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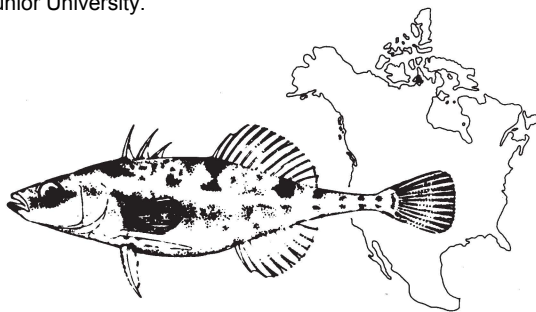
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## Historical Ecology as a Research Program

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Modern evolutionary biology is the descendant of two theories proposed by Darwin. First, all organisms are connected by common genealogy, and second, the form and function of organisms is closely tied to the environments in which they live. Of these two theories, the role of the first (phylogeny) in evolutionary explanations has been diminishing in some fields, most notably in ecology and ethology. However, the last ten years have witnessed the beginning of a reversal in this trend. With increasing frequency, ecologists (Wanntorp et al., 1990; Maurer and Brooks, submitted), ethologists (Dobson, 1985; Huey and Bennett, 1987; McLennan et al., 1988), functional morphologists (Lauder, 1982), and other evolutionary biologists (Ridley, 1983; Clutton-Brock and Harvey, 1984; Endler and McLellan, 1988) are accepting the proposition that some innovations that arose in the past have been integrated into the phenotype and function today as constraints on the evolution of other characters.

If persistent ancestral traits constrain the scope of the adaptively possible at every point in evolution, we expect better evolutionary explanations and predictions to come from restricting the genealogical rather than the ecological scope of any study. This can be shown by a simple thought experiment. Suppose we were to pick, at random, any organism from a designated tide pool and a crab from anywhere in the world. If we then asked for a list of morphological, behavioral, and ecological characteristics of the unknown organism from the designated environment and of the known organism (a crab) from an undetermined habitat, we would expect that more of the predictions would be correct for the crab than for the unknown tide pool organism. Knowing that we are dealing with "a crab" imparts more evolutionary and ecological information than the most detailed description of the tide pool. In this system, we can make better predictions by reference to genealogy than to current environments. The extent to which this would be true generally is related to the

extent to which genealogical properties should take precedence over local environmental conditions in evolutionary explanations.

Reference to phylogeny provides an historical context for evolutionary ecological explanations. For example, consider a large, white predator (species X) living in the arctic, and the question: "why is this species white?" A traditional approach to answering this question might be: (1) observation: "white" individuals are cryptic in the arctic environment; (2): hypothesis: white is selectively advantageous (i. e., at some time in the past individuals bearing white coats gained a large enough selective advantage over nonwhite individuals to promote the spread of white throughout the population/species); (3) prediction: white individuals will be "better" at acquiring either food or mates than their nonwhite counterparts; (4) test the predictions with a series of studies on mate choice and foraging behavior. The success of these studies requires that "white" is sufficiently variable to be quantified and compared among individuals. However, if coat color is a fixed trait, there is no way to test the hypothesis. Additionally, even if coat color does prove to be variable, studies concentrating on only one species are investigating only one aspect of the evolution of white coats, i.e., its maintenance in that species. This kind of analysis does not address the mechanisms by which a shift from the ancestral coloration to white occurred, nor does it address the question of the environmental conditions under which the trait arose and was fixed in the first place.

Now, let us approach the problem from an historical perspective. We begin by asking questions about *the origin of species X* and *the origin of white coat color*. Suppose that our initial investigations reveal (1) the ancestor of species X lived in an arctic habitat, and the speciation event producing species X and its closest relative occurred in that environment and (2) white coat color originated in the ancestor of X. The first step in the evolution of white coat color has now been traced: white originated in an arctic environment and its presence in species X is an ancestral legacy. Flushed with success, we turn our attention to the next problem, the potential mechanisms that promote the shift from ancestral coat color (say, brown) to white in the ancestor of X. This phase of the analysis requires that we search for correlations between white coat color and other ecological traits throughout the evolutionary history of the group of species to which X belongs. For example, one hypothesis might be that coat color in general is correlated with hunting behavior, and that white in particular is associated with hunting seals. Examining the distribution of feeding behaviors and coat color on a phylogenetic tree for this group of organisms will reveal information about the relationships between these characters through evolutionary time. Let us focus our attention on the ancestor of species X. There are three possible macroevolutionary patterns of the relationships between coat color and diet in this ancestor: (1) the shift to seal hunting arose before the appearance of white coloration. This indicates that brown, non-cryptic, individuals were capable of surviving by feeding on seals; (2) the shift to seal hunting and white coat color appeared at the same time (in the ancestor of species X). This relationship provides strong evidence that there is a causal link between color and hunting, supporting an hypothesis that white coat color conferred an adaptive advantage to its owners. This explanation could be strengthened if changes in coat color and feeding preferences co-vary throughout the evolutionary history of the entire group; (3) the shift to seal hunting arose after the appearance of white coloration. In this case, we are faced with the possibility that white individuals

could not compete successfully with other members of the community and were forced to change their feeding habits in order to survive.

Hopefully, this discussion about the evolution of white coat color in the mysterious, predatory species X has illustrated some of the new perspectives that will emerge from a phylogenetic (historical) comparison. Such an analysis allows us to investigate questions concerning (1) the evolutionary origin of a character and (2) the mechanisms promoting the spread of that character once it appeared in the population. Adopting this view clearly implies that a necessary pre-condition for any evolutionary explanation is an explicit hypothesis of phylogenetic relationships for the group of organisms being studied. The province of biological research directly concerned with the formulation, testing, and refinement of explicit hypotheses of phylogenetic relationships is phylogenetic systematics (Hennig, 1950, 1966; Wiley, 1981). It is therefore important that phylogeneticists develop research programs, complementing established research traditions, designed to incorporate historical explanations explicitly. The initial step in establishing such research programs has been the development of a rigorous, quantitative, reproducible method for discerning phylogenetic components in any system independent of theoretical assumptions or expectations peculiar to a particular discipline. This has largely been accomplished with the advent of phylogenetic systematics (Hennig, 1950, 1966; Wiley, 1981, this volume). The second step is more difficult in some ways, because it is not purely an empirical or scientific issue. In order to successfully develop complementary programs, there must be systematists willing to develop phylogenetic applications in specialized areas of research, and workers in various other fields willing to consider a broadening of their research agendas by incorporating phylogenetic explanations.

One such researcher was Herbert H. Ross. Ross (1972a,b) was particularly interested in explaining speciation patterns for a variety of groups within the most diverse taxonomic class on this planet, the insects. Based upon his discovery that only approximately one out of every thirty speciation events in these groups was correlated with some form of ecological diversification, Ross suggested that ecological change was consistent with, but much less frequent than, phylogenetic diversification. Furthermore, since he could not uncover any predictable patterns to explain the shifts that did occur, he proposed that ecological change comprised a biological "uncertainty principle" in evolution. More than a decade passed before Ross's insights were corroborated by another study. Boucot (1983) reported that the majority of ecological changes leaving some trace in the fossil record occurred out of timephase with periods of phylogenetic diversification. Like Ross, he concluded that ecological change lagged behind morphological and phylogenetic diversification, or "evolution takes place in an ecological vacuum."

Brooks (1985) consolidated the research of these authors into a discipline that he called historical ecology. Research in this discipline is primarily concerned with the investigation of macroevolutionary processes; i.e., among-species phenomena that occur over relatively long time periods and relatively large spatial scales whose effects are found in patterns of phylogenetic constraints on any system being studied (Goldschmidt, 1940). Historical ecologists make use of phylogenetic trees to produce direct estimates of the origin and persistence of various aspects of ecological diversity and associations. Initially, such researchers focused their attention upon the macroevolutionary components of ecological associations, such as host-parasite or herbivore-plant systems, or communities and biotas. Recently however, the discipline has

expanded to include the effects of two general evolutionary processes, speciation and adaptation, in the context of both evolving groups (clades) and ecological associations (systems and biotas) (Brooks and McLennan, 1991). This approach allows us to examine two kinds of macroevolutionary questions about groups of organisms. First, how did a given species arise? In order to answer this, we must explore a variety of ways in which descendant species are produced from an ancestral species (speciation). Second, how did a given species acquire its repertoire of behavioral/ecological characters? This question moves us into the more familiar realm of the relationships between an organism and its environment (adaptation). Answers to these questions provide the groundwork for asking analogous questions about the evolutionary histories of multi-species ecological associations (co-speciation and co-adaptation).

## THE PHYLOGENETIC METHOD

The foundations for historical ecology lie in the "comparative method." This is a term used by different biologists to mean different things. For some, the comparative method refers to studies in which distantly related species that live in the same habitat are examined for common morphological, ecological, or behavioral traits. Those traits in common are then explained as convergent adaptations to a common environment. For others, the comparative method refers to studies in which morphological, ecological or behavioral traits of interest are examined in light of the phylogenetic origins of those traits. It is this second form of the "comparative method," more properly called the "phylogenetic method," that is pertinent to historical ecology. Within this context, it is important for researchers to be as rigorous as possible with their phylogenetic hypotheses. It is inappropriate to use a taxonomic classification as a phylogeny because many classifications portray paraphyletic (or polyphyletic) taxa as monophyletic groups. Evolutionary explanations based on these classifications will overestimate the importance of adaptive plasticity because diagnoses for paraphyletic groups list synapomorphic traits more than once. This gives the impression that these traits are actually examples of parallel or convergent evolution and such homoplasy, in turn, is often considered strong evidence of adaptive evolution. Figure 1a depicts the phylogenetic tree for a clade of five species, showing species D and E as highly distinct from species A, B, and C on the basis of five synapomorphies (characters 6–10). Figure 1b depicts a tree reconstructed from a classification scheme that places species A, B, and C in one group, and species D and E in another group because they are "so distinct." This arrangement forces us to postulate that characters 2–5 evolved twice, overestimating the amount of adaptive evolution.

The use of paraphyletic taxa as evolutionary groups in classifications may also produce spurious, and exception-ridden, generalizations. For example, Figure 2 depicts a phylogenetic tree for a group of species, along with the distribution of particular morphological ( $M_1$  and  $M_2$ ) and functional ( $F_1$  and  $F_2$ ) traits. Taxonomic analysis of the group might produce a classification, based upon the hypothesized evolution of co-adapted trait complexes, that clustered species A and B together ( $M_1$  and  $F_1$  are co-adapted), and clustered species D and E together ( $M_2$  and  $F_2$  are co-adapted). Under such a scheme, the phylogeny of the group corresponds to the evolution of co-adapted trait complexes, with the exception of species C, for which some special explanation is now necessary. The phylogenetic tree, however, implies

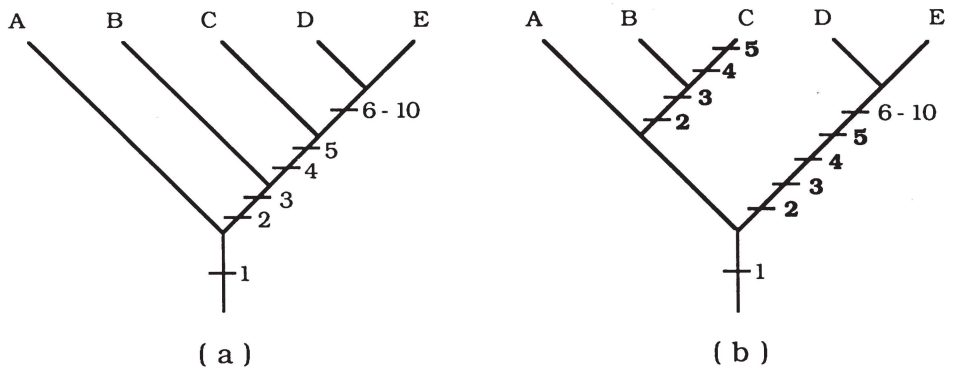


Figure 1.

