6 Preamble to Cospeciation and Coadaptation

In the preceding two chapters, the evolutionary diversification of ecological and behavioral characters was discussed as if it were a within-clade phenomenon. Obviously, the situation is more complex in nature, where each organism experiences a wide range of interactions with both closely and distantly related species; or, in the language of historical ecology, the evolutionary diversification of any given clade occurs in association with members of other clades. The evolution of ecological associations involves combinations of speciation and adaptation events within both common and independent phylogenetic contexts. This evolutionary interchange, in turn, produces four major classes of associations: the associated species and their interactions have evolved in a phylogenetic context (I in table 6.1); the associated species have evolved in a phylogenetic context, but their interactions show phylogenetic divergence (II in table 6.1); the associated species have not evolved in a phylogenetic context, but their interactions reflect ancestral attributes (III in table 6.1); and the associated species have not evolved in a phylogenetic context, and their interactions indicate phylogenetic divergence (IV in table 6.1). We expect biotas to be influenced evolutionarily by combinations of these four general classes of processes.

We are going to simplify this discussion by adopting neutral terms for a variety of biological associations. In the discussion of coevolution, one member of each association will be designated as the "host" taxon, and we will refer to the other members of the association as "associated with" or "inhabiting" the host taxon. This will relieve us, and the reader, of the burden of distinguishing among an array of ecological associations (e.g., competitive, host-parasite, insect-plant, herbivore-crop, predator-prey, mutualistic, commensal), while attempting to understand the historical ecological perspective on coevolution. When we discuss multispecies associations, we will use the general terms "biota," "ecological association," and "community" interchangeably. At the moment, the data base is not large enough for us to differentiate among these terms within a macroevolutionary context.

Table 6.1 Heuristic table depicting the four types of associations that result from the interaction between speciation and adaptation within a phylogenetic framework.

	Interactions	
Associations	Phylogenetic	Nonphylogenetic
Phylogenetic	I	II
Nonphylogenetic	III	IV

A Broad-based Coevolutionary Paradigm

In the past, ecological associations have been "diagnosed" by their geographical location, by their species composition, and by the interactions among the associated species. We believe that there is a need for a more general theory of ecological associations that includes an explicit historical component. Furthermore, we suggest that such a general theory should be a broad-based "coevolutionary" paradigm.

The term "coevolution" is generally associated with the pioneering paper by Ehrlich and Raven (1964), although the theoretical and mathematical basis of their perspective, as well as the term itself, was developed by Mode (1958). Ehrlich and Raven's perspective was population biological and emphasized the possibilities of short-term mutual adaptive interactions, although they did briefly address the macroevolutionary patterns that might result from the microevolutionary dynamic they proposed. This paper established the direction of current coevolution studies. As a consequence, the term coevolution has come to be used in a relatively restricted sense within the evolutionary framework, referring only to cases of reciprocal adaptive responses between ecologically interacting species (see, e.g., the excellent review by Futuyma and Slatkin 1983). Our sense of "coevolution" is broader, encompassing both the *degree of mutual phylogenetic association* (what we will call cospeciation) and the *degree of mutual modification* (what we will call coadaptation). As with our discussion of speciation and adaptation, we do not think there is a simple linear relationship between cospeciation and coadaptation; both aspects of ecological associations must be studied in order to produce robust explanations of their evolutionary origins.

The historical record of studies in coevolution actually begins with von Ihering's (1891) observations about the close similarities between some flatworm parasites inhabiting crayfish in New Zealand and those inhabiting crayfish in the mountains of Argentina. He postulated that the species in the two disjunct areas were derived from ancestral crayfish and flatworms that were themselves associated. Hence, von Ihering argued, South America and New Zealand must have at one time been connected by fresh water. In 1902 he presented a study of the origins of South American mammals, concluding that North and South America were not connected until the Pliocene, because the South American mammal fauna included both an autochthonous (endemic) element, which had originated in South America, and an allochthonous (invasive) element derived from North America, comprising taxa that were not known from South America prior to the Pliocene.

