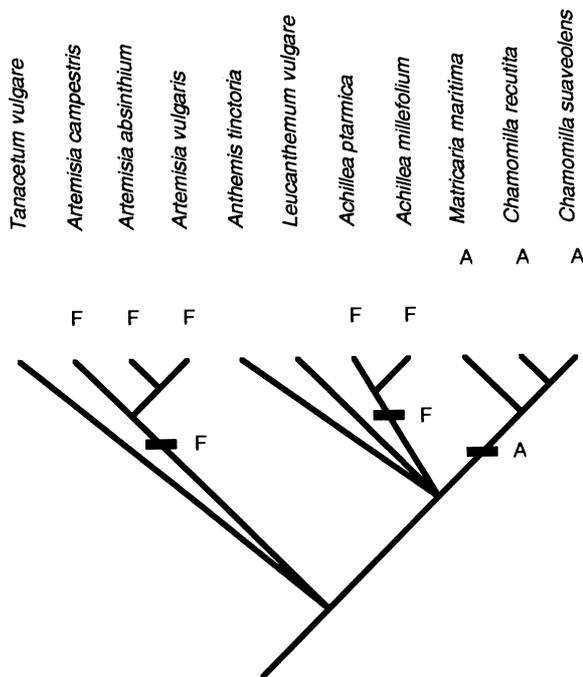


Fig. 5. Cladogram of some members of the daisy family (Asteraceae). The occurrence of two traits within species are shown on top. (A – annual life cycle, F – few-flowered capitula.) The origins of these traits are shown as bars on the cladogram.

Sillén-Tullberg (1988) tested this idea with a phylogenetic analysis of butterflies. She used the best available taxonomies, for in most cases cladograms were not available. Her focus was on the order of events: did gregariousness evolve before, with, or after warning coloration? The test was decisive: in 15 cases gregariousness had evolved after warning coloration, and in no case had it evolved before warning coloration. In three cases, the two traits could not be separated, and in five cases gregariousness had evolved in lineages without warning coloration (Fig. 4).

The evidence presented by Sillén-Tullberg speaks against the kin selection hypothesis for the origin of warning coloration. Here phylogenetic analysis provided a powerful test that falsified a specific kind of adaptational explanation and supports a critical reappraisal of a classical position in evolutionary ecology. Höglund (1989) used the same approach to study the dependence of sexual dimorphism on lek behaviour in birds.

Life history theory – Phylogenetic explanations

One of the dominant metaphors in life-history theory during the 60s and 70s was r&K-selection. It was thought that the diversity of observed life histories could be ordered along a single dimension with r-selected types at one end and K-selected types at the other. By the late 70s, examples that did not fit were

accumulating, and closer analysis of the logic leading to the predictions demonstrated that there was no clear foundation for the predicted association between K-selection and the life-history traits.

Stearns (1977) found that about half the species for which the data are reliable – for intra-specific or intra-generic comparison – fit, and about half did not. He later (Stearns 1980) suggested that our impression that most species could be arrayed along a single dimension was not due to microevolutionary processes acting within species, but to comparisons arising at the level of the family, the order, and the class. In an analysis of life-history variation in the mammals, based on multivariate statistics, Stearns (1983) found that most of the pattern of covariance in life-history traits that we call r&K-selection results from correlations with two factors: body size and phylogenetic relationship. When the influence of those factors is removed and the residuals are examined, much less of the covariance in the traits is left to be explained by microevolution operating within species. Brown (1983), in his work on snails, and Dunham and Miles (1985), in their work on reptiles, reached similar conclusions.

None of these authors had access to cladograms and they were therefore forced to use existing classifications in their studies. Pagel and Harvey (1988) provide a useful overview and critique of the strengths and weaknesses of several alternative methods of doing such analyses.

Telenius et al. (1989 and unpublished) analyzed the distributions of life history traits in eleven species of the plant family Asteraceae using a cladogram derived from a study of the tribe Anthemidae by Bremer and Humphries (in press) (Fig. 5). Three of the species were annuals, together forming a monophyletic group. The interpretation was that the annual life cycle evolved once in the common ancestor of these species and does not need special explanations in the three genera. On the other hand, few-flowered capitula occurred in the two distantly related genera *Artemisia* and *Achillea*, and was interpreted to have evolved independently within each genus. When relating the number of flowers to the type of pollinating agent, they found that few flowered capitula were correlated with a generalist pollinating agent (generalist insects or wind).