Using paraphyletic taxa as monophyletic groups overestimates the amount of adaptive evolution that has occurred in any group. (a) Phylogenetic tree for taxa A–E, indicating 10 derived traits that have each evolved once in the group. (b) Tree diagram representing a classification scheme in which taxa A, B, and C are considered one group and taxa D and E, which have 5 unique traits (traits 6–10) and are thus “very different” from A, B, and C, are considered another group. According to this classification, characters 2, 3, 4, and 5 have evolved twice.

that the correlation of  $M_1$  and  $M_2$  with  $F_1$  and  $F_2$  is the result of common phylogenetic history. The presence of  $M_1$  and  $F_2$  in species C indicates different rates of evolutionary divergence in morphology and function, demonstrating the relative evolutionary *independence* of morphology and function in the group. Hence, there is actually no evidence of co-adapted trait complexes in this case. Most commonly accepted classifications contain paraphyletic groups, and thus cannot serve as independent templates for estimating the influence of phylogenetic constraints and adaptive plasticity on the evolution of those organisms. One cannot simply equate “taxonomy” with “phylogeny” and use current classifications for studies of historical ecology. However, given the current dearth of phylogenetic trees available, a number of ecologists who have tried to incorporate phylogenetic information into their explanations have been forced to rely on current classifications.

Phylogenetic systematics provides three sets of techniques useful to studies of ecology and evolution: (1) tree optimization, (2) consensus analysis, and (3) tree mapping (or parsimony analysis at the level of clades).

### Tree Optimization

Tree optimization is used to determine how many times and at which points in a 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 and PHYSYS. They give consistent results, differing only in the way in which they interpret convergent and parallel evolution (including evolutionary reversals). Convergent evolution of similar traits in different lineages is considered to be one of the strongest types of evidence for adaptation; however, convergence is often asserted without demonstration by phylogenetic analysis (Fig. 3a and 3b). Phylogenetic systematics provides a strong test of homoplasy because it is the homoplasious

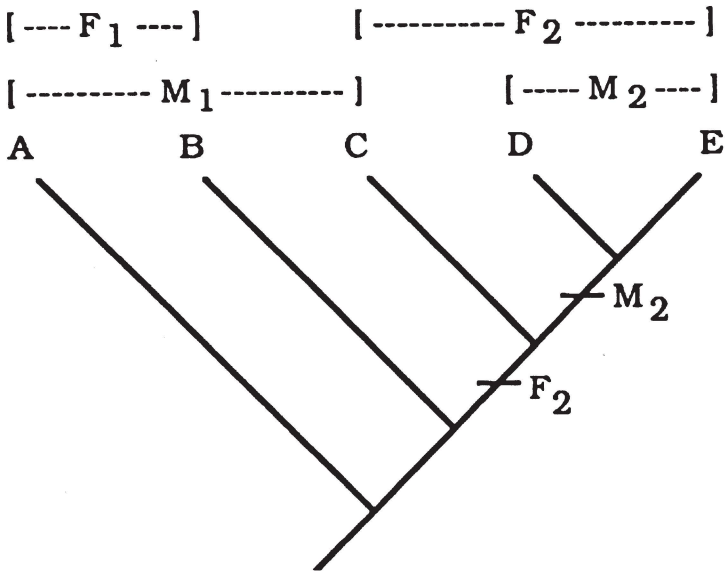


Figure 2. Paraphyletic taxa used as monophyletic groups may provide misleading and exception-ridden generalizations about evolution. If taxa A and B are considered one group, and taxa D and E another, there is a perfect correlation between morphology and function (M<sub>1</sub>/F<sub>1</sub> and M<sub>2</sub>/F<sub>2</sub>), suggesting the existence of co-adapted trait complexes. Taxon C remains an exception, having M<sub>1</sub> and F<sub>2</sub>. When the five taxa are viewed in their proper phylogenetic context, the evolutionary hypothesis suggests that the transitions M<sub>1</sub> to M<sub>2</sub> and F<sub>1</sub> to F<sub>2</sub> are not coupled; hence, there is no evidence of co-adapted trait complexes.

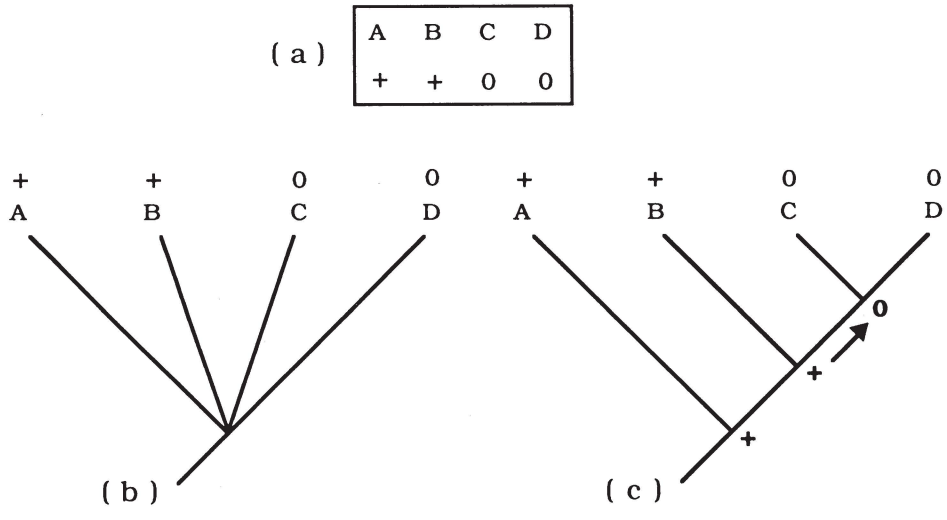
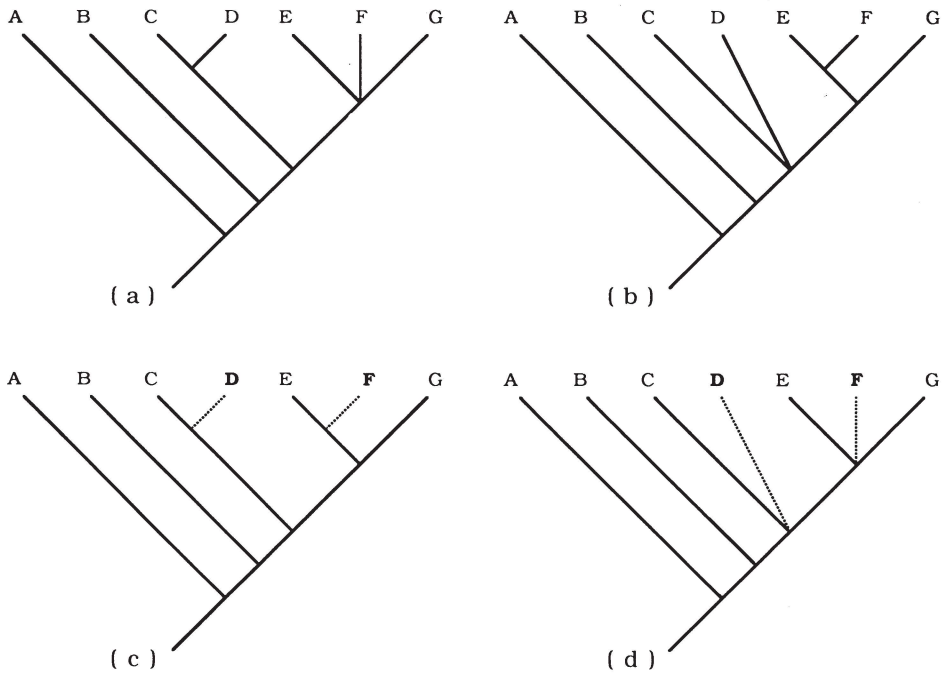


Figure 3. Tree optimization. (a) Distribution of character states "0" and "+" among species A-D. (b) Distribution of character states "0" and "+" among species A-D with unresolved phylogenetic relationships. In this case it is impossible to determine how many times "0" and "+" have evolved and which state is ancestral to the other state. (c) Distribution of character states "0" and "+" optimized on phylogenetic tree of taxa A-D; trait "+" is interpreted as being a persistent ancestral trait in A and B, with "+" evolving into "0" in the common ancestor of C + D. (Redrawn and modified from Funk and Brooks, 1990)



**Figure 4.**

Consensus analysis. (a) and (b) are two partially-resolved trees for the same taxa. (c) The Adams consensus tree for 4a and 4b. (d) The Nelson consensus tree for 4a and 4b. Dashed lines indicate the ambiguous placement of taxa D and F (Redrawn and modified from Funk and Brooks, 1990)

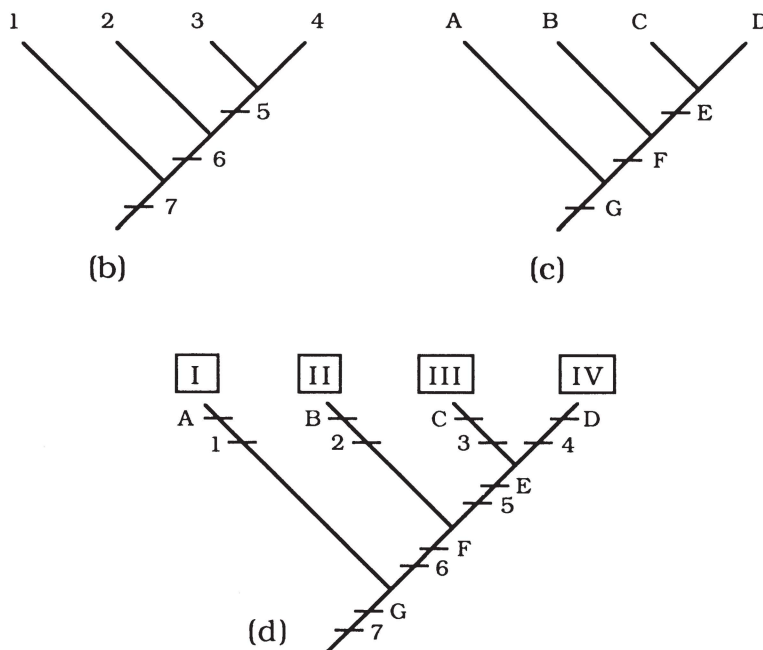
characters that are highlighted against a background of presumed evolutionary homology. Putative convergences are identified *a posteriori* from phylogenetic analyses based on a set of characters for which no postulate of convergence was proposed *a priori*. Convergences in quantitative or qualitative traits can be identified by optimizing such characters onto phylogenetic trees constructed using other data (Fig. 3c). Once convergence has been identified, adaptive hypotheses can be constructed by looking for similarities in environments inhabited by taxa exhibiting the convergent traits.

### Consensus Trees

Consensus trees provide a summary when more than one cladogram for a group is available. Consensus trees are not valid hypotheses of phylogenetic relationships (Miyamoto, 1983), but they are excellent tools for locating problem taxa and characters, and for highlighting areas of agreement (see Funk and Brooks, 1990, for applications of consensus analysis). There are two basic types of consensus trees. Adams consensus trees (Adams, 1972) indicate those portions of alternate trees that do not conflict with each other. Nelson consensus trees (Nelson, 1979, 1983) indicate only those portions of alternate trees that are identical. Figures 4a and 4b are alternative cladograms for the same taxa (A–G); Figure 4c is an Adams consensus tree and Figure 4d is a Nelson consensus tree (sometimes called a strict consensus tree).



	Species	1	2	3	4
(a)	Species	A	B	C	D
	Area	I	II	III	IV



**Figure 5.** Brooks Parsimony Analysis (BPA). (a) The distribution of species of two hypothetical fish clades in 4 different areas. (b) Phylogeny for clade comprised of species 1–4 with interior branches numbered for parsimony analysis. (c) Phylogeny for clade comprised of species A–D with interior branches labeled for parsimony analysis. (d) The area cladogram supported by the phylogenies of the two clades. Note that there is complete congruence in this example.

### Parsimony Analysis (Brooks Parsimony Analysis, BPA)

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. We can document such covariation, and departures from it, by tree mapping or parsimony methods. 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 1 are sympatric in area III—area III is the taxon, and A and 1 are the characters) (Fig. 5a–c). 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 (Fig. 5d). Those species that covary with respect to the summary cladogram have covarying 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 parsimony mapping methods, see Brooks (1988a, 1990), Wiley (1988a, b), Mayden (1988), Funk and Brooks (1990), and Brooks and McLennan (1991).

