chapter 8. One basic theme underlying this and subsequent chapters is that spatial and resource allocation are important components of community evolution. Spatial allocation patterns are revealed by studies of cospeciation in a geographical context (historical biogeography), whereas resource allocation patterns are revealed by studies of cospeciation in an ecological context. As a consequence, historical ecologists investigating both aspects of cospeciation will uncover the extent to which phylogenetic influences have shaped these components of community and biotic structure.

For this reason, it is important to emphasize two generalities that emerge from this chapter. First, we have presented a single methodological approach for documenting patterns of both spatial and resource allocation (the latter in terms of co-occurring species). Wiley (1988a) has termed this approach BPA, for *Brooks parsimony analysis,* because it was first outlined for use in studies of host-parasite associations (resource allocation) by Brooks (1981) and extended to studies of biogeography (spatial allocation) by Brooks (1985). As we have noted above, BPA has required substantial modification, most recently by Wiley (1988a,b) and Brooks (1990), from the original formulation. As a result of this modification, BPA is now robust enough to be used as a general analytical tool for documenting macroevolutionary patterns of spatial and resource allocation. However, beware of the assumptions that it is either a "perfect" method (something not yet produced by scientists) or the best possible formulation. Both Page (1987, 1988) and Simberloff (1987, 1988) have called for statistical tests of cospeciation hypotheses (see the discussion in chapter 6). Since these tests are designed to examine a different set of questions (degrees of congruence among phylogenetic trees) than those addressed by BPA (pinpointing particular instances of incongruence), the development of and interaction between both methodologies will add depth to our evolutionary explanations.

The second generalization that emerges from this chapter is that this modified version of BPA is sensitive to a variety of evolutionary influences (see, for example, the study of Amazonian birds by Cracraft and Prum 1988). This is an encouraging result, for it frees us of concerns that BPA might be a reductionist approach that attempts to force data to conform to an "all cospeciation" model. In fact, the results of the numerous studies presented in this book imply that entire clades do not generally evolve as a result of a single speciation mode. We therefore do not expect all members of an association to conform to a single cospeciation scenario, but rather to represent the unique interaction of historical (vicariance/cospeciation) and nonhistorical (dispersal/resource-switching) events.

8 Coadaptation

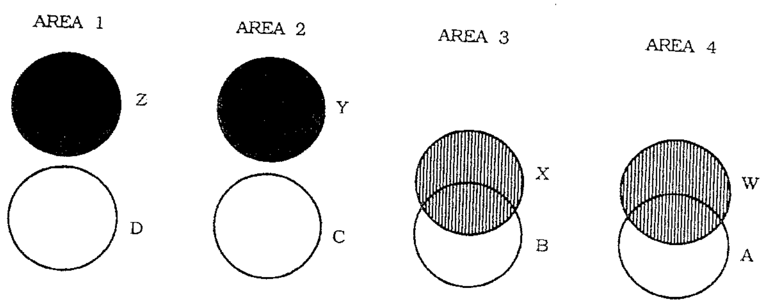
Studies of cospeciation attempt to uncover the patterns of geographical or ecological association between and among clades. When we asked questions about how species came to be geographically and ecologically associated, we were investigating the most obvious characteristic of ecological association patterns, species composition (cospeciation; chapter 7). We will now build upon that base to show you that it is possible to uncover the influences of adaptive interactions between species in shaping these macroevolutionary patterns (coadaptation). In essence, we will be embarking upon a search for causal explanations of cospeciation and resource/host switching.