Von Ihering's proposal that close ecological associations between parasites and hosts could be used as indicators of phylogeny and ancient geographical configurations was supported by other systematists. Fahrenholz (1913) examined the relationships between catarrhine (Old World monkeys) and hominoid (great apes) primates based on their blood-sucking lice, with an eye on the possibility that the associations might indicate something about phylogenetic relationships. He postulated that the information derived from the occurrence of related lice on different primates demonstrated that the catarrhine primates were more closely related to hominoids than to any other primate group, a conclusion that remains the consensus view today. Additionally, Kellogg (1896, 1913), who studied birds and their associated biting lice, Harrison (1914, 1915a,b, 1916, 1922, 1924, 1926, 1928a,b, 1929) and his associate Johnston (1912, 1914, 1916), who studied a variety of vertebrate and associated parasite systems, and Metcalf (1920, 1922, 1923a,b, 1929, 1940), who studied the opalinid protists inhabiting frogs, all thought that contemporaneous host-parasite associations held keys to answering evolutionary questions. Metcalf, in fact, recognized that all the preceding studies had a common basis. He called studies using the interactions between species and their geographic locations or ecologically associated species to infer phylogenetic relationships and paleontological conditions the "von Ihering method."

The von Ihering approach, using biogeographical and ecological association data, and the Fahrenholz approach, using only data from ecological associations, inspired two generations of parasitologists to formulate abundant evolutionary "rules" about the evolution of hosts and parasites (see references in Brooks 1979b, 1985). The studies underlying these rules had two things in common: because the systems under investigation showed rather obvious patterns of phylogenetic association, they were based in systematics rather than in ecology; and they were plagued by the lack of a rigorous analytical testing? method for [documenting] their hypotheses. The early development of this systematic perspective was paralleled by an ecologically based research paradigm, based on efforts to understand patterns of host utilization by phytophagous insects (e.g., Verschaffelt 1910; Brues 1920). Because the associations often showed no clear phylogenetic component, this tradition tended to develop without the influence of systematic information. Instead, researchers were interested in uncovering the ecological ties between organisms, that is, the particular cues being used by insects to locate their host plants. The Ehrlich and Raven (1964) paper was the ultimate synthesis of this line of research.

And so today we have two very different perspectives on "coevolution," each of which has a long history and has developed independent sets of models, explanatory hypotheses, and research methods. Needless to say, coevolution, like any evolutionary change, represents the complex outcome of numerous processes; therefore, we believe that a robust theory of coevolution must incorporate both perspectives. Furthermore, we think that the methodological rigor provided by phylogenetic systematics now makes it possible to begin integrating the two approaches. In fact, if the inclusion of both systematic and ecological information in recent texts on coevolution is a barometer of change, then the integration has already begun (Futuyma and Slatkin 1983; Nitecki 1983; Wheeler and Blackwell 1984; Kim 1985).

The coevolutionary paradigm that will emerge from this integration is based on attempts to answer three questions: (1) How did the species come to be in this area? This is the central question in historical or comparative biogeography. (2) How did the species come to be in this association? Within any group of geographically associated species there will be nonrandom ecological interactions, ranging from casual to obligatory, among some of those species. The problem lies in determining which components, if any, of the associations among extant organisms can be traced through a history of association between the ancestors of those organisms. (3) How are the members of an association interacting with one another? This question focuses our attention on the details of specific interactions between organisms by examining information about the origins and the modifications of these interactions within a phylogenetic framework.

Cospeciation

The production of both microevolutionary and macroevolutionary patterns in biological associations, in analogy with our discussion of diversification within and among clades, relies on two evolutionary processes, speciation and adaptation. Questions 1 and 2 above are concerned with speciation patterns and thus address biological associations at the level of the interacting clades. This is the focus of chapter 7. Most researchers approach this problem from a macroevolutionary perspective; however, microevolutionary theorists have recently included implications for cospeciation in their models (e.g., Kiester, Lande, and Schemske 1984).

Studies of cospeciation attempt to uncover the patterns of geographical or ecological associations among clades. There are two components to these patterns. First, two or more species may be ecologically associated today because their ancestors were associated with each other in the past. In this case the contemporaneous relationship is a persistent ancestral component of the biotic structure within which the interacting species reside. This is referred to as **association by descent** because each of the species has "inherited" the association. Second, two or more species may be associated because at least one of the species originated in some other context and subsequently became involved in the interaction by colonization of a host or dispersal into a geographical area. This is referred to as **association by colonization** (Brooks 1979b; Mitter and Brooks 1983; Brooks and Mitter 1984). In the first case the associated species share a common phylogenetic history (fig. 6.1a); in the case of association by colonization, they do not (fig. 6.1b). Both association by descent and association by colonization may be manifested in geographical patterns or in purely ecological patterns of species co-occurrence. Of course, any species that originally appears as a colonizing influence in an ecological association can become phylogenetically associated in the subsequent evolutionary history of that association (fig. 6.2).