## SPECIATION: EMERGENCE OF MACROEVOLUTIONARY PATTERNS

Speciation is one of the two evolutionary processes upon which historical ecology is based (the other being adaptation). Mayr (1963) recognized three general classes of speciation: (1) reductive speciation, in which two existing species fuse to form a third. Harlan and DeWet (1963) proposed the term "compilo-species" for cases in which one species absorbs another, although examples of this phenomenon have not been documented to date; (2) phyletic speciation, in which a gradual progression of forms through a single lineage (anagenesis) are assigned species status at different points in time. Although the endpoints of such a continuum may be recognizably "different," separation of the intermediate forms into distinct groups is an inherently arbitrary exercise (Hennig, 1966; Wiley, 1981). Additionally, since we consider each individually evolving lineage to be a single species, "phyletic speciation" can only represent intraspecific evolutionary change; i.e., change preceding or following, but not correlated with, speciation; and (3) additive speciation, which involves lineage splitting (cladogenesis) and reticulate evolution. The majority of examples of speciation represent cases of additive speciation. No single mechanism is responsible for the initiation of additive speciation (Wiley, 1981). Several mechanisms have been proposed, and we will consider each as a distinct "model" of speciation. It is important to remember that, whatever the process, speciation does not just produce species; it produces sister species. Since this irreversible production of groups which are each other's closest relative introduces an historical component into the process, speciation cannot be studied without first determining the sister group relationships within the system of interest. Assuming that two species are or are not "closely related," and basing hypotheses of the speciation model involved in their production on this assumption, will, in most cases, ultimately lead to confusing and contradictory results.

Wiley (1981; see also Wiley and Mayden, 1985) suggested that the various models of additive speciation could be studied by establishing phylogenetic, biogeographic, and population biological predictions corresponding to each model. In order to begin such extensive studies, three assumptions concerning the nature of the data must be satisfied. First, character evolution must provide a reliable basis for reconstructing sequences of speciation events, that is, speciation has left a trace of its actions that we can detect. This assumption requires that one of two processes be occurring; either character evolution is tightly coupled with speciation or character evolution occurs at the same or higher rate than lineage splitting. Thus, even if the divergence of particular characters is not driving the divergence of the lineages, there will be an historical trail of character anagenesis highlighting speciation events. Although the second condition represents the traditional perspective of evolutionary biologists, the recent advent of punctuated equilibrium models (Eldredge and Gould, 1972) has strengthened the proposition of a causal relationship between character modification and speciation. The first assumption is violated if gene flow is halted permanently between populations at a faster rate than character change is occurring. If this happens, the traits present in each species will represent a combination of (i) characters that existed prior to the isolation of the populations, providing information about common ancestry (symplesiomorphies) and (ii) evolutionary modifications that occurred subsequent to the population's isolation, providing

information about the unique status of the population (autapomorphies). Since derived traits are not shared between populations under these circumstances, sequences of speciation events will be difficult or impossible to determine.

The second assumption is that there have been no extinctions in the clade. If we are to use phylogenetic trees to study particular modes of speciation, we must have confidence that sister species are each other's closest relatives; and not, in reality, more distantly related due to the extinction of several unknown intermediate species. Consider the following hypothetical example. Two groups of fish, demonstrated to be sister species on the basis of a phylogenetic analysis, are located on either side of a mountain range. Based on these observations, we might hypothesize that the disjunct distribution was caused when the upheaval of the mountains separated the ancestral species into two populations, which subsequently diverged in isolation. Unfortunately for our theory, a group of enthusiastic paleontologists discover an abundance of fossil evidence suggesting that at least two other species fall between the extant representatives. Hence, the current disjunction of fishes B and C was probably derived through a series of speciation and extinction events; only one of which need be associated with the tectonic activity.

The third assumption postulates that the influence of geographical separation during the evolutionary divergence of a clade has not been obscured by rampant dispersal of the descendant species. Pairs of sister-species or clades that show such dissemination may be identified by large-scale sympatry; however, uncovering such sympatry creates a problem because it is difficult to determine whether the current distribution pattern existed during the speciation of the group, or whether it represents widespread dispersal following speciation in isolation.

It is probably true that many groups will not satisfy all the assumptions; however, until a larger data base is established, it is impossible to determine whether these nonconformists need be accorded the status of an overwhelming majority or a confounding minority. We are confident that numerous clades will emerge in which phylogenetic patterns and distribution patterns are congruent with predictions from particular speciation models.

## Documenting Modes of Speciation

There are several putative modes of speciation, each of which involves a distinct combination of factors. Wiley (1981) and Funk and Brooks (1990) have summarized the predictions of the major modes in terms of phylogenetic patterns as follows:

### Sympatric speciation

Sympatric speciation occurs when one or more new species arises with no geographic segregation of populations. Mechanisms underlying this speciation mode include hybridization, ecological partitioning, sexual selection, and evolution of asexual or parthenogenetic populations (e.g., through apomixis). Phylogenetic support for postulates of sympatric speciation requires that the sympatric species be true sister-species, that is, each other's closest relatives. This, in turn, is based on the assumptions that no other, more closely related, species have become extinct since the formation of the two sympatric species, and that present-day sympatry reflects

sympatry at the time of speciation. These latter two criteria are obviously difficult to document.

Speciation by hybridization is a particularly important phenomenon among plant groups, as well as among certain groups of freshwater fishes and lizards. There are three classes of phenotypic and ecological outcomes of this mode of speciation: (1) The hybrids can segregate phenotypically and ecologically with one of the two parents. Since the hybrids are subjected to the same selective regime as the parents, and the parents are already surviving in the environment, it is likely that the hybrids will survive as well. Mixed stands of such "species-groups" have been documented (Funk, 1985). Interspecific competition may occur under these conditions, since new genetic information has been added to the system without enlarging the available resource base. (2) Hybrids may represent mixtures or intermediate forms of parental attributes. The genotypic and phenotypic flexibility of these individuals may allow them to survive in a wider range of habitats than either parent, reducing the likelihood of competition between parent and offspring. (3) Hybrids could represent a unique phenotypic and ecological system. In this case, survival is more problematic because the new combination must correspond to one allowed by un- or under-exploited resource bases in the local environment. However, such hybrids, if they survive, should face no competition from either parent. Each of these three pathways of survival open to species of hybrid origin implies different microevolutionary scenarios. These scenarios can be tested if one has a phylogenetic tree that indicates parental identity and the degree of similarity between parents and descendants. Funk (1985) presented a protocol using consensus tree analysis to document and to assess such data.

#### Allopatric speciation I (vicariant or geographic speciation)

This mode of speciation results from the physical separation of an ancestral species into two or more relatively large and isolated populations, with subsequent lineage divergence by the fragmented populations in isolation. In this case, sister-species will be allopatric, the ancestral species' distribution may be estimated by summing the distribution of the descendant species, and the points of geographic disjunction between species correspond to the historical boundaries established by the physical changes. Because the mechanism initiating speciation is independent of any particular biological system, a variety of species inhabiting the same area should be fragmented in the same way by the physical events, and could all speciate in accordance with that geological pattern. Hence, we would expect the biogeographic distribution patterns indicated by the phylogenies for a number of different groups would be the same. The majority of published examples of vicariance biogeography are putative cases of this mode of allopatric speciation (see Wiley, 1988a, for a summary).

#### Allopatric speciation II (peripheral isolates allopatric speciation)

This mode supposes that a new species arises on the periphery (periphery may be ecologically or physiographically defined) of a larger ancestral population. The parental species, which occupies the central range, must be demonstrably plesiomorphic in all characters relative to the descendant species in order to be readily

recognized. The descendant species, by contrast, must exhibit one or more autapomorphic traits and occur in a peripheral locality relative to the putative ancestor. Since the conditions under which different species' populations may invade and or be isolated in peripheral habitats will depend on the abilities of each species, replicated biogeographic patterns are not expected for different clades undergoing peripheral isolates speciation. However, under special circumstances, such as sequential dispersal along an island chain, there may be repeated biogeographic patterns following Hennig's Progression Rule (Hennig, 1966; see Wiley, 1981). Wiley (1981) also suggested that speciation in species comprising demes with restricted gene flow, such as asexual clades, should correspond to this class of phylogenetic patterns. Published studies purporting to demonstrate evidence of peripheral isolates allopatric speciation include: Hart (1985a, b) for plants in the Andes, Lynch (1982) for toads of the genus *Ceratophrys* in eastern South America, and Wiley (1981, 1988a) for fishes of the genera *Xiphophorus* and *Heterandria* in Central America. However, not all the groups in these studies satisfy all the criteria discussed above.

### Parapatric speciation

Parapatric speciation results from population differentiation into descendant species despite some gene flow and geographical overlap during the process. This produces sister-species that exhibit parapatric (partially abutting) geographic distributions. As with peripheral isolates allopatric speciation, the probability of parapatric speciation is clade dependent; therefore, repeating biogeographic patterns are not expected. An interaction between allopatric and parapatric mechanisms occurs when speciation initiated in allopatry continues even when the diverging populations subsequently become parapatric (allo-parapatric speciation of Wiley, 1981). Depending on the population size, this mode may or may not produce replicated biogeographic patterns among clades.

## Frequency of Modes of Speciation

Lynch (1989) has presented an analysis of more than 60 documented cases for vertebrate speciation. His study suggests that 71% of the cases are due to vicariant (allopatric mode I) speciation, 15% are due to peripheral isolates (allopatric mode II) speciation, and 6% are due to sympatric speciation (the remaining 8% comprised cases for which an assignment could not be made unambiguously). He also concluded that many of the putative cases of peripheral isolates allopatric speciation were really microvicariance, suggesting that peripheral isolates allopatric speciation might be no more common than sympatric speciation among vertebrates. Lynch's study suggests that the majority of speciation events result from the physical partitioning of information systems rather than environmentally-driven diversification.

## Macroevolutionary Trends in Diversity: Species Number

The term diversity has been used in a variety of ways by biologists. Some researchers associate "diversity" with the number of species in a group, the number of individuals in a population, or the relative number of individuals of different

species in a given community or ecosystem. Others associate "diversity" with the ecological or behavioral diversification among members of a group, the ecological or behavioral variation among members of a population, or the ecological or behavioral differentiation among the members of a community or ecosystem. In this section, we will address macroecological questions concerning the number of species in different groups. The goal of this research is to determine if there are clades of "unusually high" or "unusually low" species number, and to attempt to explain those groups. The major drawback to such studies is the absence of a rigorous definition of what constitutes "unusual." Nonetheless, there is a perception that some groups are more speciose than other "equivalent" groups, and that there is an evolutionary explanation for this. It has been tempting to think that highly speciose groups are somehow "better" or "more successful" than average whereas groups of low species number are somehow "less successful" than average.

Mayden (1986) suggested that assessing differences in species number between or among groups required two things. First, all groups under examination must be monophyletic. Because phylogenetic systematics stresses the recognition of monophyletic groups, it is an appropriate starting point for studies of this component of diversity. Second, the groups being compared must be of equal antiquity. A number of methods have been proposed for documenting the relative ages of clades. Stratigraphic and biogeographic analyses attempt to use environmental parameters as independent indicators of age. The use of "genetic distances" attempts to use a hypothetical "internal clock" that is universally informative about evolutionary rates. Phylogenetic systematics uses yet another criterion, sister-group relationships, since, by definition, each of two sister-groups is the same age.