Evolution of species associations – Insects and host plants

Insect-host plant associations have been studied with increasing intensity ever since the publication of the pioneering work on butterfly–host plant co-evolution by Ehrlich and Raven (1964). There has been particularly vigorous debate over the evolutionary processes creating the patterns of insect-host plant associations seen today. Several different process models have been formulated (e.g., Ehrlich and Raven 1964, Jermy 1976, 1984, Smiley 1978). Only recently, however, has it been realized that these models predict different types of fit

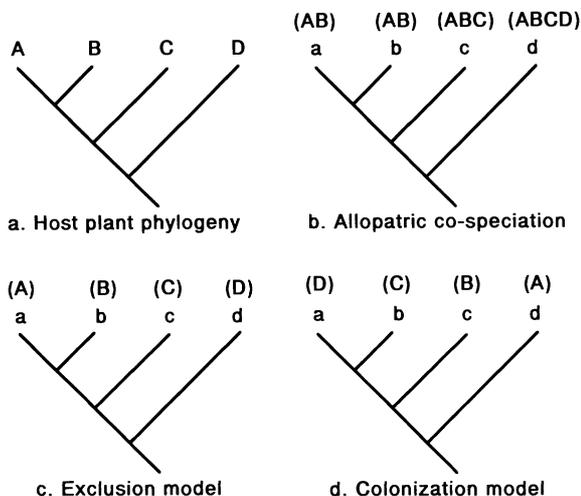


Fig. 6. Different models for the evolution of insect-host plant associations and examples of the type of fit between insect and plant phylogenies they predict. All species are assumed to be sympatric. This means that the allopatric co-speciation model is represented by the extreme case where all species have secondarily become sympatric. Lower case letters refer to insect species and upper case letters to plant species. Letters in brackets refer to host plant records of insect species.

between insect and plant phylogenies, and thus can be tested using phylogenetic methods (Mitter and Brooks 1983, Miller 1987).

To exemplify this approach, we briefly discuss three models for the evolution of insect-host plant associations and the type of fit between insect and host plant phylogenies they predict (cf. Fig. 6). We also cite a few case studies supporting two of the models.

Allopatric co-speciation (Brooks 1979)

In this model, congruence between insect and host plant phylogenies is expected because of simultaneous allopatric speciation in insect and host plant lineages, i.e., vicariance events. We expect some of these co-speciation events to persist as concordant insect and host plant vicariance patterns. Because in this model co-speciation is independent of any changes in host preference or host suitability, there are no general predictions about changes in the host plant range of the insects that can be attached to it. However, when sympatry between lineages is established subsequent to a co-speciation event, we may expect a tendency towards broadening of the host plant range of the insects (Fig. 6b). Until lately, this model has received very little attention in the literature on insect-host plant associations.

Exclusion model (Ehrlich and Raven 1964, Berenbaum 1983)

This is the "classical" coevolution model and may be summarized as follows. Phytophagous insects reduce

the fitness of their host plants. Therefore, plants which by chance acquire traits (defence mechanisms) that make them unpalatable to phytophagous insects will increase their fitness, and the new defence mechanism will spread throughout the plant species. In the absence of phytophagous insects the plant lineage will then rapidly radiate. However, sooner or later some individual insects will overcome the new defence mechanism and be able to feed on the previously protected plant group. These individuals will increase their fitness because they will avoid competition from other phytophagous insects. Therefore, the ability to overcome the new defence mechanism will spread throughout the species. In the absence of competitors, the insect lineage will diversify to exploit the previously protected plant group. Exactly as the allopatric co-speciation model, the exclusion model predicts a non-random congruence between insect and plant phylogenies (Fig. 6c). However, according to the exclusion model, the co-speciation events will be found to be sympatric (rather than allopatric) and not associated with persistent vicariance patterns. Furthermore, co-speciation events will tend to be associated with specialization in the insect, i.e., narrowing rather than broadening of the host plant range of the insects. We should expect some insect lineages to specialize on single host plant clades because the insects have overcome the defence system of the plants; we should expect other insect lineages to be excluded from certain host plant clades because the insects have not overcome the defence systems of the plants (when insect phylogenies are mapped on host plant phylogenies it is sometimes possible to detect such exclusion events because they appear as extinctions of insect lineages; see Brooks 1988).

Colonization model (Jermy 1976, 1984)

According to this model, diversification of phytophagous insects took place after the radiation of the host plants and was independent of plant speciation. The insects colonized new host plants numerous times during their evolution. If this model is correct, we expect little or no congruence between insect and plant phylogenies (Fig. 6d). A special type of the colonization model was proposed by Ehrlich and Raven (1964), who suggested that host shifts occur predominantly between plants with similar secondary metabolites.