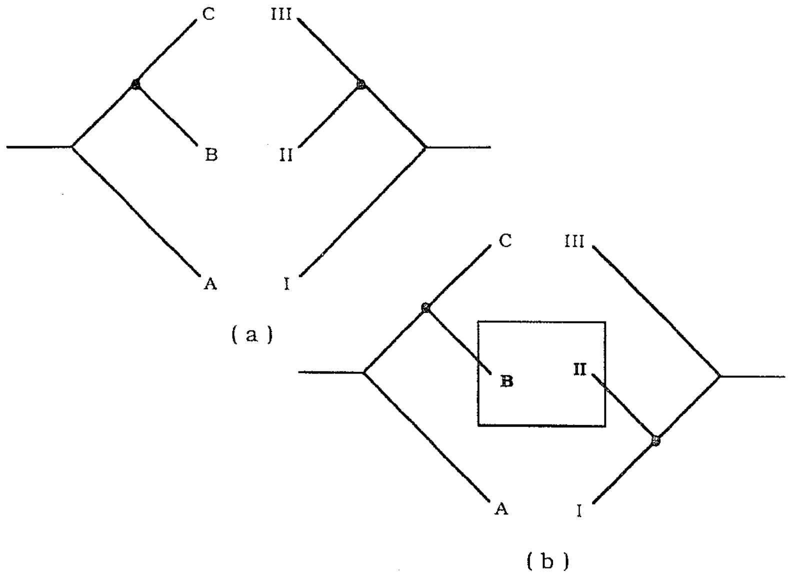
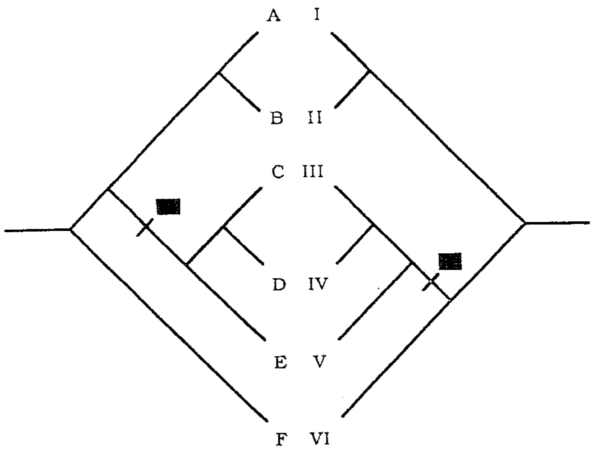


Fig. 6.1. Hypothetical example of the two components of cospeciation. (*a*) Association by descent: all species associations, A with I, B with II, and C with III, are the result of common history; that is, the ancestor of A + B + C was associated with the ancestor of I + II + III and the ancestor of B + C was associated with the ancestor of II + III. (*b*) Association by colonization: in this case, species II is hypothesized to have colonized species B. In this example, A–C and I–III may be two different groups of species or a group of species and a group of areas inhabited by the species.



■ = association due to colonization of the ancestor of the C + D + E clade by the ancestor of the III + IV + V clade

Fig. 6.2. Hypothetical example of the interrelationships between association by descent and association by colonization. Taxa A, B, and F are historically associated with taxa I, II, and VI, respectively. However, the ancestor of the III + IV + V clade colonized the ancestor of the C + D + E clade. Subsequent to that colonization, the interaction between the two ancestors was carried through two speciation events: (1) an association between taxa E and V and between the ancestor of C + D and the ancestor of III + IV, followed by (2) an association between C and III and between D and IV. This particular pattern of association through shared speciation demonstrates the existence of a historical interaction growing out of an original colonization event.

Cospeciation in a Geographical Context: How Did the Species Come to Be in This Area?