A monophyletic group that is commonly perceived as "unusually" speciose is the passeriform birds. One explanation of this diversity is that passeriforms, as a group, possess some "key adaptation" that has allowed them to become "more successful" evolutionarily than other birds (but see Raikow, 1986). Kochmer and Wagner (1988) suggested that the small size of passeriforms relative to other birds was the key adaptation. They contended that species of relatively small organisms have more chances for ecological specialization (the other component of diversity) and hence should become more speciose as a result of their relatively greater success at carving up environmental resources. Fitzpatrick (1988) also suggested that passeriforms' relatively small size was their key adaptation, but attributed their evolutionary success to their role of ecological generalists. Two steps are required for the clarification of this problem: (i) a refinement of the data base for foraging habits within the passeriforms and, minimally, their sister group and (ii) a phylogenetic analysis of the relationships within the passeriforms and, minimally, their sister group. This is the only way to determine whether the foraging mode displayed by the passeriforms is a plesiomorphic (ancestral) trait or a derived trait. For example, suppose the passeriforms are ecological generalists. If the sister group of the passeriforms includes species that are also generalists (at least primitively within the group), then the presence of that foraging mode among passeriforms is not a unique attribute of song birds. Rather, the propensity to be an ecological generalist has been inherited from some common ancestor that gave rise to groups some of which are, and others of which are not, unusually speciose. This result would not support the hypothesis that the evolutionary success of passeriforms is due to their role as ecological generalists. Historical ecology, then, calls for both an increase in and a collaboration

between experimental and phylogenetic programs. This in itself makes such research efforts exciting.

Simpson (1944) was among the first modern evolutionary biologists to consider general explanations for groups of unusually low species numbers. Simpson considered all such groups "relicts" of one form or another, recognizing that different processes could produce different kinds of relictual groups. Phylogenetic relicts are "living fossils," members of groups that have existed for a long time without speciating very much. Such low speciation rates could be due to phylogenetic or developmental constraints on phenotypic diversification, or could be due to unusually pronounced ecological specialization, leading to choice of specialized habitat that acted as strong long-term stabilizing selection. Numerical relicts, by contrast, are the relatively few surviving members of once more-speciose groups that have been depleted by extinction. Brooks and Bandoni (1988) have suggested that phylogenetic relicts, whether the product of evolutionary constraints or stabilizing selection, should be ecologically conservative, whereas numerical relicts should be ecologically diverse. Clearly, the integration of phylogenetic and ecological information may be of great use in explaining differences in species numbers among low-diversity and high-diversity groups, but this field requires much development.

## ADAPTATION

The search for a functional (adaptive) fit between an organism and its environment is one of the dominant themes in evolutionary biology (see, e.g., Lewontin, 1978; Dunbar, 1982; Coddington, 1988). There are three components to adaptation: origin, diversification, and maintenance of characters. Microevolutionary studies concentrate on the maintenance of traits in current environments where the processes shaping the interactions between the organism and its environment can be observed and measured directly. Having untangled this complicated web, these researchers then extrapolate backwards to the processes involved in the character's initial appearance in, and subsequent spread through, the ancestral species. Even if we assume that all evolutionary innovations are adaptations, it is still relevant to ask whether the innovation arose in the species at hand, and hence possibly in the environment at hand, or whether it arose in an ancestor and possibly in a different environment. The inheritance of the trait from ancestors should always be considered as the evolutionary null-hypothesis. Only traits demonstrated to be novel in the species at hand (autapomorphies) are candidates for explanations that invoke environmental conditions unique to a particular species. If we do not assume that all innovations are adaptations, i.e., if we assume that "adaptive evolution" is not synonymous with "evolution," then we must ask just what are the criteria for recognizing particular key innovations as adaptations (Coddington, 1988). For example, the European oak is well known for its habit of retaining its leaves far into the winter. This is especially notable in young specimens and makes them conspicuous in the deciduous woodland they inhabit. Several theories have been proposed explaining leaf retention as an adaptation (Otto and Nilsson, 1981; Nilsson, 1983). Wanntorp (1983) used phylogenetic analysis to show that all oaks of warmer climates are evergreen, and close relatives of the common oak are semi-evergreen. Leaf retention is ancestral in oaks and needs no special, adaptive, explanation in the European oak.

## Adaptive Change in Qualitative Traits

Historical ecology complements microevolutionary studies by providing direct estimates of phylogeny which can be used as a template for reconstructing the historical patterns of character origin and diversification. Such a template can help biologists to focus their search for the processes underlying adaptation. For example, it has long been thought that the development of aposematic, or warning, coloration required the involvement of kin selection (Fisher, 1930; Harvey et al., 1982). The idea was straightforward: while some mutants with warning coloration would be eaten, or damaged and killed, because predators were thought to learn slowly and to kill their prey before determining their toxicity, their similarly-colored siblings would be avoided. Under this hypothesis, gregariousness should evolve first, provide a context in which kin-selection could work, then be followed by the evolution of aposematic coloration. Sillén-Tullberg (1988) tested this idea by referring to the best available taxonomies (explicit phylogenetic hypotheses do not yet exist for many groups) for a number of butterfly lineages. Her focus was on the order of events: did gregariousness evolve before, with, or after warning coloration? In 15 cases, gregariousness evolved after warning coloration, and in no case did it evolve before warning coloration. In three cases, the two traits arose on the same branch of the tree, and in five lineages gregariousness evolved without warning coloration. This observation makes sense when one remembers that butterfly eggs and larvae are exposed, small, relatively immobile, and a good source of nutrition. A predator that finds an aggregation should consume all the individuals in it. On these grounds, it is unlikely that gregariousness would evolve before unpalatability, and this indeed appears to be the case. The evidence presented by Sillén-Tullberg argues for individual selection of warning coloration and against the kin-selection hypothesis for its origin.

Historical ecological methods can also be used to establish whether or not phylogenetic diversification could have involved interspecific competition. Let us consider the Compositae genus *Montanoa* Cerv. *Montanoa* has 30 taxa, 25 of which are shrubs or vines and five of which are trees growing to approximately 30 meters in height. All species have wind-dispersed seeds. The trees all have daisy-like flowers, grow in cloud forests at higher elevations than other species in the genus, and three that have been examined chromosomally are high-level polyploids. One species grows in each of the following locations: Guerrero, México; Chiapas, México, and northern Guatemala; Costa Rica; Venezuela and Colombia; and the Santa Marta Mountains, Colombia. All five species have a number of similar morphological and anatomical characters that allow them to survive in cloud forests; none has ever been found at lower elevations. They are members of four different clades, their sister-species being shrubs living at adjacent lower elevations in each case (Funk, 1982). One could speculate that in each case natural selection had favored the evolution of the same kind of strategy for surviving in cloud forests. One might also be tempted to explain the absence of sympatry between the tree and shrub forms as an example of competitive exclusion. However, an understanding of the phylogenetic constraints involved in this system leads to a different interpretation.

Among composites, it is common (1) for polyploids to be larger than diploids, hence, "trees versus shrubs" may simply be a consequence of ploidy level, and (2) for polyploids to be produced so the parallel and convergent appearance of polyploids in this group is not a surprising phylogenetic pattern. Physiologically, composites are



relatively inefficient water conductors so it is unlikely that the large tree forms could survive outside of high-moisture habitats like cloud forests. On the other hand, greenhouse experiments (Funk, pers. comm.) indicate that the seeds of shrub-like species of *Montanoa* cannot survive under conditions of high moisture. The developmental constraints on size, moisture requirements, and moisture tolerance lead to three predictions: (1) any polyploid seed that is produced too far from a cloud forest to disperse into a high moisture zone will never germinate; (2) no diploid seed that disperses into a cloud forest will survive in the high moisture conditions; and (3) no polyploid seed that disperses outside a cloud forest will germinate successfully in the low moisture conditions. The convergent evolution of tree-like species indicates a certain degree of developmental plasticity in polyploid production (something common among composites). The habitat segregation between trees and shrubs results from developmental constraints on moisture requirements/tolerances in the clade leading to strong selection against diploids in cloud forests and against polyploids in more mesic environments. No matter how many times the tree-like polyploid forms evolve, they will never occur sympatrically with any diploid species so the necessary initial conditions for inter-specific competition will never be established.

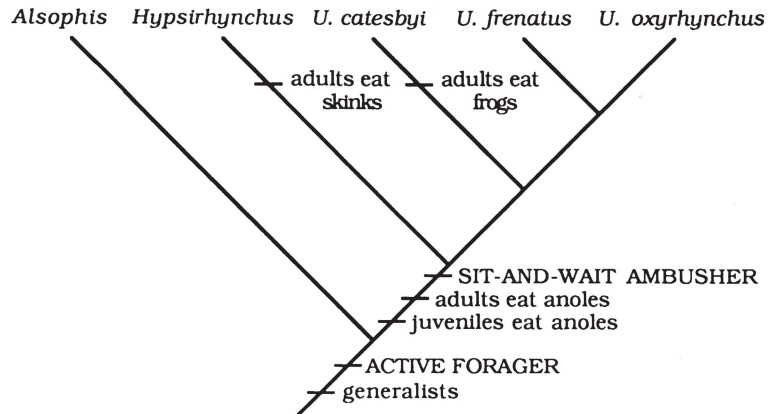
On the zoological side, snakes on Hispaniola exhibit a variety of feeding strategies utilizing local frogs and lizards as prey. Some are generalists and some are specialists; some are active foragers and others are sit-and-wait ambushers. Traditionally, the differences in the foraging and feeding behaviors of each species have been explained as adaptive responses to inter-specific competition. Henderson et al. (1988) provided ecological and phylogenetic data for some members of *Hypsirhynchus*, *Uromacer*, and *Alsophis*, using *Antillophis*, *Ialtris*, and *Darlingtonia* as outgroups (Fig. 6).

Their analysis suggests that the active foraging, generalist feeding mode employed by *Alsophis cantherigerus* is plesiomorphic in these snakes. The change to a sit-and-wait foraging strategy occurred in the common ancestor of *Uromacer* and *Hypsirhynchus* and has been retained in all its descendants. These relationships emphasize the importance of historical constraints on foraging behaviors in these groups. *Uromacer catesbyi* is reported to show both active and sit-and-wait behaviors. This raises some interesting points about the control of these two behaviors, which have been treated as alternative character states in the analysis. The most parsimonious phylogenetic explanation is that active foraging has re-evolved in *U. catesbyi*. However, when this problem is examined in light of the snake's diet, a new explanation presents itself. All the "sit-and-wait" species on the island feed predominantly on some type of anoline lizard, except for *U. catesbyi*, which eats frogs. Perhaps the appearance of "active" foraging is associated with this shift to such a novel prey item. Observations recorded in the literature also suggest that *U. catesbyi* is the worst sit-and-wait predator in the genus *Uromacer*, and that it is frequently seen chasing its prey, presumably after missing them by the first strategy! Further field observations are required to discover whether *U. catesbyi* does indeed display both foraging modes (which requires quite a complex phylogenetic explanation) or whether its chasing behavior is simply a by-product of its inability to capture frogs very efficiently. Additional resolution of the relationships among all the colubrid snakes in this area is also required before this problem can be adequately formulated. For example, three species of colubrid were not included in the study group because information on their feeding habits and behavior is lacking. Of these, all are active foragers: one feeds

Figure 6.

Feeding habits of colubrid snakes on Hispaniola Island mapped onto a phylogenetic tree for the group.

*U.* = *Uromacer*.



on frogs almost exclusively, one feeds on anoles primarily and frogs secondarily, and the feeding habits of the third are unknown. Interestingly, the most plesiomorphic member of the study group, *Alsophis*, is an active forager feeding on, among other things, frogs. Although the recurring association between active foraging and feeding on frogs is a tantalizing one, without further phylogenetic analysis such a relationship is, for the moment, speculative.

Although foraging mode is phylogenetically conservative among these colubrid snakes, there has been moderate evolutionary divergence in the group with respect to the principal prey item. All species retain the plesiomorphic juvenile feeding preference for anoles, and *U. oxyrhynchus* and *U. frenatus* carry this preference into adulthood. *Hypsirhynchus ferox* becomes more specialized on teiid lizards (*Ameiva*) and *U. catesbyi* switches to frogs (*Osteopilus*). These species pinpoint profitable foci in the search for adaptationist explanations of ecological diversity in this group of snakes. Although there has been a trend within the group toward an increase in dietary specialization, only three of the eight branches on the phylogenetic tree are characterized by any shift in feeding mode. It is therefore unlikely that such diversification has been driven solely by competitive interactions favoring niche partitioning. Instead, phylogenetic analysis suggests that the observed ecological diversity is a reflection of more than one factor, only one of which might be competition.