Two examples – gall midges and butterflies

Only few studies using a phylogenetic approach to examine the evolution of insect-host plant associations have been published so far. Roskam (1983, 1985) used cladograms to investigate the evolution of the association between *Semudobia* gall midges and their host plants, birches (*Betula* spp.). The cladograms are highly congruent, because all four speciation events in the *Semudobia* cladogram correspond with dichotomies in the *Betula* cladogram (no. 1–4 in Fig. 7). Of the two descendant species after the first speciation event in the

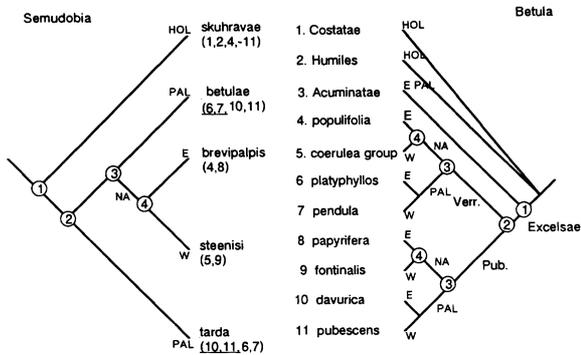


Fig. 7. Evolution of the association between birches, *Betula* spp. and gall midges, *Semudobia* spp. Numbered nodes refer to co-speciation events; numbers in parentheses refer to host plants of gall midges (main host underlined). HOL = Holarctic, PAL = Palearctic, NA = Nearctic region; E = East, W = West; Pub. = Sect. Pubescentes, Verr. = Sect. Verrucosae. From Roskam (1985).

gall midges, one (*S. skuhravae*) retains a broad host range and now induces galls in bracts of fruit catkins of birches belonging to all sections of *Betula* except *Acuminatae*, which hosts no gall midges. The other, the stem species of the remaining *Semudobia* species, is specialized on birches belonging to the section *Excelsae*. The narrow host range of the latter species is explained by the exploitation of a new resource, deciduous fruits, a derived condition only present in birches belonging to the sections *Excelsae* and *Acuminatae*. After the second speciation event in the gall midges there is only weak specialization in the descendant lineages (Roskam and van Uffelen 1981), leading to a “doubling” of the host plant records of the remaining *Semudobia* species. The third and fourth co-speciation events are vicariance events, for there is a corresponding pattern of allopatric speciation in *Semudobia* and *Betula*. Even if there is one possible exclusion event, which could indicate the evolution of a novel defence mechanism in birches belonging to the section *Acuminatae*, the overall pattern in *Semudobia* and *Betula* is clearly best fit by the allopatric co-speciation model.

Host plant relationships in the butterfly family Papilionidae were considered strong evidence for the exclusion model by Berenbaum (1983). Miller (1987) compared cladograms of butterflies in this family with traditional classifications of their host plants. He found very little congruence between insect phylogeny and plant classification. Thus, the evolution of papilionid host plant associations is characterized by numerous host plant shifts. Furthermore, these shifts tend to occur between plants with similar secondary metabolites, thus supporting the colonization model of Ehrlich and Raven (1964) but not the exclusion model. Patterns supporting the colonization model (not necessarily the Ehrlich and Raven variant) have also been reported in the tephritid fly genus *Rhagoletis* (Berlocher and Bush 1982) and in

Heliconius butterflies (Mitter and Brooks 1983). We are not aware of any studies to date that support the exclusion model.

It is important to recognize that even if colonization of new host plants is frequent, important aspects of insect-host plant relationships may still be historically constrained. For instance, Nylin (1988) showed that the polyphagous nymphalid butterfly *Polygonia c-album* displays a distinct preference for hosts in the order *Urticales*, and larvae also grow faster on these hosts. A preliminary phylogenetic analysis (Nylin, unpubl.) reveals that the polyphagous genera *Polygonia* and *Nymphalis* evolved from an ancestor specialized on *Urticales*. Thus, despite the colonization of many new hosts, the ancestral ties with *Urticales* persist in *Polygonia c-album*.

Insect-host plant associations constitute only one example of coevolving species associations for which phylogenetic methods promise to give new insights. The majority of phylogenetic studies in coevolution published to date have been based on helminth and arthropod parasites of vertebrates (see Brooks 1988 for a review). The possible coevolution between other interacting components of ecosystems, such as predator – prey or pollinator – plant associations, has been little discussed in phylogenetic terms. The most useful methods for comparing phylogenies of putatively coevolving groups, consensus trees and parsimony mapping, are reviewed below.

Community ecology – Regional explanations of local diversity

Ricklefs (1987) argues convincingly that community ecology has relied mostly on local-process theories in explanations of patterns strongly influenced by regional processes. Local explanations rely on the action of competition, predation and disease to explain patterns of species diversity in small areas, from hectares to square kilometres. The community is seen as maintained in a saturated equilibrium by biotic interactions.