One of the fundamental advances of the past twenty years in evolutionary biology has been the formal articulation of two different perspectives on the general manner by which species achieve their geographical distributions. These perspectives may be categorized loosely as "island biogeography" (MacArthur and Wilson 1967), which calls attention to the propensity for organisms to move about, and "vicariance biogeography" (Croizat, Nelson, and Rosen 1974; Rosen 1975, 1985; Platnick and Nelson 1978), which reminds us that those movements may not be unconstrained (see Cain 1944, Camp 1947, and Wulff 1950 for early examples of this type of research). Since both research programs have contributed valuable insights into the problem of species co-occurrence, we are advocating the following "fusion" perspective: a species may be represented in a particular area because it evolved elsewhere and dispersed into that area, or it may occur in the area because it evolved there. In the first instance, the dispersal may have occurred a long time ago or relatively recently; in any event, there is no reason to expect the species' history to be congruent with the history of the area into which it dispersed. In the second instance, the species' history must be congruent with the history of the area (allopatric speciation mode I). It is likely that many, if not most, ecological associations contain both vicariant and dispersalist elements; therefore, it is important to have a method that elucidates the relative roles that geological changes and colonization have played in determining the patterns of species origin and geographic occurrence.

The first methods developed in this area were designed to provide qualitative documentation of general biogeographic distribution patterns based upon the sister-group relationships of members of different clades. Rosen (1975) presented an approach using "reduced area cladograms" in which distributional elements not common to all clades were eliminated from the data base, resulting in a simplified area cladogram depicting the "general pattern" (fig. 6.3).

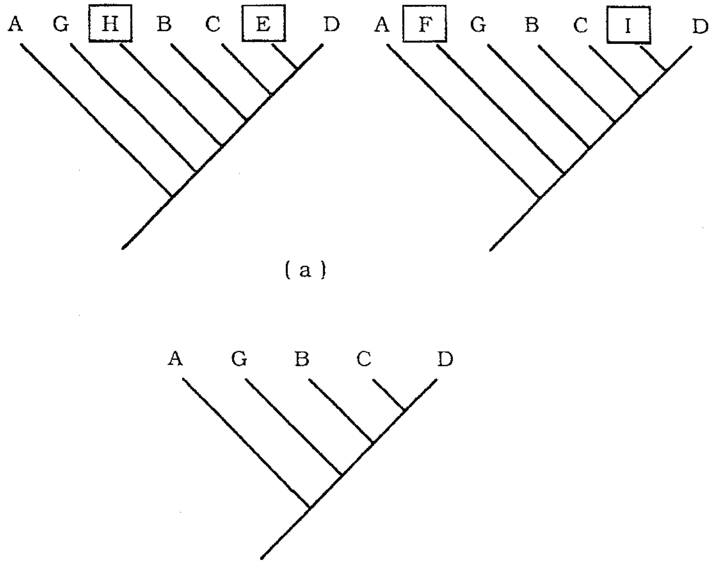
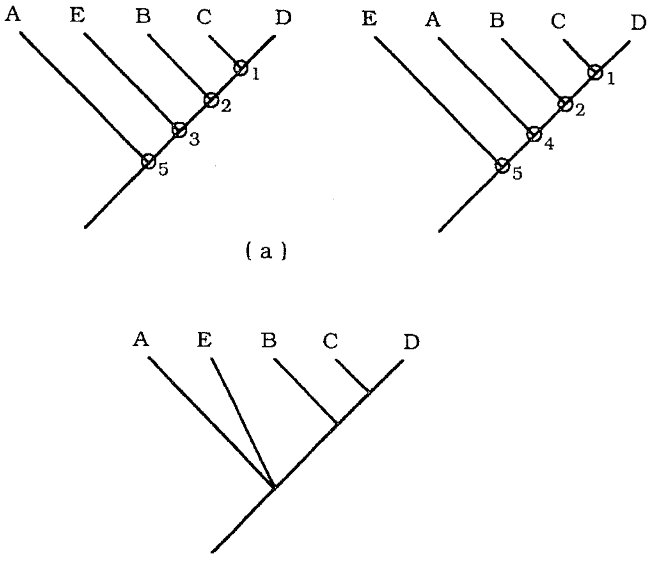


Fig. 6.3. "Reduced area cladogram" approach to historical biogeography. (*a*) Phylogenetic trees for two different clades, with geographic distributions of member species (*letters*) noted, indicate that some areas (A, G, B, C, D) contain members of both clades. (*b*) When the taxa inhabiting other areas (E, F, H, I) are removed from the two phylogenetic trees, reducing the number of taxa being considered, the biogeographical relationships for each clade appear identical.