### Adaptive Change in Quantitative Traits: Integrating Statistical and Phylogenetic Approaches

Over the last decade, a renewed interest in the genealogical aspects of evolution has emerged in the form of a new research program that attempts to strengthen our examination of adaptive hypotheses by considering the effects of phylogenetic constraints on quantitative traits. The reasons for this are twofold: first, it utilizes the kinds of data already collected by ecologists, and second, it is in the variability of quantitative traits, shown by statistical analysis, that the effects of natural selection can be most easily detected. A number of studies have demonstrated that much of the variation and covariation of quantitative traits present in a clade arises at higher taxonomic levels (e.g., Brown, 1983; Stearns, 1983; Dunham and Miles, 1985; Cheverud et al., 1985). One explanation of these findings is that even quantitative

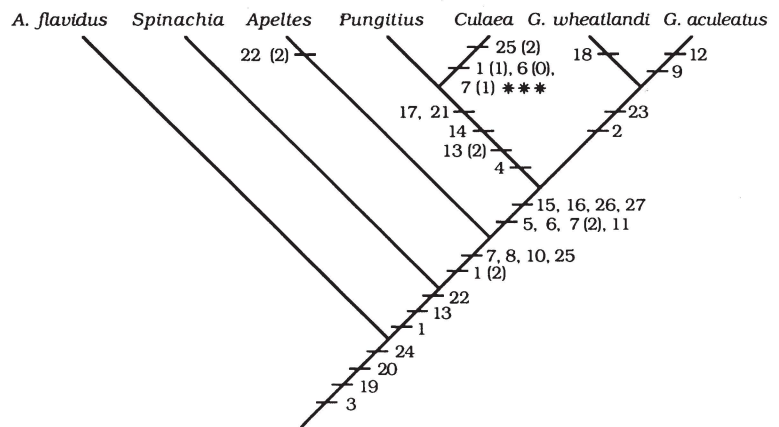
variation is progressively delimited within clades by constraints peculiar to those clades.

This proposition could be examined by: (1) constructing a phylogenetic tree for a given group, (2) mapping onto it the evolutionary innovations that are hypothesized to be acting as clade-specific constraints, and (3) calculating the deviations from the mean values for the quantitative traits thought to be constrained in a clade-specific fashion using a nested analysis of variance or covariance. Those evolutionary innovations hypothesized to be constraints could then be associated with positive or negative residuals of the quantitative trait for each clade. The result would be an hypothesis, based on correlation, about a putative causal link between the evolutionary innovations and the quantitative traits. This information could then be used to test alternative hypotheses about such links, for some hypotheses would be ruled out by the pattern observed. For example, allometric relationships such as size-fecundity or adult weight–birth weight vary within clades. Most of the variation is not among species, but among genera, sub-families, or families (Harvey and Clutton-Brock, 1985; Pagel and Harvey, 1988; Harvey and Pagel, 1991). Within a given species, the clade-level constraints function as boundary conditions on life-history evolution, and they have been used in predictions of optimal life histories (e.g., Stearns and Koella, 1986). In a multivariate analysis of life-history variation in the mammals, Stearns (1983) found that most of the patterns of covariance formerly attributed to r- and K-selection resulted from correlations with two factors: body size and phylogenetic relationship. When the influence of those factors was removed from the data and the residuals examined, very little of the original covariance remained to be explained by microevolution operating within species. Work by Brown (1983) and Dunham and Miles (1985) provided empirical support for that expectation. Brooks and Wiley (1988) suggested that r- and K-selection represented the range of alternate manifestations of energy processing in biological systems and, as such, should be primarily correlates of body size and history. When phylogenetic relationships are taken into consideration this postulate is supported by the empirical data.

### Adaptive Change in Ethological Traits: Integrating Experimental and Phylogenetic Approaches

Comparative ethology is founded upon a tradition of incorporating both phylogenetic (historical) and environmental (selective) factors in explanations of behavioral evolution (Darwin, 1872; Whitman, 1898; Wheeler, 1928; Lorenz, 1941; Tinbergen, 1964). The last two decades have witnessed an increase in studies involving the environmentally-based maintenance of behaviors with a concomitant decrease in the number of evolutionary questions examined within a phylogenetic framework (but see Dobson, 1985; Coddington, 1986; Sillén-Tullberg, 1988). For example, the form of a species' mating system is hypothesized to result primarily from selection imposed by local environmental conditions (Vehrencamp and Bradbury, 1984). McLennan et al. (1988) examined this hypothesis using stickleback fishes (family Gasterosteidae). They constructed a cladogram for sticklebacks based solely upon behavioral traits (Fig. 7). The resulting tree had a high consistency index (90.3%) and a low F-ratio (7.3), indicating a high overall level of historical constraint and a low degree of evolutionary plasticity for the behavioral traits used to construct the tree.

**Figure 7.**  
Phylogenetic tree for  
gasterosteid fishes derived  
from behavioral characters.  
Numbers = characters;  
\* = homoplasious traits.  
(Redrawn and modified  
from McLennan et al.,  
1988)



When the distribution of species' mating systems and habitat preferences were examined on the tree an intriguing result emerged.

Within the Gasterosteidae, *Pungitius* and *Gasterosteus* are habitat generalists. *Gasterosteus aculeatus*, for example, exists as marine, estuarine, anadromous, and freshwater populations. Among the freshwater populations, habitats range from ephemeral, weed-choked ditches to large, oligotrophic lakes. At the other end of the spectrum, the fifteen- and fivespined sticklebacks are habitat specialists: *Spinachia spinachia* is restricted to marine habitats and *Culaea inconstans* to freshwater ones. *Apeltes quadracus* falls somewhere between these extremes, preferring brackish habitats but venturing into freshwater areas on occasion. Although they live in vastly different environments, all gasterosteids exhibit a male territorial (character 20), polygynous (character 19), paternal care (Fig. 7, character 24) mating system. The presence of these behavioral patterns is thus a reflection of tight phylogenetic constraints on mating system evolution within this family of fishes. So, examination of the relationship between the form of the mating system and the environment on this coarse level of analysis reveals that this system is more closely tied to phylogeny than to the environment. However, the discovery of this phylogenetic influence is only the first step in developing a comprehensive evolutionary picture. We might next ask what factors were responsible for the initial success of that mating system, and what factors are responsible for its current maintenance throughout the entire family? Answering this requires an analysis of the fitness components of the mating system for each species (i.e., female fecundity, adult survival rates, female encounter rate; see Vehrencamp and Bradbury, 1984, for a detailed discussion). The results of such an analysis will provide a more robust estimate of the relative roles for the effects of both phylogenetic heritage and environmental factors in the evolution of this mating system.

The study by McLennan et al. (1988) illustrates three of the benefits of utilizing the phylogenetic approach in the study of behavioral evolution:

#### Differentiation between character origin and character maintenance

Current behavioral patterns represent an interaction of past (historical constraints) and present (environmental selection). Studies of the evolutionary signifi-

cance of a character should evaluate both factors to avoid confusing character maintenance with character origin and diversification. For example, the presence of circle fighting behavior (Fig. 7, character 11) in all members of the monophyletic group *Gasterosteus* + *Pungitius* + *Culaea* suggests that circle fighting arose in the ancestor of this clade. Any questions about the environmental context in which fighting arose must be based on assessments of the relationship between the ancestor in which the trait appeared and the environment at that time. Studies of fighting behavior in the four contemporaneous species are studies about the maintenance of fighting, not its origin.

### Examination of current evolutionary hypotheses

Phylogenetic systematic analysis can be used to assess the support for existing hypotheses of behavioral evolution. For example, Tinbergen (1953) predicted that increasing levels of aggression should be accompanied by increasing ritualization of aggressive behaviors. Within the gasterosteids, experimental evidence suggests that *Spinachia* is the least aggressive, and *G. aculeatus* the most aggressive, of the sticklebacks (Wootton, 1976). The phylogenetic diversification of aggressive behaviors parallels this change (Fig. 8); there is a macroevolutionary transition from chasing to threatening to fighting behavior. This analysis thus provides corroboration for Tinbergen's hypothesis, and an unexpected bonus. Examination of the tree reveals that each evolutionary change in an aggressive display (traits in capital letters in Fig. 8) is accompanied by a change in a submissive display (traits in lower-case letters in Fig. 8).

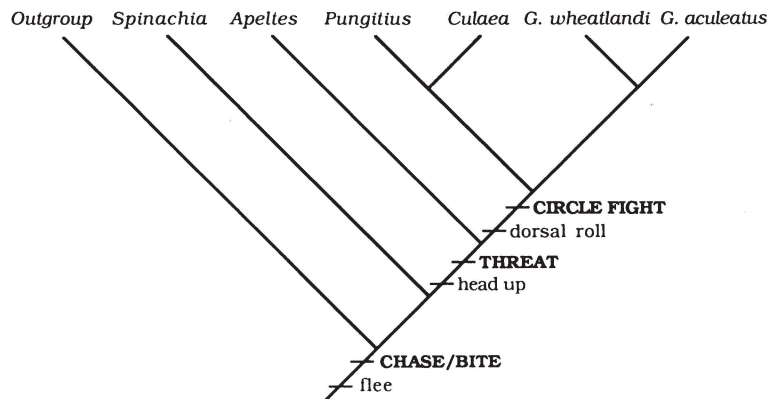
### Experimental predictions

Phylogenetic analysis of patterns and relationships between characters provides a framework of predictions for experimental examination. Consider the following question: "what is the evolutionary significance of sexually dimorphic breeding coloration in the three-spined stickleback, *Gasterosteus aculeatus*?" Based upon the macroevolutionary relationships between breeding colors and breeding behaviors depicted on the gasterosteid tree, three predictions, relevant to a discussion of nuptial coloration in *G. aculeatus*, can be proposed (see McLennan et al., 1988; McLennan, 1991, for details of these predictions): nuptial coloration is (i) weakly associated with male/male interactions (intra-sexual selection), (ii) moderately associated with parental care (natural selection), and (iii) strongly associated with male/female interactions (intersexual selection). These predictions, construed as evolutionary null hypotheses, were tested in laboratory studies of an anadromous, three-spined, population. In brief, the following experimental results were obtained:

- (a) **investigation of the endogenous rhythm of color change across the territory acquisition/nest building (male/male interactions), courtship (male/female interactions), and parental stages of the *G. aculeatus* breeding cycle:** The results corroborated the phylogenetic predictions. Each male displayed (i) his most intense, widely dispersed color signal during courtship, (ii) a second, but significantly lower, peak in color during fry guarding, and (iii) virtually no color development during territory acquisition, maintenance, and nest building (McLennan and McPhail, 1989).

**Figure 8.**

Phylogenetic tree for gasterosteid fishes showing origin and diversification of characters involved in aggressive and submissive interactions. Upper-case letters = aggressive behaviors; Lower-case letters = submissive behaviors (Redrawn and modified from Brooks and McLennan, 1991).



- (b) **investigation of the relationship between male color and female behavior:** When given a choice of two competing, territorial males, females from this population spawned almost exclusively with the most intensely colored male (McLennan and McPhail, 1990; see also Milinski and Bakker, 1990). Once again, the phylogenetic prediction that intersexual selection has played a significant role in shaping male nuptial coloration in the gasterosteids is confirmed by experimental investigation.