However, independent lines of evidence suggest that regional diversity plays a strong role. That there are four to five times more mangrove species in Malaysia than in Costa Rica and four times more chapparal plant species in Israel than in California, that the number of cynipine wasps on a species of California oak is strongly related to the total number of cynipines recorded from the whole range of the oak species, that local species richness in Caribbean birds is strongly related to total regional bird diversity, are all observations that one cannot explain on the assumption of local, saturated equilibria – otherwise similar states would be attained in systems experiencing similar conditions. The explanation of local community structure in these systems should include historical and biogeographic information – from cladistics and biogeography.

The communities of helminth parasites inhabiting South American freshwater stingrays provides a striking

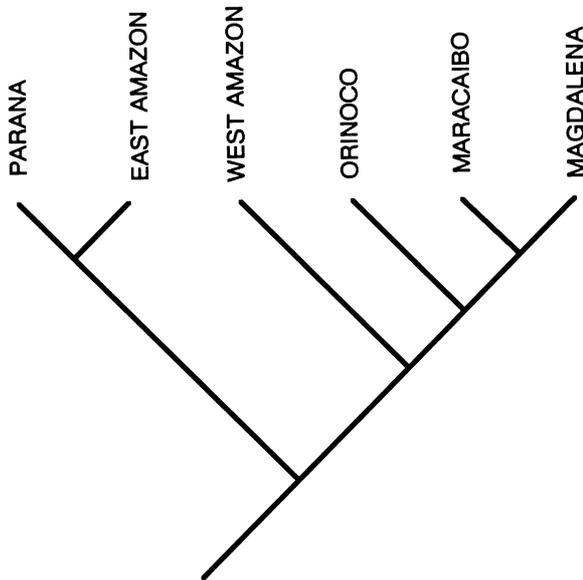


Fig. 8. Area cladogram of the river systems in South America, based on the relationships and distribution of sting ray parasites (Brooks 1985). The Paraná separated first, then the East Amazon, the West Amazon, the Orinoco, and last the Maracaibo and Magdalena river systems.

example. Brooks (1985) showed that the degree of historical influence on helminth community diversity differed among six river areas in South America. The Paraná system, the western Amazon, the Orinoco and the Magdalena systems all contain species whose phylogenetic relationships correspond to the geological history of the areas in which they occur (Fig. 8). The Orinoco community also has many species that colonized from other river systems. Therefore, it has the highest diversity although it is not the oldest. In two other areas, the Maracaibo basin and the eastern Amazon, the helminth communities also appear to have been partly derived from colonization events. The Maracaibo community has representatives from three different source areas (the Magdalena, Orinoco and western Amazon), while the eastern Amazon has representatives from only a single source area (the Paraná). The historical assembly of these communities has differed among the river systems. The community of the Paraná system has almost entirely evolved locally, while that of the Orinoco has a large colonist component. Equilibrium explanations may be relevant for the latter, but absolutely not for the former system, where instead an historical explanation is required. Again, the cladistic approach shows its strength already in suggesting the appropriate framework in which the problems should be formulated.

Radiations – are they adaptive?

The general definition of adaptive radiation is that an ancestor colonizes a new adaptive zone, followed by radiation of descendant lines occupying the many empty niches. There are several examples of adaptive radiations in the literature, however, few were examined from a phylogenetic stand-point.

Brooks et al. (1985) studied how much of the diversification among the families of digenetic trematodes (a group of parasitic flatworms) could be explained by adaptive changes in life history traits. They picked out traits assumed to have adaptive value, e.g., host type. They pointed out: “the ecological factors we used... are the same ecological factors that have been used to support adaptationist explanations of digenetic evolution”. A cladogram, based on morphological characters (Brooks et al. 1985), was used to map the “adaptive” traits on. They discovered that only one fourth of the branch points, i.e., speciation events, were accompanied by changes in any of the “adaptive” traits.

As a result of such findings, several classical cases of adaptive radiation should be subjected to cladistic analysis in which the putative adaptations and the putative environmental conditions with which they should be associated are introduced on the cladogram. Until such analyses show to what extent adaptations are associated with radiations, the word “adaptive” should be dropped from the catch phrase “adaptive radiation”.

The related subject of adaptive zones has seen the beginning of a cladistic treatment. Mitter et al. (1988) tested the common suggestion that insect lineages which evolved phytophagy entered new adaptive zones and were able to diversify as a result of overcoming this major obstacle in evolution. They showed that phytophagous clades of insects are consistently more species-rich than their non-phytophagous sister clades, thus supporting the notion that entering a new adaptive zone is followed by subsequent radiation.