Coadaptation can be investigated from two different, but not mutually exclusive, perspectives: coevolution and community evolution. We will use the term "coevolution" to encompass both phylogenetic co-occurrence and mutual adaptive interactions between species. Thus construed, coevolution is not a "process" in the classical sense; it is a descriptive term applied to a variety of evolutionary forces produced from the interplay between macroevolutionary (cospeciation and host switching) and microevolutionary (mutual adaptive responses by members of associated species) processes. Cospeciation and host switching (discussed in chapter 7) produce the phylogenetic context within which coadaptation occurs; and coadaptation, in turn, provides information about the processes involved in the evolutionary diversification of biological associations within this historical structure. *Coadaptation is manifested in the degree to which the coevolving species affect, or have affected, each other's genetic makeup, or the way in which they influence each other's ecology.*

1. 2.

Hmm...

The other perspective on coadaptation comes from research aimed at discovering the ways in which multispecies ecological associations evolve and are maintained. Unlike coevolutionary research, studies in community evolution are not based on the assumption that strong and often highly specialized ecological interactions are occurring between species (although this may be the case). Because they are not individual entities tied together by the bonds of reproduction and development, communities do not evolve in the same way species evolve; they are "assembled" through time. If they are more



(a) DISTRIBUTION OF FISH SPECIES IN WATER COLUMN

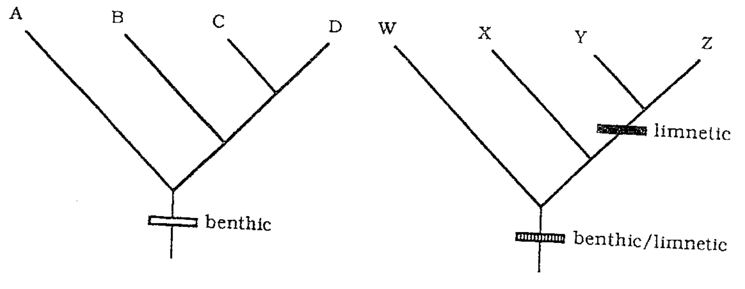


Fig. 8.1. The influence of history at the community level. (*a*) Distribution of foraging preferences. *White circle* = species foraging in the benthos; *striped circle* = species foraging in both the benthos and the limnos; *black circle* = species foraging in the limnos. (*b*) Phylogenetic relationships for clade A–D, based on nonecological data. (*c*) Phylogenetic relationships for clade W–Z, based on nonecological data.

than arbitrary units, randomly dispersed through time and space, *we should be able to document the effects of both macro- and microevolutionary processes on their evolutionary assemblage.*

Consider the following hypothetical example of the interaction between past and present at the community level (elaborated from Mayden 1987a). Imagine discovering that two fish species in a large lake (area 1; fig. 8.1a) do not overlap ecologically; say, for example, one is a benthic forager (species D) and one is limnetic (species Z). A possible explanation for such habitat separation is that it represents the effects of competition between these two species in the past. Is this a reasonable hypothesis? The short answer to this question is, we don't know. The longer answer is, without a phylogeny for the fishes and a record of their relatives' interactions with each other, it is

impossible to ascertain whether the association in our research lake is a result of interactions between Z and D or a historical legacy of interactions between their ancestors. So, after extensive fieldwork, we uncover species C (benthic) and Y (limnetic) in area 2, species X (demonstrates both foraging modes) and B (benthic) in area 3, and species W (demonstrates both foraging modes) and A (benthic) in area 4 (fig. 8.1a). As luck would have it, phylogenies exist for the two clades, based on morphological data. When the foraging modes are optimized on the trees, we discover that foraging on the benthos is plesiomorphic for all members of the A + B + C + D clade. These species have not changed their foraging habits, interactions with members of the other clade notwithstanding. Conversely, foraging on both benthic and limnetic prey was primitive for the W + X + Y + Z clade, but something happened during the interaction between the ancestor of Y + Z and the ancestor of C + D, and the former moved out of the benthic into the limnetic realm. So, while this does rule out a role for interspecific competition between past populations of species D and Z in shaping the current foraging modes in these fishes, it does not rule out the possibilities that competition was either involved in the habitat shift in the appropriate ancestors or is maintaining the divergent foraging habits today.