### Macroevolutionary Trends in Diversity: Adaptive Radiations

The concept of adaptive radiations has played an important role in both evolutionary ecology, as an explanation for differences in diversity among groups, and in systematics, as a rationale for including grade groups in classifications. And yet, there is little in the way of published expectations about the macroevolutionary patterns that should characterize adaptive radiations. We must determine the criteria by which adaptive radiations can be assessed, and then ask how many putative speciation events on a given phylogeny are marked by such changes. From this analysis of the relative proportion of the clade's evolution that has been "adaptive," one could argue for or against an explanation of "adaptive radiation" in any given case. Ross (1972a) investigated changes in biogeographical dispersal (a species occurring in a non-vicariant area with respect to its relatives), divergence in ecological life history traits or behavior from the plesiomorphic condition, and host shifts for a variety of insect groups. He concluded that adaptive changes (any of the above three) occurred about once every 30 speciation events. More recently, Andersen (1982) presented a monographic revision of the Gerromorpha, a group of semi-aquatic hemipteran insects. He demonstrated that ecological correlates of speciation could often be used as diagnostic traits at what he considered to be generic levels and higher. This indicates a high degree of phylogenetic concordance and conservatism in ecological diversification that corroborates Ross's observations. Brooks et al. (1985) studied the putative adaptive radiation of the digenetic trematodes, a group of endoparasitic flatworms. They used the following criteria for adaptive changes: (1) morphological homoplasy (whether correlated with functional change or not); (2) changes in development of invasive larvae that increased the numbers of such colonizing stages;

changes in the ecological life history traits involving the first intermediate host (3), the second intermediate host (4), or the final host (5); and (6) changes in the mode of infection of the second intermediate host. Their study concluded that approximately one out of every four family-level groups was characterized by some form of adaptive change in any one of the above six criteria. Coddington (1988) has suggested a number of additional criteria by which adaptive evolution can be assessed. These include (in increasing order of explanatory value): (1) the appearance of homoplasy correlated with functional change on a phylogenetic tree; (2) the appearance of predicted homoplasy correlated with predicted functional changes; and (3) the appearance of particular structural change correlated with particular functional change, regardless of homoplasy. In his study, Coddington discussed a number of examples and found that in no case could the conclusion of adaptive evolution be supported by invoking any of his criteria. Additional studies, such as those reported in Brooks and Wiley (1988), corroborate the notion that only a small proportion of rigorously documented evolutionary diversification has been demonstrably adaptive by these criteria.

It is clear that the term adaptive radiation means different things to different people. It is also clear that relatively few studies have assessed the degree of adaptive radiation for a clade using any empirical criteria, and that those studies that have attempted such assessments have found the adaptive radiation postulate unsatisfactory. As a result of findings discussed above, several classical adaptive radiations should be subjected to phylogenetic analysis in which the putative adaptations and the putative environmental conditions with which they should be associated are included, as much as possible, on the cladogram. Coddington (1988) has demonstrated that one such classic example, the case of the Galapagos finches, has no rigorous analytical base from which any conclusions about adaptation or adaptive radiations can be drawn. Until such analyses show the extent to which adaptations are associated with radiations, the word "adaptive" should be eliminated from the catch phrase "adaptive radiation."

## HISTORICAL ECOLOGY OF ECOLOGICAL ASSOCIATIONS

Ecological associations do not evolve in the same sense that species evolve; rather, they are "assembled." However, some of the "assembly rules" may be evolutionary. For instance, ecological associations are (1) spatially localized, although their boundaries are often fuzzy, (2) comprised of particular species, and (3) characterized by particular interactions among the species. These components impart a high degree of predictability to ecological associations, and historical ecology attempts to determine how much of that predictability is due to historical constraints. Such constraints comprise the "assembly rules" that may be integrated with "production rules" to provide robust causal explanations for the structure and function of ecosystems. Historical ecology asks three types of questions about ecological associations: (1) how did their component species come to be in the same geographical area; (2) how did particular species come to be intimately connected within the association; and (3) how did the traits that characterize those intimate interactions among species within the association come to be?

## Research Programs I: Biogeography

There are two macroevolutionary explanations for the occurrence of a given species in a given area. The first is that the species evolved in place; that is, its ancestor (or a population of its ancestor) inhabited the area in which the species now occurs. This phenomenon is called vicariance. Species within a given ecological community that have evolved *in situ* will exhibit covarying geographic distribution patterns with respect to their patterns of phylogenetic relationships. The second explanation is that the species evolved elsewhere and subsequently dispersed into the area under investigation. Community members will exhibit independent geographic distribution patterns. If the phylogenetic trees for the various members of an ecological association are treated as multi-state characters of their areas, and a parsimony mapping exercise performed using these areas as taxa, the resultant tree of area relationships will partition out the historical (vicariant) and non-historical (dispersal) geographical components of any ecological association. Those portions of phylogenetic trees congruent with the resultant area tree represent the historical portion of the species associations (explanation 1 above); incongruent portions represent episodes of dispersal (explanation 2 above). For a review of methods and studies performed to date, see Wiley (1988a, b).

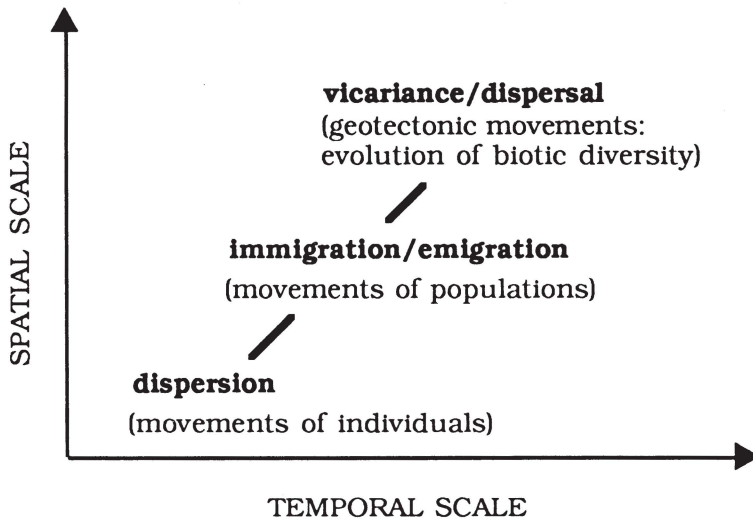
### Spatial scaling effects

The question of historical components in biogeography touches on many researchers' interest in macroecology—scaling effects. Brooks (1988b) suggested that phylogenetic studies in biogeography could be related to the biological relationships between temporal and spatial scaling effects. The longer the time scale chosen for observation of a biological system, the greater the degree of historical constraint involved in producing the observed patterns of diversity. In a complementary manner, the larger the spatial scale chosen for study, the greater the degree of historical constraint expected in producing the observed patterns of diversity and distribution.

On the smallest spatial scales, biogeographic patterns result from micro-habitat distribution and vagility of the organisms being studied. As the observation arena increases, the number of species comprising the biogeographic patterns increases. On intermediate spatial scales, particular communities, ecosystems, or biotas form the units of pattern. Processes dominating these spatial scales are species composition phenomena, immigration-emigration dynamics, and biotic expansion and contraction. Finally, on large spatial scales groups of biotas form the units of study. Since most species occur allopatrically from their closest relatives (see section on speciation: Lynch, 1989), it should follow that the larger the spatial scale, the greater the likelihood that the relevant biogeographical patterns will involve groups of phylogenetically-related species. Figure 9 presents a heuristic view of biogeography unified by scaling effects and phylogenetic constraints.

There are three important consequences of these scaling effects: (1) the larger the spatial scale chosen for a particular analysis, the greater the likelihood of finding vicariant elements in the members of any ecological association; (2) in order to detect historical constraints in the organization of any fairly localized ecological associa-





**Figure 9.** Heuristic representation of the relationships among spatial scaling effects, temporal scaling effects, and production of biomass and diversity with respect to patterns and processes in biogeography. (Redrawn and modified from Brooks, 1988b).

tion, it is necessary to examine a number of different associations; and (3) if ecological associations reflect organized patterns of energy use (the ecological hierarchy), increasing the spatial observation arena will increase the the proportion of historically determined (the genealogical hierarchy) energy use patterns (see Brown and Maurer, 1987, 1988; Maurer and Brooks, 1991). We will return to these points when we discuss the evolution of multi-species ecological associations.

## Research Programs II: Coevolution

The macroevolutionary perspective on coevolution parallels the macroevolutionary perspective on biogeography. Two or more species may exhibit a non-random interaction because their ancestors interacted with each other. In this case the interaction is a persistent phylogenetic constraint on the organization of the ecological association. Conversely, the species may have evolved in association with other species and subsequently become involved in the interaction seen today. In this case, there has been a departure from phylogenetic constraints. The macroevolutionary aspects of coevolution of interacting species may be divided into two separate processes: *co-speciation* and *co-accommodation* (Brooks, 1979). Co-accommodation involves the the degree of mutual modification (factors like host preference and host suitability), while co-speciation involves the degree of phylogenetic congruence (concomitant speciation), or incongruence, between host and parasite lineages. Brooks (1979, 1980, 1981, 1985, 1988a), Mitter and Brooks (1983), and Brooks and Mitter (1984) suggested a role for phylogenetic analysis in studies of putatively coevolved and coevolving species. Several discussions have centered around the proper use of the term "coevolution"; does it signify reciprocal modification of interacting species, with phylogenetic components possible but not part of the process, or phylogenetic association, regardless of degree of mutual modification? The few studies published indicate that historical constraints (congruent portions of host and parasite phylogenies for co-speciation, persistent ancestral ecological traits for co-accommodation) are widespread in many groups but conspicuously lacking in

some. For a discussion of parsimony methods used in comparisons of host and parasite phylogenies and of representative studies published to date, see Brooks and McLennan (1991).

Insect-host plant associations have been studied with increasing intensity ever since the publication of the pioneering work on butterfly-host plant coevolution by Ehrlich and Raven (1964). In this area of study, debate over evolutionary processes responsible for extant patterns of insect-host plant associations has been particularly vigorous. In contrast, parasite-host associations have tended to be studied from a phylogenetic perspective with the majority of research based on helminth and arthropod parasites of vertebrates (see Brooks, 1988a, for a review of studies). Finally, there is a dearth of studies investigating the possible coevolution of other interacting components of ecosystems (such as predator-prey systems). Based on research spanning the past 25 years, three major classes of models of coevolutionary processes, with their phylogenetic expectations, can be recognized:

#### Allopatric co-speciation (Brooks, 1979)

This model predicts congruence between host and parasite phylogenies based upon simultaneous allopatric speciation in parasite and host lineages, i.e., vicariance events. Since co-speciation is independent of any changes in co-accommodation, no general predictions about changes in co-accommodation are associated with this model. Hence, we would expect no predictable relationships between co-accommodation and degree of phylogenetic congruence for associates showing this type of coevolution. There may be a trend toward broadening of the co-accommodation whenever sympatry between two components of co-speciating clades is established subsequent to the speciation events. This model appears to represent the majority of helminth parasites-vertebrate systems (see, e.g., studies cited in Brooks, 1988a) and appears to be the primary form of association for copepod ectoparasites of elasmobranchs (Deets, 1987; Benz and Deets, 1988; Deets and Ho, 1988). However, it has received very little attention in the literature on insect-host plant associations until recently.

Roskam (1985) used phylogenetic analysis to investigate the evolution of the association between gall midges (*Semudobia* spp.) and their host plants, birches (*Betula* spp.). All four speciation events in the *Semudobia* cladogram correspond to dichotomies in the *Betula* cladogram. Of the two descendant species after the first speciation event in the gall midges, one (*S. skuhravae*) retains a broad host range and induces galls in bracts of fruit catkins of all betulid birches except the gall midge-free *Acuminatae*. 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 deciduous fruits, a derived condition only present in birches in the sections *Excelsae* and *Acuminatae*. After the second speciation event in the gall midges, there is only weak specialization in the descendant lineages, leading to a "doubling" of the host plant records of the remaining *Semudobia* species (Roskam and van Uffelen, 1981). The third and fourth co-speciation events are vicariance events, for there is a corresponding pattern of allopatric speciation in *Semudobia* and *Betula*. This study reveals the importance of co-speciation in the association between *Semudobia* and *Betula*, with only minor changes in

the host ranges of the gall-midges. The one major change in host range is readily explained as the exploitation of a new resource. The pattern of host plant associations in *Semudobia* gall midges is best fit by the allopatric co-speciation model.

### Sequential coevolution (Jermy, 1976, 1984)

According to this model, proposed for insect-plant systems, diversification of phytophagous insects took place after the radiation of the host plants and was *independent* of it. If, as suggested, the insects colonized new host plants many times during their evolution, insect and plant phylogenies should show no congruence. Miller (1987) compared cladograms of butterflies (Family Papilionidae) with traditional classifications of their host plants and found very little congruence between insect phylogeny and plant classification. The evolution of papilionid host plant associations is therefore characterized by numerous host plant shifts. Berlocher and Bush (1982) and Mitter and Brooks (1983) have performed or reported similar studies with similar results for other groups of phytophagous insects.