Combining cladograms with statistical analysis

In this section we will discuss the possibility of combining cladistics with statistical methods, i.e., analyses of variance, covariance and correlation. Such methods are widely used by ecologists, for the simple reason that most traits studied are quantitative and show considerable variation. In contrast, cladistics and other systematic methods prefer qualitative traits with little variation within taxa. By combining the two approaches it might be possible to find answers to some basic questions in ecology. For instance: one Great Tit laid eight eggs this year. The reason that it laid amniote eggs in the first place goes back to the relationship between birds and dinosaurs and does not need a special explanation. But why eight eggs and not seven or nine? To what extent was this due to the Great Tit being a member of a certain order of birds, or suborder, superfamily,

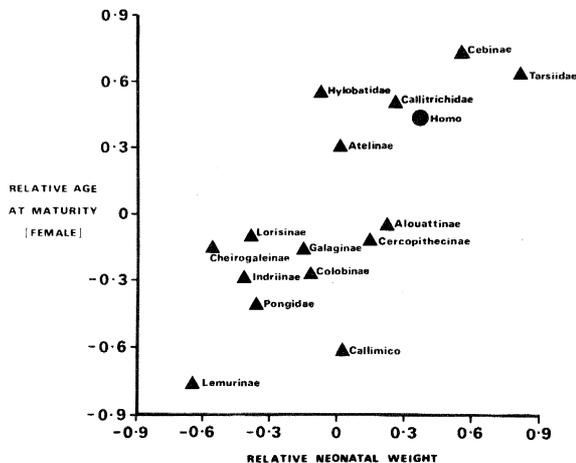


Fig. 9. The relationship between relative birth weight and relative adult weight in Primates. Relative measures were calculated as deviations from the line of best fit among different subfamilies. The allometric relationship does not arise among species, but at higher taxonomic levels (from Harvey and Clutton-Brock 1985).

family (Paridae), genus (*Parus*) or species (*P. major*), and what part of the explanation belongs in the field of population ecology or the study of environmental effects and physiology? The answers to these questions will vary depending on the species studied. For example, the whole bird order Procellariiformes lays a single egg, while clutch sizes vary considerably within the family Passerinae.

There are also related questions. Quantitative traits, studied by ecologists, are often interrelated in allometric relationship or tradeoffs. Are the deviations from the ancestral state at each phylogenetic level coupled with changes in associated traits (e.g., adult sizes with number of eggs) or with changes in life style (niche shifts, feeding habits etc.)?

Allometric relationships such as size-fecundity or adult weight-birth weight vary within clades. Often, one finds that most of the variation is not among species, but among genera, sub-families or families (Harvey and Clutton-Brock 1985, Pagel and Harvey 1989). Within a given species, such relationships function as the boundary conditions on optimality problems in life-history evolution – as tradeoffs, and they have been used in predictions of optimal life histories (e.g., Stearns and Koella 1986). Such predictions can be surprisingly accurate, and it would therefore be interesting to have a method that would partition the prediction into components contributed, through the constraining allometric relationship by the family, sub-family, genus and so forth.

Tracing the history of constraints

A number of studies have demonstrated that much of the variation and covariation of quantitative traits pres-

ent in a clade arises at higher taxonomic levels (e.g., Brown 1983, Stearns 1983, Dunham and Miles 1985). One explanation of this result, not well tested, is that variation is progressively delimited within clades by constraints peculiar to those clades. It would therefore be of interest to study if the distribution of characters on the cladogram suggests their involvement in constraints. To find out, one could construct a cladogram and include in it the evolutionary innovations for each clade thought to act as clade-specific constraints. These innovations would be associated with deviations from mean values of the quantitative traits, e.g., life history traits thought to be constrained in a clade-specific fashion. These deviations could be calculated from a nested analysis of variance or covariance. By associating the evolutionary innovations hypothesized to be constraints with positive or negative residuals of the quantitative trait for each clade, one could generate a hypothesis, based on correlation, about a putative causal link between the evolutionary innovations and the quantitative traits. At the same time, such information could be used to test alternative hypotheses about such links, for some hypotheses would be ruled out by the pattern observed.