The Platnick and Nelson (1978) and Nelson and Platnick (1981) approach, called "component analysis" (see also Humphries and Parenti 1986), relied on the use of "consensus trees" (Adams 1972; Nelson 1979, 1983) to summarize the common biogeographic elements (for a discussion of the limitations of consensus trees see Miyamoto 1985 and Wiley et al. 1990). In this method, elements that depart from the general pattern are depicted as ambiguities (fig. 6.4). The possibility that these ambiguous elements actually represent instances agreeing with the general pattern is then investigated by invoking one of two assumptions.

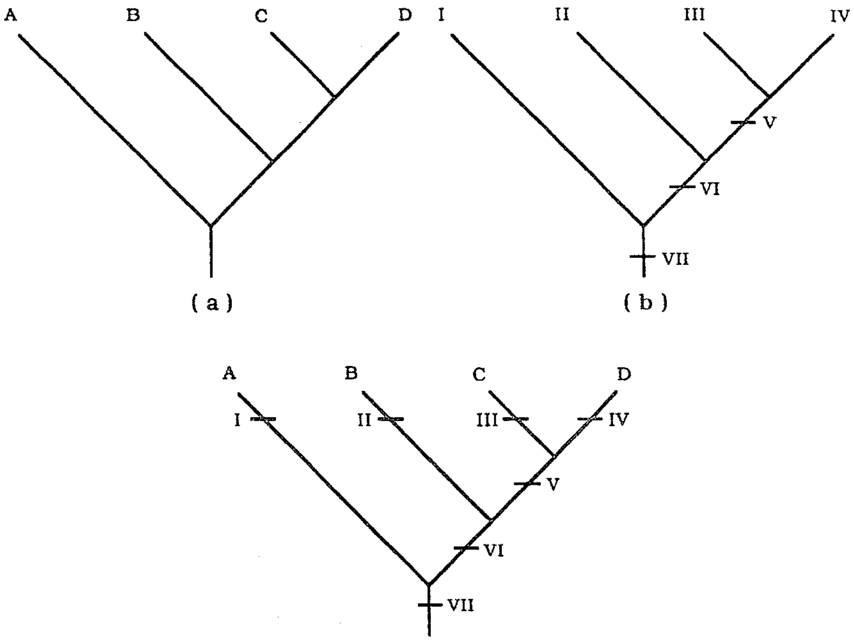
Both the reduced-area-cladogram and the component-analysis approaches have been criticized by ecologists and by systematists. Simberloff (1987, 1988) and Page (1987, 1988) pointed out that removal of ambiguous or conflicting data might make it appear that there is more evidence for general patterns than the data actually support. These authors also objected to the lack of statistical significance tests (but see Simberloff 1987) to determine the probability that apparent general patterns are due to a common cause (vicariance: allopatric speciation mode I) or to a series of unrelated parallel speciation events (Endler 1982). Wiley (1988a,b) and Zandee and Roos (1987) also criticized component analysis for obscuring evolutionarily relevant aspects of biogeographic patterns. They called for methodological changes that would allow an integration of the exceptions with the more general patterns. The methodology we will present in chapter 7 is based on the changes proposed by Wiley and Zandee and Roos and further modified by Brooks (1990). This approach is not designed to ask, either qualitatively or quantitatively, if there is a single general distribution pattern that might explain all of the data. Rather, it is based on the assumption that any given biota is likely to be a combination of species that (1) evolved where they now occur and (2) evolved elsewhere and dispersed into the area where they now occur.



(a)

(b)

Fig. 6.4. "Component analysis" approach to historical biogeography. (*a*) Phylogenetic trees for two different clades, with geographic distributions of member species (*letters*), are compared by enumerating nodes that link different combinations of areas. There are five different nodes: (1) CD, (2) BCD, (3) EBCD, (4) ABCD, and (5) AEBCD. Nodes 1, 2, and 5 are common to both phylogenetic trees. (*b*) The common biogeographic relationships for both clades are those supported by those three nodes indicated in the consensus tree.



(a)

(b)

(c)

Fig. 6.5. Hypothetical example of optimizing the phylogeny for the study group onto the area cladogram for the geographical region under investigation. (*a*) Area cladogram. (*b*) Phylogeny. (*c*) Phylogeny optimized on area cladogram.