At the moment, little of the research in either coevolution or community ecology has used phylogenetic information; therefore, this chapter will serve more to indicate future research possibilities than to present a data base from which generalizations can be derived.

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

Coevolutionary associations have been studied with increasing intensity ever since Ehrlich and Raven (1964) published their pioneering work on butterfly–host plant interactions. The debate concerning the evolutionary processes underlying extant association patterns has been particularly vigorous, but, until recently (Futuyma and Kim 1987), the discussions generally have not incorporated phylogenetic components into the testing protocol for the various coevolutionary models (see, e.g., Futuyma and Slatkin 1983). Many examples have been assigned coevolutionary status simply because of the complexity of the ecological interactions (e.g., Sussman and Raven 1978; Moran 1989). Most of the models of coevolution are based on microevolutionary (population genetical and population ecological) processes. This state of affairs is hardly surprising given the wealth of experimental and field data available at that level, compared to which the number of macroevolutionary studies places a distant, but nevertheless optimistic, second. Three major classes of coevolutionary models have emerged from this vast data base. If these models are realistic representations of the processes that have affected coevolutionary interactions, we should be able to find some phylogenetic patterns characteristic of each model.

Allopatric Cospeciation

Allopatric cospeciation (Brooks 1979b), or the "California model," is based on the assumption that hosts and associates are simply sharing space and energy. As the null model for historical ecological studies of coadaptation, it predicts *congruence between host and associate phylogenies* based solely upon simultaneous allopatric speciation in associate and host lineages, that is, vicariance events (fig. 8.2). Like any null model, *support for the hypothesis of cospeciation offers relatively weak explanatory power.* For example, discovering that a particular set of associations has resulted from allopatric cospeciation eliminates coevolutionary models based on host switching, but does not allow us to distinguish the effects of a historical correlation from the effects of some mutual interaction that maintains or promotes the association and its diversification. And even if we assume the latter, the delineation of cospeciation patterns by themselves, no matter how detailed, does not allow us to differentiate among a variety of ways in which the associated species might be causally, rather than casually, intertwined.

One possible way to untangle correlation from causation with respect to cospeciation patterns is to examine the basis of the specificity in the associations. For example, Smiley (1978) presented a version of the cospeciation model based on the assumption that there is a general evolutionary tendency towards specialization, in this case specialization in host choice, by associated species. This model postulates that as an evolving associate lineage becomes progressively more specialized, it will be associated with fewer and fewer hosts, and cospeciation events will increase accordingly (fig. 8.3). In this case the degree of cospeciation is the result of an evolutionary trend inherent in the associated species and not of mutual adaptive modifications between host and associate.

HJK?

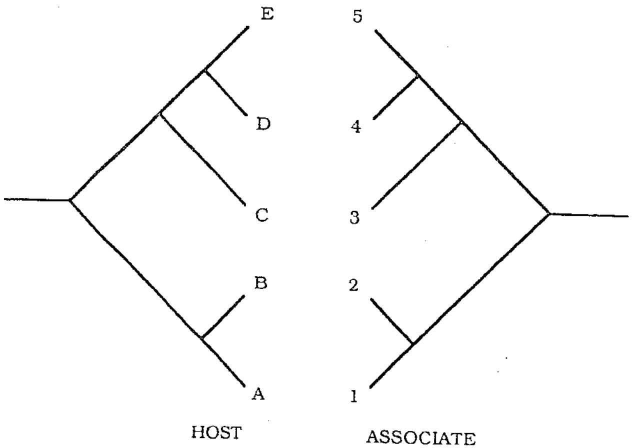


Fig. 8.2. The allopatric cospeciation, or California model, of coevolution. Complete congruence between the phylogeny for the hosts (taxa represented by *letters*) and the phylogeny for their associates (taxa represented by *numbers*) is due solely to simultaneous cospeciation.