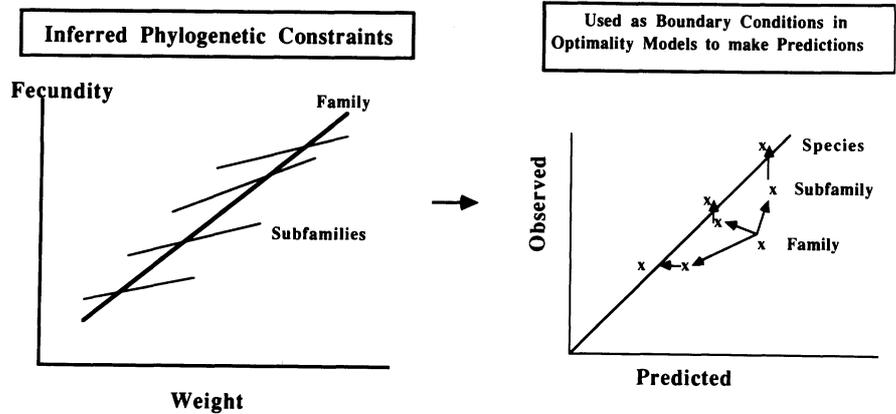
Phylogenies and the comparative method

New and refined methods aimed at finding answers to questions like those outlined above are constantly arriving. The methods trace their roots to comparative ecology. In recent years it has been realized that individual species cannot be treated as independent data points in analyses using the comparative method (Clutton-Brock and Harvey 1977, 1979). This is because related species may share a character because of so called “phylogenetic inertia” (i.e., constraints on development; e.g., Clutton-Brock and Harvey 1979, Felsenstein 1985) or because, being similar species, they probably share many aspects of their ecological niches which may influence the evolution of the trait under study (e.g., Ridley 1983, 1989, Grafen 1989). Nested analysis of variance could be used to find the taxonomic level which contributes the most to the variance in the studied trait, and then means can be compared for taxa at this level instead of species means. Similar techniques were adopted in several major comparative studies, such as Stearns’ (1983) analysis of life history traits in mammals.

The major drawback of this method is that phylogenies are used only to find the taxonomic level to study. Means for higher taxa are not necessarily (or even probably) independent (Felsenstein 1985, Bell 1989). Also, more or less equal variance may exist at several levels, and (importantly if we are interested in studying how traits affect each other in evolution) covariance between traits may be greater at levels other than the one where variance in the dependent trait is greatest (Bell 1989).

Harvey and coworkers (cf. Pagel and Harvey 1988) have developed methods to get estimates of the con-

Fig. 10. Inferring phylogenetic constraint. – Left. When plotted on a graph, the observed life history data for different species generates a line for each subfamily. This line represent the phylogenetic boundary conditions at this taxonomic level. Estimates of constraints for each subfamily, in turn, generate the boundary conditions at the family level and so forth. – Right. The inferred constraints are then used as boundary conditions in optimality models to predict the optimal life history traits, or trade-offs between traits. The predictions are plotted against observed values. In this graph, the distance between the points represents the amount of change in the trait at each taxonomic level.



straining relationship at different taxonomic levels in a given classification. Because many of the existing classifications are not based on cladistic principles, however, they do not reflect phylogeny. To use these methods fruitfully, therefore, it would be necessary to follow the roundabout way of first making a cladistic analysis and then translating the result into a new classification. One would then make an estimate of the constraining relationships for each level of interest in the cladistic classification: for example, for one family, for each of three subfamilies, then for each species in each subfamily. Using these average constraints for each level, one would then make a prediction of the optimal life history trait as though each of those levels represented a real population of organisms – the average family-level ancestor, the average subfamily-level ancestor and so forth. Presumably, as more and more precise information on constraints entered the calculations, the predictions would come closer and closer to the observations. This approach to more precise predictions could be plotted on a graph of predictions vs observations, and the magnitude of changes from family to subfamily to species would give one a visual impression of the importance of constraints acting at each level (Fig. 10).

There are several problems with this approach, including the assumption that one can actually estimate the constraint in the putative common ancestor. Another problem is the indirect use of cladograms in this and similar methods. Even if cladograms have been used to construct the classification, the delimitation of families, genera etc. depend on idiosyncrasy. This means that one loses much information on relationship and that it becomes difficult to compare relevant clades.

Even if two subfamilies are both monophyletic, they are directly comparable only if they are of equal age (e.g., sister groups). A more direct approach would be to dispense with classification and use the cladogram directly to identify the ancestral state for each component.

Ridley (1983) proposed a solution for discrete characters. Cladistic methods (parsimony assignments of traits to phylogenies) could be used to count the number of times a trait has evolved independently. Felsenstein (1985) showed how phylogenies could be used also in comparative studies of quantitative data. The major problems with such approaches, of which Grafen's (1989) "phylogenetic regression" is another example, are practical. They require that the phylogenies are known. This led Bell (1989) to suggest his comparative method, where nested analyses of variance and covariance are used to partition variance between taxonomic levels, much in the same way as the methods developed by Clutton-Brock and Harvey (1977, 1979, 1984) with a major difference: for the logical reasons mentioned above, Bell does not measure correlations between groups but instead within groups. However, his method still suffers from the problems associated with using non-cladistic classifications or using phylogenies only indirectly as mentioned earlier.