### “Classical” coevolution (Ehrlich and Raven, 1964)

The classical coevolution model, also proposed for insect-plant systems, may be summarized as follows. Phytophagous insects reduce the fitness of their host plants. Plants that by chance acquire traits (defense mechanisms) that make them unpalatable to phytophagous insects will therefore increase their fitness, and the new defense mechanism will spread throughout the plant population. However, some mutant insects will, in their turn, overcome the new defense mechanism and be able to feed on the previously protected plant group. These insects will increase their fitness because they will avoid competition with other phytophagous insects. The ability to overcome the new defense mechanism will spread throughout the insect population, and this insect population will specialize on the previously protected plant group. The predictions of the classical coevolution model are that (1) relatively primitive and relatively derived portions of the insect and plant phylogenies will be congruent, and (2) portions of the host phylogeny will include non-parasitized species (these representing the descendants of ancestors that developed defense mechanisms). Brooks (1988a) presented a theoretical example of this pattern. We are not aware of any phylogenetic studies to date that support this model, which is ironic because it was the study by Ehrlich and Raven (1964) that sparked the recent interest in coevolution among evolutionary ecologists.

It has also been postulated that the co-speciation events under this model will be associated with narrowing rather than broadening of the host plant range, where host specificity is taken as an indication of the degree of reciprocal adaptation. Coevolution for a group then may be characterized as more or less tight depending on the frequency of co-speciation events found, which represent extremely tight coevolution. Smiley (1978) presented an evolutionary scenario without reciprocal adaptations but with a tendency toward extreme specialization in phytophagous insects. This scenario leads to essentially the same phylogenetic predictions as the classical coevolution model.

### Research Programs III: Community Ecology

Ricklefs (1987) referred to the "eclipse of history" in community ecology as having a profound and adverse effect on the field. He argued convincingly that community ecology has relied predominantly on local-process theories for its 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 kilometers. Under this view, the community is maintained in a saturated equilibrium by biotic interactions. Independent lines of evidence from quite different communities, however, suggest that regional diversity influences local diversity. Despite similarities in local environments, there are four to five times more mangrove species in Malaysian swamps than in Costa Rican swamps and four times more chaparral plant species in xeric areas of Israel than in xeric areas of California. 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. Local species richness in Caribbean birds is strongly related to total regional bird diversity. These observations cannot be explained by postulating local, saturated equilibria, since equilibrium theory predicts that similar states would be attained in systems experiencing similar conditions.

The explanation of local community structure in these systems should include historical information about the biogeographic and coevolutionary components of communities. Ross (1986) and Mayden (1987), for example, reported a high degree of phylogenetic constraints in the structuring of fish communities. If a number of associated species show ecological shifts at equivalent points in phylogeny, it would be possible to find evidence of ecological reorganization and to ask if it appeared to be episodic or stochastic. Such questions have been broached by Erwin (1985) for neontological data and by Boucot (1978, 1982, 1983) for paleontological data. Boucot (1983) suggested that periodic episodes of massive ecological reorganization in the fossil record are a major source of "punctuated" change in community structure.

The communities of helminth parasites inhabiting Neotropical freshwater stingrays are good model systems for illustrating historical constraints on community structure. Brooks (1985) showed that the degree of historical influence on helminth community diversity differed among six areas in South America. The Parana system, the western Amazon, the Orinoco, and the Magdalena system all contain species whose phylogenetic relationships correspond to the geological history of the areas in which they occur. Because the Orinoco community also has species that colonized from other river systems, 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 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 Parana).

Within each of the communities identified for the freshwater stingray parasites, there are differences in patterns of host utilization. This represents differences in one form of ecological life history traits. The Parana community, which is the oldest, comprises four species of parasites whose occurrence in the region is due to historical association (vicariance) with the areas. Each of those four species is known to inhabit

more than one stingray host species. Hence, in terms of hosts utilized, there is as much historical association as there is host-switching. The western Amazon (six vicariant and one colonizing species) and Magdalena (five vicariant species) communities, by contrast, exhibit much more restricted host associations (one host switch in each case). The Orinoco community comprises two portions, a vicariant portion with five species of parasites showing only one host switch, and a colonizing portion with six species of parasites showing eight host switches. The eastern Amazon, with three species, all of which occur in the area because of colonization (themselves or an ancestor), exhibit two host switches as well. Finally, the Maracaibo area comprises three parasite species, two derived by colonization, exhibiting two host switches.

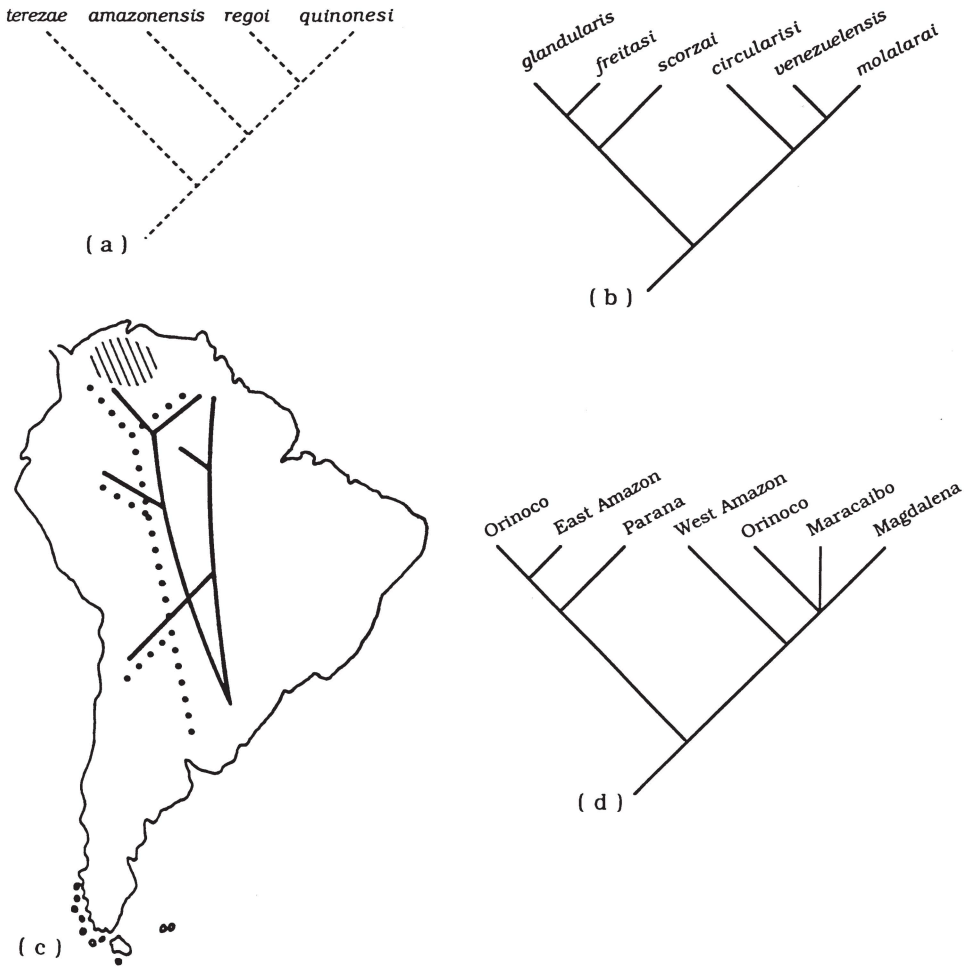
Because the historical assembly of these communities has differed among river systems and has led to quite different species diversities in similar environments, it would be misleading to try to construct a general explanation for each of them based on equilibrium assumptions. General explanations in community evolution may be apparent only when groups of communities are studied.

### Integrating the Scaling Effects and the Phylogenetic Approaches

The freshwater stingray parasite study provides an example of the relative importance of understanding spatial and temporal (phylogenetic) scales in studies of community evolution. If a single stingray species in a single area is chosen for study, we obtain data such as those reported by Brooks (1988b) for *Potamotrygon histrix* in the delta of the Orinoco River. Some of the parasites were found wherever *P. histrix* were found, while others appeared to have more restricted distributions (possibly due to sampling error). If we expand the scope of the study to include another stingray species (*Potamotrygon reticulatus*) in the same area, we find that one of the parasite species inhabiting *P. histrix* also occurs in *P. reticulatus*. And if we include non-stingray species in the study, we find that the majority of parasite species seem to inhabit only stingrays, while a few also inhabit teleosts.

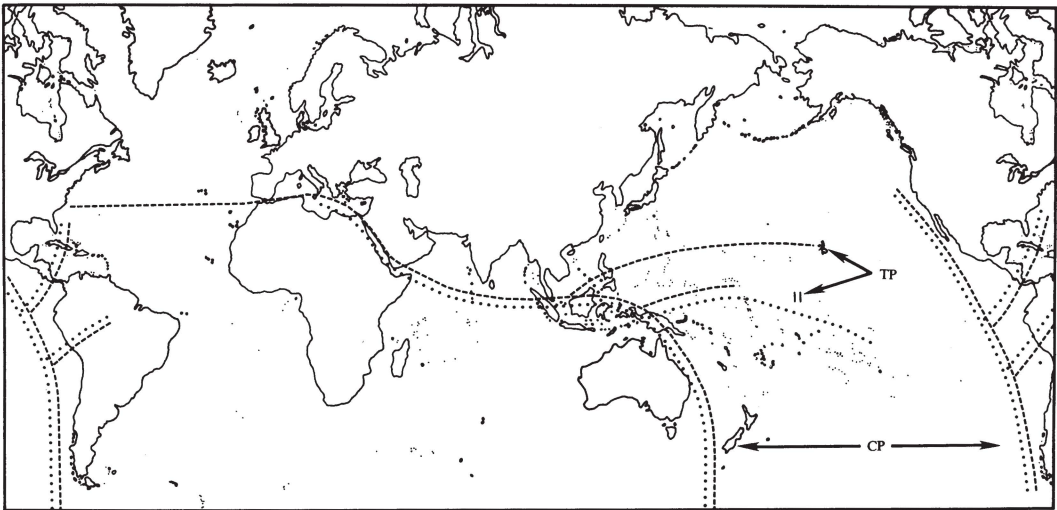
Now expand the study to include all stingrays and all their parasites from all the river systems in South America. Some of the rays and some of their parasites are found in restricted areas and others occur in more than one area. Because the spatial scale has increased and we are dealing with more than one community, we expect the degree of phylogenetic constraint on the patterns observed to increase. When we examine the phylogenetic components of the associations between areas and hosts, we find a great deal of phylogenetic constraint in the composition and patterning (with respect to host utilization) of the various communities that was not evident from observations of a single community (Fig. 10). There is a fit of approximately 75% (estimated by the consistency index) between the parasite phylogenies and the history of the areas in which they occur, and there is also approximately a 75% fit of the parasite phylogenies to the stingray phylogeny. In just over 50% of the observed cases, the host-parasite-geography co-occurrences can be completely explained by reference to history.

Finally, we expand the spatial scale to include the parasites (and their hosts) that are most closely related to those found in freshwater stingrays (Fig. 11). Potamotrygonids and their parasites appear to have originated from Pacific marine ancestors that were isolated in South America by the Andean orogeny (see also



**Figure 10.** Historical biogeography of parasitic helminths inhabiting neotropical freshwater stingrays. (a) Phylogenetic tree for members of the tapeworm genus *Acanthobothrium* inhabiting neotropical freshwater stingrays. (b) Phylogenetic tree for members of the tapeworm genus *Rhinebothroides*, all of whose members inhabit neotropical freshwater stingrays. (c) Map of South America with phylogenetic trees from 10a and 10b superimposed; shaded area is Maracaibo region. (d) Area cladogram for neotropical areas of endemism based on phylogenetic relationships of parasites inhabiting freshwater stingrays. (Redrawn and modified from Brooks, 1988b)

Brooks and Deardorff, 1988). A similar origin has been suggested for freshwater needlefish (Collette, 1982) and for freshwater anchovies (Nelson, 1984). This links the evolution of freshwater stingrays and their parasites with the evolution of Pacific stingrays and their parasites, while at the same time suggesting that the historical origins of the freshwater rays and their parasites are parts of a larger story involving other groups of organisms. That is, as the spatial and temporal scale of a study increases, the diversity encompassed by the relevant ecological patterns of association grows larger.