If nonbiological data can be used to reconstruct the geological history of an area, we can use phylogenetic optimization methods to map the phylogeny of any clade onto this "area cladogram" (fig. 6.5). Since the geological history serves as an independent variable, optimizing the phylogenetic data on the area cladogram is analogous to regressing the evolutionary history of the taxa onto the geography. Given this, we can potentially identify the species in any biota that co-occur due to a common history of allopatric speciation, and those that are present due to dispersal from another area.

At the moment, actual geological data for specific studies may exist only in a historical ecologist's utopia. If these data are not available, a secondary source of information can be extracted from the phylogenetic relationships of co-occurring groups of organisms. If we have phylogenies for two or more clades whose members are associated geographically, we may ask if any of the taxa share a common history of speciation. The assumption here is that points of congruence among the phylogenies of geographically associated species identify episodes in which the clades experienced common speciation events. Such studies assess (1) historical geological relationships among areas if the speciation events took place as a result of geographic isolation (allopatric speciation mode I) or (2) the degree to which biotas share common histories if speciation resulted from colonization over common routes (allopatric speciation mode II; see reviews by Wiley 1988a,b).

It is important to determine which components of an ecological association are linked with either vicariance or dispersal events, in order to assess the context in which particular interactions emerged. However, when discussing "cospeciation in a geographical context," the possibility of shared phylogenetic histories among geographically co-occurring species is investigated without making assumptions about the type or extent of their ecological interactions. In fact, beyond occupying the same general area, the study species need not interact at all. In a simple sense, we are interested in asking to what extent speciation has been promoted by the active movements of organisms and to what extent it has been promoted by the active movements of the earth. The robustness of such studies depends on whether we have an explicit independent "evolutionary history" for the areas and how many clades we are able to analyze phylogenetically.

Cospeciation in an Ecological Context: How Did the Species Come to Be in This Association?

Speaking of "cospeciation in an ecological context" does not imply that historical biogeography is not an ecological phenomenon. We use this nomenclature to refer to cospeciation analyses in which the geographic context of the ecological associations is not considered; only the associations themselves are investigated. This is conceptually and analytically analogous to biogeographic studies, except that in this case one taxon, designated as the "host," replaces the concept of "area" in a historical biogeographic analysis.

This type of research is the "genealogical descendant" of the von Ihering method. If the "host" phylogeny is articulated, it serves as an independent variable onto which the phylogenetic relationships of the taxa associated with the host can be optimized (cf. the area cladogram reconstructed from geological evidence). If the host phylogeny is unknown, the history of the associations can be inferred by substituting the names of the hosts for the names of the associates on the phylogenetic tree of the associates. The latter method provides the weakest hypothesis of historical association, because data from the associated taxa are used to reconstruct host relationships and are then mapped back onto those relationships. Because of the inherent circularity in such an approach, it should only be used in a preliminary study (or as a last resort when no other information is available). And finally, if we have phylogenetic information about more than one clade associated with the same "host" group, we may ask questions about common histories of association between members of the host group and members of the associated groups.

We will use a single analytical method for both types of cospeciation analysis (see chapter 7). This application is based on the assumption that, on the macroevolutionary scale of cospeciation, areas and "hosts" can be equated to "taxa" in the phylogenetic analysis and the actual taxa, in turn, can be equated to characters for the areas and "hosts." Cracraft (1988) delineated two problems that may arise when microevolutionary phenomena are replaced with their macroevolutionary counterparts in phylogenetic analyses (see also Sober 1988). The first possible problem surrounds the use of hosts or areas as taxa and stems from the possibility that species inhabiting areas or in an association may represent multiple historical origins. By contrast, "real" taxa have only a singular origin. Now, in a phylogenetic systematic analysis the unique history of a taxon is demonstrated by the homologous characters (shared derived characters). The explanation for homology, common history, is the same for phylogenetic analyses at all levels of biological organization. Therefore, the same methodological principles should be applicable to the history of clades or to the history of associated clades. By contrast, the explanations for homoplasy invoke different processes at different levels of analysis. When we speak of homoplasious traits for individual taxa, we postulate multiple origins of traits mediated by the effects of natural selection and/or common developmental pathways. In cospeciation analysis, homoplasies indicate episodes of colonization, called "dispersal" in biogeography and "resource switching" in coevolutionary studies (when the homoplasies are parallelisms or convergences), or of extinction (when the homoplasies are reversals). So long as we are aware of the level at which we are analyzing evolution, we should be able to invoke appropriate mechanisms to explain departures from common history. Hence, the analytical method produces patterns of phylogenetic congruence for those elements sharing a common history and phylogenetic incongruence for those having independent histories, calling the elements in the analysis "characters" or "taxa" notwithstanding. The question, then, is one of interpretation and not of analysis.