In summary: each method has its own specific drawbacks – practical or logical. It could be argued, however, that the requirement that the phylogeny should be known is not really an argument against a particular method. As Felsenstein (1985) remarks: "phylogenies are fundamental to comparative biology; there is no doing it without taking them into account".

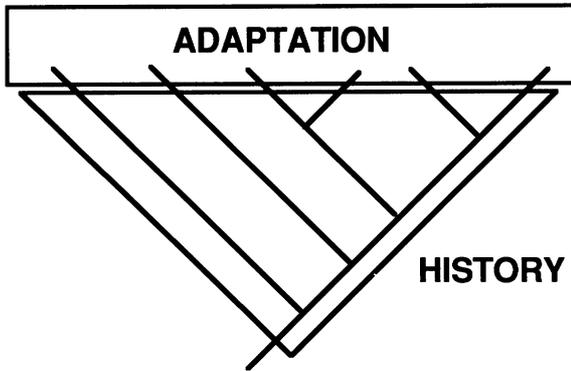


Fig. 11. Recent adaptation is “the tip of an iceberg of constraint”.

Procedure

Standard phylogenetic checks

Making certain phylogenetic checks standard practice would strengthen adaptational analysis.

Identifying candidates for adaptation

In studies focused on one species, cladistic analysis will identify those unique traits that could be given adaptational explanations at this level as autapomorphies. In a wider sense, cladistics can be applied as a tool to refer explanations to the proper phylogenetic level: the level where they appear as apomorphies. Because all traits appear as apomorphies at some level, a plesiomorphic trait that is given an historical explanation at one level, is of course a candidate for an adaptational explanation at some more general level (where it appears as an apomorphy). This approach has been underappreciated. Its power is neatly exemplified in Wanntorp's discussion of leaf retention in oaks (1983). Coddington (1988) discusses such cladistic tests of adaptational hypotheses.

Identifying the level at which statistical independence is attained

In comparative work on two or more species, one should determine at what level the traits involved can be treated as independent of one another. This point is old (Lack 1968), often repeated (Ridley 1983, 1989, Clutton-Brock and Harvey 1984, Felsenstein 1985, Pagel and Harvey 1988), and little heeded. The sum of ancestral traits – the “Bauplan” of Gould and Lewontin (1979) producing the “phylogenetic inertia” of Cheverud et al. (1985) – constrains the scope of the adaptively possible at every point in evolution (Brundin 1972). Some adaptations that occurred in the past characterize higher taxonomic levels, are integrated into both genotype and phenotype and function as constraints on lower levels (Fig. 11).

Identifying convergences

Independent derivation of similar traits in different lineages indicate convergence, one of the strongest types of evidence for adaptation. Convergence is often asserted without being demonstrated through cladistic analysis. Convergence can be demonstrated only a posteriori however, (e.g., Coddington 1985). After the cladistic analysis has been performed, it manifests itself as homoplastic traits that are in conflict with the general cladistic pattern. Purely numerical techniques could be used, for example, to identify convergence in quantitative characters. Once convergence has been identified, one can construct causal hypotheses by looking for similarities in the environment (Telenius et al. 1989). In Stearns' (1983) analysis of life history traits in mammals, for example, the similarity between beaver and coypu was striking. These two large, aquatic rodents are only distantly related cladistically. The similarities are thus homoplasies, convergences, which can be explained as adaptations to a shared life style leading to similar selection pressures on life history traits.

Analysis of coevolution

Mitter and Brooks (1983) and Brooks and Mitter (1984) suggested a role for phylogenetic analysis in studies of supposedly coevolved and coevolving species. The few studies published indicate that historical constraints are widespread in many groups but conspicuously lacking in some. Not enough is yet known to make any strong generalizations (see Brooks 1988 for a review).

Cladistic methods for ecological research

Phylogenetic systematics has developed three sets of techniques useful for studies of ecology and evolution:

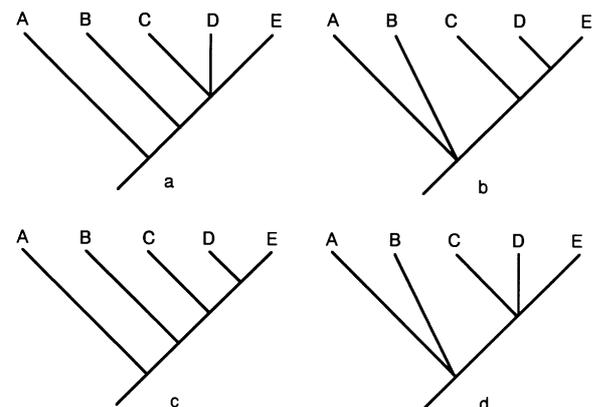


Fig. 12. Consensus trees: a and b are two cladograms of the same group of organisms based on independent data sets. c is an Adams consensus tree, and d is a Nelson, or strict consensus tree. The Adams tree is completely resolved, since the resolution found in either tree is not contradicted by the (lack of resolution in the) other. The Nelson tree only acknowledges the component CDE, since it is the only part identical to both trees.