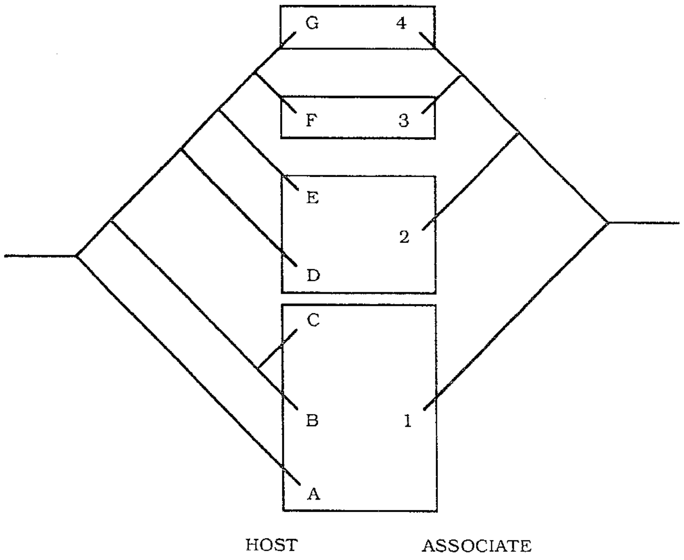
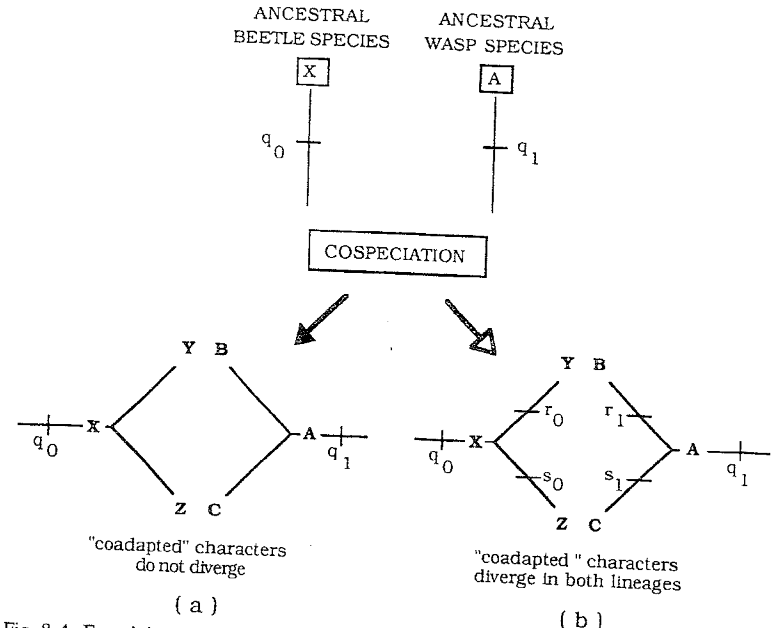


Fig. 8.3. Interaction between cospeciation and specificity displayed by the associate species. In this scenario, the degree of cospeciation increases through time due to some inherent drive towards increasing host specificity in the associate lineage.

Alternatively, the association may be maintained by the presence of certain host resources that are of adaptive value to an associated species. If an associate species requires a specific resource and/or a resource with a restricted distribution among host groups, then it is possible that the phylogenetic association between the host group and the associated group is due to the distribution of the resource. Consider a hypothetical ancestral beetle species X characterized by trait q_0 that serves as a cue for members of a parasitic wasp species A (other examples of q_0 might be a chemical cue that triggers feeding in a phytophagous insect, a chemical cue that triggers settling behavior in larvae, or a visual cue that triggers orientation in a vertebrate or insect polli-



"coadapted" characters do not diverge

(a)

"coadapted " characters diverge in both lineages

(b)