The second problem arises from a perception that this approach forces data into a single model of evolutionary process, and as such is unrealistically reductionist and may obscure the influence of independent lineages in the evolutionary assemblage of biotas and other ecological associations. Kluge (1988) suggested that the vicariance explanation should be the null hypothesis for studies of cospeciation in geographically associated species. He advocated this explanation because it is based on the assumption that speciation has occurred as a result of active geological changes and this, in turn, does not require a supposition about the involvement of any particular biological process. Like Kluge, we believe that what we call cospeciation analysis uses common phylogenetic history as a null hypothesis: not in an a priori attempt to favor one explanation over another, but as the background against which the influences of independent elements can be most efficiently highlighted.

Macroevolutionary patterns of species co-occurrence result from the interactions of the geographical and ecological components of biological associations. The current data base supports an interpretation that there is a substantial phylogenetic component in some geographical and ecological associations. However, there is also evidence of associated taxa "escaping" from this underlying phylogenetic structure. Cospeciation analyses that include both historical and nonhistorical influences on geographic distributions and ecological associations will thus be richer than analyses that concentrate on either one component or the other. In chapter 7 we will discuss how this approach can be used to ferret out information about the assembly of biotas with complex evolutionary histories.

Coadaptation

How Are the Members of an Association Interacting with One Another?

Since cospeciation analysis does not incorporate assumptions concerning particular adaptive processes, such analysis will not provide any information about the ways in which associated lineages are influencing, or have influenced, each other's evolution. This falls into the domain of coadaptation studies, which are designed to uncover the adaptive components within the macroevolutionary patterns of association between and among clades (Mitter and Brooks 1983; Brooks and Mitter 1984). Brooks (1979b) referred to this as the degree of **coaccommodation** among ecological associates, but coaccommodation refers more to an evolved state than to a particular evolutionary process. *Investigations of this putative coevolutionary process attempt to establish whether there is evidence for coadaptation in an association and, given the presence of such evidence, to discern whether this is a legacy of history or a result of current interactions between the associated species.* Although the microevolutionary and macroevolutionary levels of coevolution are closely linked by the process of coadaptation, surprisingly few phylogenetic studies have examined this problem. The studies that are available will be discussed in chapter 8.

Studies of coadaptation must begin with a cospeciation analysis to provide the phylogenetic background against which episodes of mutual modification can be highlighted. Without this analysis, it is impossible to objectively differentiate scenarios based on the assumption that current associations reflect historical associations from other scenarios that presuppose little or no history of interaction. We will examine coadaptation from the perspectives of (1) pairs of very closely interacting clades and (2) larger multiclade associations. Type 1 associations are more commonly investigated by students of coevolution, whereas type 2 associations pertain to studies of the evolution of communities.

The Evolution of Closely Interacting Clades

Most theoretical information about coadaptational influences on coevolution comes from the studies of population biologists who stress the degree of mutual modification, or reciprocal adaptation, of the population ecology or population genetics of ecologically associated species. Three general classes of ecological "models" have emerged as a result of this research. **Allopatric cospeciation** is the "null" coadaptation model, because it assumes that the evolutionary associations between the taxa are due to cospeciation events that do not necessarily reflect any mutual interaction or evolutionary modification (reciprocal adaptation). Being the null model, allopatric cospeciation is, by itself, a weak hypothesis of coadaptation. For example, discovering that current associations are due to allopatric cospeciation rules out coevolutionary models based on an assumption of resource switching, but does not allow us to ascertain whether the association is merely a historical correlation or is due to some mutual interaction that maintains or promotes the association and its diversification. This model predicts congruence between the phylogenies of associated taxa. The second class is **Resource-tracking,** or **colonization,** models, in which diversification of each associated taxon occurs independently. For example, plant-eating insects may have colonized new host plants many times during their evolution (Mitter, Farrel, and Wiegemann 1988). In each case the colonization is hypothesized to have been the result of the evolution of insects that cued in on a particular biotic resource that was present in at least one plant species. Since this host switching involves the "tracking" of a resource that is shared among a group of hosts that do not form a clade, this model predicts no congruence between the phylogenies of the interacting taxa. Finally, there is the **evolutionary arms-race,** or **exclusion,** class of models. Briefly summarized, this classical model of coevolution proposes the following sequence of evolutionary interactions: Members of taxon A (say, spiders) reduce the fitness of members of taxon B (say, butterflies). Butterflies that, by chance, acquire traits (defense mechanisms) that increase their resistance to spiders, increase their fitness, so the new defense mechanism will spread throughout the population. However, some mutant spiders will, in their turn, overcome the new defense mechanism and be able to feed on the previously protected butterfly group. These spiders increase their fitness because they will avoid competition from other spiders; therefore, the ability to overcome the new defense mechanism will spread throughout the spider population, and this population will feed on the previously protected butterfly taxon. This model predicts some degree of congruence between the associated taxa's phylogenies, with "gaps" in the historical association due to the time lag between the evolution of "defense" and "counterdefense" traits. In chapter 8 we will show that distinguishing among these coevolutionary models is more complex than originally thought.