(1) tree optimization, (2) consensus analysis and (3) parsimony mapping.

Tree optimization

Tree optimization is used to determine how many times and at which points in phylogeny a trait has arisen. Several methods have been developed for optimizing traits on trees, many of which are available as options on the computer packages PAUP (Swofford 1989) and Hennig 86 (Farris 1988). They give consistent results, differing only in the way in which they interpret convergent and parallel evolution (including evolutionary reversals). For those interested in phylogenetically conservative traits, this presents no problems. Those interested in phylogenetically plastic traits are often presented with more than one way to interpret their data (Coddington 1988).

Consensus trees

Consensus trees provide a summary when more than one cladogram for a group is available (e.g., based on different data sets, such as morphology and behavioural ecology as in the stickleback example above). Consensus trees are not valid summaries of data (Miyamoto 1983), but they are excellent for locating problem taxa and characters and for highlighting areas of agreement. There are two basic types of consensus trees. Adams consensus trees (Adams 1972) maintain all those portions of alternative trees that do not conflict with each other. Nelson consensus trees (Nelson 1979, 1983) maintain only those portions of alternative trees that are identical. Fig. 12a,b are alternative cladograms for the same taxa (A-G); Fig. 12c is an Adams consensus tree and Fig. 12d is a Nelson consensus tree (sometimes called a strict consensus tree).

Parsimony mapping

Species occur in various associations. Geographically-associated species are sympatric. Ecologically-associated species are synecological, symbiotic or syntopic. Each association is diagnosed by its component species. Historical effects in such associations will be manifested in patterns of co-variation of the phylogenies for the component groups. Documenting such co-variation, and departures from it, is accomplished by tree mapping or parsimony methods (Brooks 1981). In terms of phylogenetic analysis, this is accomplished by treating the cladograms for the associated groups each as a multi-state character of the association. Each particular association is treated as a "taxon" (e.g., species A and species X are sympatric in area III; area III is the taxon, and A and X are the characters). The species, plus codes for their phylogenetic relationships taken from their cladograms, are used as characters of the various associations, and a phylogenetic analysis is performed to obtain a summary cladogram for the associations. Those species that co-vary with respect to the summary cladogram have co-varying histories with respect to the

associations; those that depart from the pattern show an escape from the historical constraints at the point indicated by the incongruence. For a more complete discussion of the technical aspects of mapping methods, see Brooks (1988), Wiley (1988) and Funk and Brooks (in press).

Conclusions

If ecology and cladistics are to achieve a happy marriage, they will have to be able to communicate clearly. That this might not be straightforward is indicated by the fact that each field is dominated by different methodological paradigms. If ecology has a central methodology, it is statistics, in particular the analysis of variance and covariance. This predisposes one to think of quantitative traits, normal distributions and the partitioning of variance. Cladistics, on the other hand, predisposes one to think of qualitative traits, matrices of presence-absence values and parsimonious trees. Thus, phylogenetic systematics and ecology not only ask qualitatively different questions – roughly, history and relationship vs process and adaptation – but they also use qualitatively different methods to get their answers. The initial challenge in developing a methodology that could bring the two fields together is, first, to identify questions that both methodologies address, and second, to define clearly how the two methodologies can be coupled, in all technical detail, to achieve a common answer to which each has made a significant contribution. Some progress has been made, but much remains to be done. Ecologists who put phylogenetic methods into their tool-kit will see new problems and turn old ones on their heads. Systematists that work on organisms important in ecological research will contribute alternative explanations to a sister field and bring rigor to the analysis of adaptation.

We have stressed the rapprochement of ecology and systematics, but that emphasis resulted from the historical accident that a resurgence of interest in comparative analysis in ecology coincided with the development of interesting new methods in systematics. In principle, any field of biology with a comparative component stands to gain from introducing the phylogenetic view as one of its tools.

Acknowledgements – We wish to thank all participants of the "Adaptation and History" workshop at Tovetorp for a memorable week in the frosty spring of 1987. We also wish to thank the Nordic Council for Ecology which provided the economic means for bringing us all together, and the ethologists of Stockholm University for generously letting us take over their field station during that week.

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