**Figure 11.**

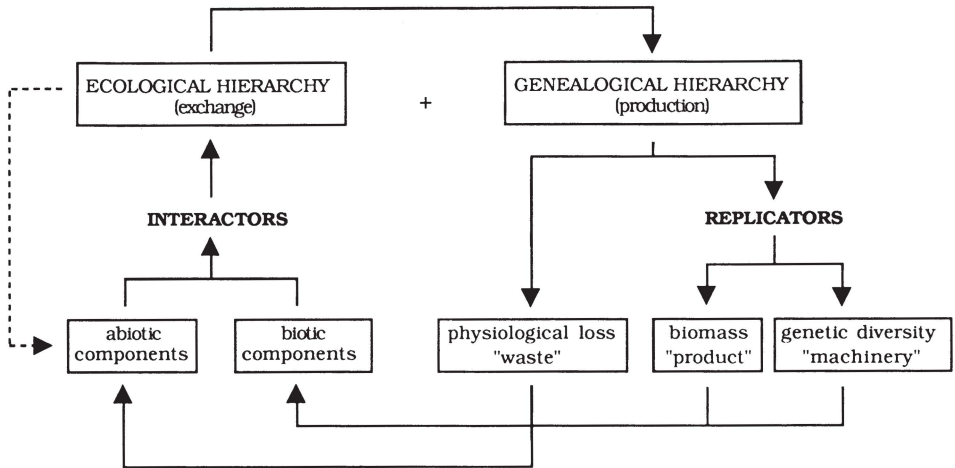
Historical biogeography of parasitic helminths inhabiting neotropical freshwater stingrays and their marine relatives, based on phylogenetic trees for species groups in the tapeworm genus *Rhinebothrium* and the nematode genus *Echinocephalus*. Note both circum-Pacific (CP) and trans-Pacific (TP I and II) distribution patterns, with the parasites in freshwater stingrays representing part of the circum-Pacific pattern. (Redrawn and modified from Brooks, 1988b)

A more quantitative approach is possible. Mayden's (1988) studies on the communities of freshwater stream fishes in North America include a number of different river systems. His findings suggest a high degree of historical constraints. Other contributions in this volume report similar findings. This is exactly what we would expect from the scaling effects predictions.

## EXPANDING THE EVOLUTIONARY FRAMEWORK

Evolutionary theory is experiencing a period of intensive re-examination. Some researchers assert that the synthetic theory of evolution, or neo-Darwinism, is essentially a complete theory. Others argue that there are gaps in the theory which can be addressed only by integrating traditional principles and research programs with new ideas. The mechanisms of evolutionary constraint are being examined on many levels, from phylogenetic to basic physico-chemical laws. We believe that a richer theory, based upon the incorporation of microevolutionary and macroevolutionary information, is emerging from these debates. Historical ecology may play a role in this emergence because it provides us with a way to integrate the study of macroevolution with the study of microevolution in a non-reductionist manner.

Although we think that historical ecology stands by itself as an interesting research program, we would like to try to place it within this broader conceptual context. Descriptively, the combination of "production" by biological systems and "exchanges" between such systems and their surroundings forms the biological economy. The production component comprises physiological dissipation ("waste"), biomass maintenance and accumulation ("product"), and genetic and



**Figure 12.**

The biological economy. Production components comprise the genealogical hierarchy and exchange components comprise the ecological hierarchy. Production stems from replicators and exchanges stem from interactors. (Redrawn and modified from Brooks and Wiley, 1988)

epigenetic information maintenance and accumulation ("machinery"), or the arena of replicators. The exchange component represents the intersection of all environmental resources and the useful resources as determined by what it takes to "run the machinery," or the arena of interactors. The source of the "machinery" requirements is the machinery plus the product (i.e., replicating organisms organized into demes, populations, and species, or the genetically diverse biomass). The source of the environmental resources are (1) abiotic materials and energy, (2) physiological dissipation products (production "waste"), and (3) biomass (production "product"). The exchange component, which represents the source of energy and matter for living systems, is the ecological hierarchy. The production component, which represents the fate of matter and energy taken up by living systems, is the genealogical hierarchy (Salthe, 1985; Eldredge, 1985; Brooks, 1988b; Brooks and Wiley, 1988; Maurer and Brooks, 1991). Figure 12 depicts the relationship between the two hierarchies in terms of exchange and production.

There are a variety of views about the causal nature of the two-hierarchy structure of biological systems (Salthe, 1985; Eldredge, 1985; Brooks and Wiley, 1988). Living systems are open thermodynamic systems. Open systems are characterized by changes in entropy ( $dS$ ) decomposed into two components, one describing entropy changes resulting from exchanges between the system and its surroundings ( $d_eS$ ) and the other describing entropy changes resulting from production by spontaneously irreversible processes occurring within the system ( $d_iS$ ). So long as the production term is positively entropic, the second law of thermodynamics is satisfied. Or,

$$dS = d_eS + d_iS, \quad d_iS > 0$$

Most of the thermodynamic activity of biological systems is accounted for by the exchange term,  $d_eS$ , in which the degrading effect of biological systems on their environments can be seen. However, accounting for the exchanges does not explain



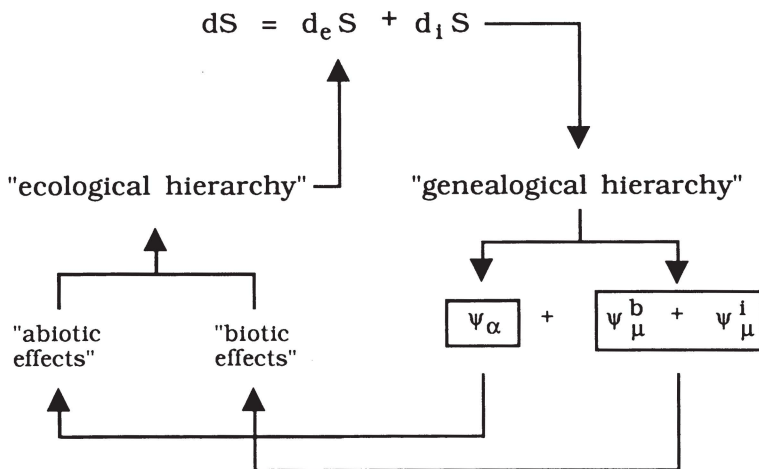


Figure 13. Major components of thermodynamic production (dissipation) and exchange in biological systems.  $\psi_\alpha$  = energy dissipation in the form of physiological waste;  $\psi_\mu^b$  = energy dissipation in the form of biomass accumulation;  $\psi_\mu^i$  = energy dissipation in the form of information diversity. (Redrawn and modified from Brooks and Wiley, 1988)

the particulars of the biological systems that carry out the exchanges with the environment. For that, we must examine the internal production aspects,  $d_i S$ , of biological systems. Prigogine and Wiame (1947), Zotin (1972), and Brooks and Wiley (1988) have associated  $d_i S$  with the fate of energy and matter taken up by biological systems from their environments. Symbolically,

$$d_i S = \psi = \psi_\alpha + \psi_\mu^b + \psi_\mu^i$$

where  $\psi$  represents fate or dissipation into production,  $\psi_\alpha$  represents "external dissipation" (physiological loss, or "waste"),  $\psi_\mu^b$  represents "bound dissipation" associated with biomass maintenance and accumulation ("product"), and  $\psi_\mu^i$  represents "bound dissipation" associated with the diversity of genetic and epigenetic information ("machinery"). Figure 13 depicts the integration of the biological economy (Fig. 12) with the behavior of open thermodynamic systems (see also Brooks and Wiley, 1988; Brooks, 1988b; Maurer and Brooks, 1991).

Production in living systems involves dissipation in all three components of  $\psi$  at all times. However, the relative importance of dissipation into each of the components depends on the time scale chosen for observing the behavior of the system. Over very short time scales, no changes in biomass or genetic diversity are seen, so all biological behavior is manifested in  $\psi_\alpha$ , physiological dissipation in the form of metabolic heat from the system. In thermodynamic terms, biological systems observed over very short time scales behave like "dissipative structures." On more intermediate time scales, the behavior of biological systems is dominated by processes associated with the accumulation of biomass ("product"). This takes a number of forms, from ontogeny to reproduction to ecological succession. On the longest time scales, the behavior of living systems is dominated by the tendency to accumulate genetic and epigenetic diversity ("machinery"). There is a common self-organizing phenomenology associated with these intermediate to long time scale production processes (Brooks and Wiley, 1988; Maurer and Brooks, 1991). The degree of self-organization is proportional to the degree of historical, or phylogenetic, constraints acting on the system. These constraints act to slow the rate of change, thereby increasing the time scale on which such changes are manifested. Thus, we expect that the longer the time scale, the greater the proportion of historical

components in the behavior of any living system. In addition, the longer the time scale, the greater the relative contribution of  $\psi_{\mu}^i$  to the observed patterns, hence, the greater the range of genetic and epigenetic diversity encompassed by patterns of organization relevant to that time scale.

If we adopt the two-hierarchy model as a working world view, it is appropriate to ask questions about the genealogical context of ecological and behavioral traits, and about the ecological context of genealogy. To paraphrase Darwin (1872:219), if there are phylogenetic constraints on ecological and behavioral diversification, it is possible that closely related species may display the same traits despite living in different environments. Further, contemporaneous species may exhibit ecological or behavioral traits that originated in environments quite different from those in which the species find themselves today. Hence, phylogenetic constraints may limit the ways in which and the extent to which species adapt to different and changing environments. On the other hand, two or more closely related species may live in similar habitats and yet exhibit divergent ecological or behavioral characteristics, indicating a certain degree of independence between the rules characterizing the genealogical and the ecological hierarchies.

## SUMMARY

For historical ecology to succeed, ecologists and phylogenetic systematists have to be willing and able to communicate clearly. Each field is dominated by different methodological paradigms and qualitatively different questions: origin, diversification, and association of traits for phylogeneticists; and maintenance and association of traits for ecologists. Bringing the two fields together requires that we identify questions of interest to both and clearly define how research programs in each field can be applied to enhance explanations to which each has made a significant contribution. The potential rapprochement of ecology and systematics implied by historical ecology results from the resurgence of interest in comparative analysis in ecology at a time when methods for documenting the patterns of evolutionary origin and diversification have been developed to an unprecedented degree in systematics.

A variety of biologists are beginning to use phylogenetic information in evolutionary ecology and adaptation theory. Their motivations differ, however. Some use traditional data, collected to answer traditional questions, adding a phylogenetic component to distinguish past local adaptive effects from present local adaptive effects. These workers assume that microevolutionary theory is an essentially complete general evolutionary theory. They expect that the results of adding phylogenetic components to their studies will produce no surprises, but will mostly "tidy up." This is the "thesis" or "Ghost of Research Past" position. For many of these workers, it is sufficient to equate "phylogeny" with "current taxonomy."

Other workers who examine the relationship between ecology and phylogeny represent an "antithesis" perspective. These workers tend to doubt the traditional descriptions and explanations in evolutionary ecology, and use phylogenetic analysis to demonstrate the shortcomings of previous research. This is the "Ghost of Research Present," which focuses on gaining better-resolved descriptions of the evolution of ecology and behavior. Such work tends not to be concerned with any particular underlying explanatory framework.

We believe that a "synthesis" of descriptive and explanatory frameworks is

necessary. It is for that reason that we introduced historical ecology by placing it within macroecology, and by placing macroecology within the unified theory of evolution. This research area is large and unexploited, so we refer to it as the "Ghost of Research Yet to Come." Just as we think evolutionary change results from an integration of traits established in the past with novelties of the present, to produce the future, we also think that traditional (microevolutionary) evolutionary ecology, population biology, comparative ethology, and community ecology will integrate with historical ecology to expand, strengthen, and unify evolutionary theory in the future.

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