These models, developed by population biologists interested in microevolutionary processes, are more useful in explaining particular interactions than in investigating the coevolutionary dynamics of entire clades. On a macroevolutionary time scale the dynamics of many, if not all, clades of ecological associates may include contributions from one, two, or even all three of the above processes. We will provide some evidence of this in chapter 7, when we document the degree of congruence and incongruence between "host" and "associate" phylogenies, and in chapter 8, when we discuss the coevolution models in detail.

The Evolution of Interacting Biotas

Because of the complexity of the systems, there has been a tendency in community ecology to base models of community species composition and structure on one particular process (reviewed in Brown 1981; McIntosh 1987). Many of these processes, including interspecific competition, random colonization, predation, and disturbance, have been widely studied, so a wealth of information is now available. Given this, perhaps the time has come to return to the viewpoint, articulated so succinctly by Hutchinson (1957), that most biotas represent a complex interaction among a variety of different influences. In other words (Brown 1981),

> success in understanding complex systems usually comes from . . . taking them apart from the top down, inducing the processes underlying their organization from patterns in the relationships of the components to each other. The alternative approach of trying to recreate the entire system by assembling the components rarely works because if the system is really complex, there is an overwhelming number of possibilities.

In chapter 8 we will use this top-down approach to the study of community evolution. Starting from the macroevolutionary patterns of evolution, we will attempt to distinguish the relative contributions of the following influences on species composition and species interaction in a community: (1) **Phylogeny:** the species occurs in the association because of cospeciation, and the traits involved in interactions amongst members of the association are plesiomorphic. This represents a potential cohesive influence in the evolution of biotas. (2) **Colonization by "preadapted" species:** the species occurs in the association because of colonization, but still exhibits plesiomorphic interaction traits (i.e., these traits were brought into the new association during the colonization event and have been retained during the evolutionary diversification, if any, of the interacting clades). (3) **Colonization by competitive exclusion:** the species occurs in the association because it colonized the area and successfully competed with the resident species. In this case, either the colonizer or the competing resident(s), or both (all), exhibit evolutionarily derived (apomorphic) interaction traits relevant to the competition (i.e., the plesiomorphic condition in both species was originally the same trait, and now one or both species exhibit a different trait). (4) **Stochastic ("nonequilibrium") phenomena:** the species is a resident (associated by descent) but exhibits an apomorphic trait that is not due to competitive "displacement" by a colonizer. This indicates a certain degree of evolutionary "wandering" by resident species, which has been "allowed" by the overall structure of the association.

Summary

Evolution results from a dynamic interaction of several processes on many different levels. In chapters 4 and 5 we discussed some of the interesting questions that can be asked by examining the effects of two of these processes, speciation and adaptation, at the level of evolving clades. In chapters 7 and 8 we will allow our gaze to sweep across a broader evolutionary landscape to encompass the influences of speciation and adaptation at the level of evolving ecological associations. There is a continuum of interactions among species composing a biota. In some cases, the interactions are so predictable and pronounced that they play a role not only in the maintenance of associations but also in their evolution. Ecological associations do not evolve in the same way that species evolve; rather, they are "assembled" evolutionarily, and some of the "assembly rules" are phylogenetically based. Information from the studies discussed in the following chapters can be combined to produce robust explanations for the evolutionary "assemblage" of multispecies ecological associations.