Fig. 8.4. Examining the potential for coadaptation within the framework of cospeciation. In both of the scenarios, preliminary phylogenetic analysis has uncovered complete congruence between host and associate phylogenies. (*a*) Host (X to Y + Z) and associate (A to B + C) speciate simultaneously; descendant species retain the plesiomorphic coadapted trait complex (q_0 in the host; q_1 in the associate). (*b*) Host and associate speciate simultaneously, and diversification in the coadapted trait complex (q_0 to $r_0 + s_0$ in the host; q_1 to $r_1 + s_1$ in the associate) is congruent with the speciation events.

nator). The wasp's reliance on q_0 is denoted by its possession of the coevolved trait q_1. Now let us follow two evolutionary scenarios involving speciation in the beetle lineage producing descendant species Y and Z, as well as speciation in the wasp lineage producing descendant species B and C (fig. 8.4).

The evolutionary association between species Y and B, on the one hand, and between Z and C, on the other, represents an instance of cospeciation. Although both scenarios depicted in figure 8.4 produce congruent host and associate phylogenies, the processes underlying this congruence are somewhat different in each case. In the first scenario (fig. 8.4a), q_0 and q_1 are phylogenetically conservative so the associations are maintained, at least in part, by the common coadapted trait complex q_0q_1. We have evidence here for "adaptively constrained" coevolution because speciation in both lineages has occurred without changes in the causal basis for the primitive host-associate interaction. In the second scenario (fig. 8.4b), the cospeciation of

the beetle and wasp clades is matched by the diversification of the adaptively significant trait complex. Species Y and B now interact through the coadapted characters r_0 and r_1, while the association between Z and C is maintained by traits s_0 and s_1. This scenario, representing "adaptively driven" coevolution, provides ecological evidence that the observed cospeciation patterns are more than casual historical associations.

OK but how can we know ~~db~~ ancestor

In figure 8.4a we have evidence that the critical host resource is a plesiomorphic trait. If this primitive resource is phylogenetically widespread, then the potential for the associated species to switch among hosts from different clades is increased dramatically. Such host switching, based on the "tracking" of a resource common to hosts that do not form a clade, is the province of the "resource-tracking" models of coevolution.

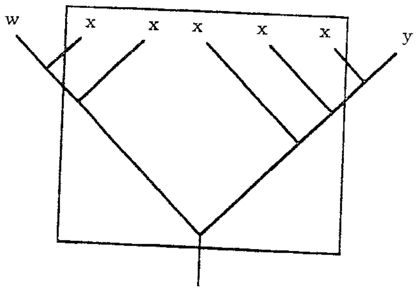
Resource Tracking

This class of models, which can also be referred to as **colonization** models, is based on the concept that hosts represent patches of necessary resources which associates have "tracked" through evolutionary time (Kethley and Johnston 1975). Three pieces of information are required in order to thoroughly examine the explanatory power of these models: a phylogeny for the hosts, a phylogeny for the associates, and an explicit description of the resource. Depending on the phylogenetic distribution of the resource, one of three general macroevolutionary patterns will be produced.

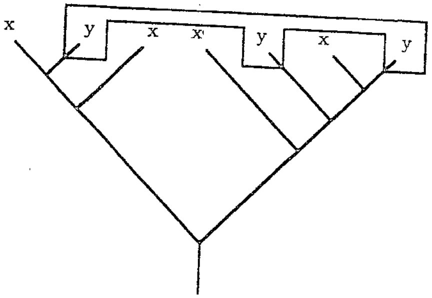
spatially explicit?

The **sequential colonization model** (Jermy 1976, 1984), originally designed to explain insect-plant coevolution, proposes that the diversification of phytophagous insects took place *after* the radiation of their host plants. The insects are hypothesized to have colonized new host plants many times during their evolution. In each case the colonization was the result of the evolution of insects responding to a particular biotic resource that already existed in at least one plant species. That resource, in turn, is postulated to have been either **plesiomorphically** (fig. 8.5a) or **convergently** (fig. 8.5b) widespread, so the predicted macroevolutionary pattern is that *host and associate phylogenies will show no congruence* (fig. 8.5c).

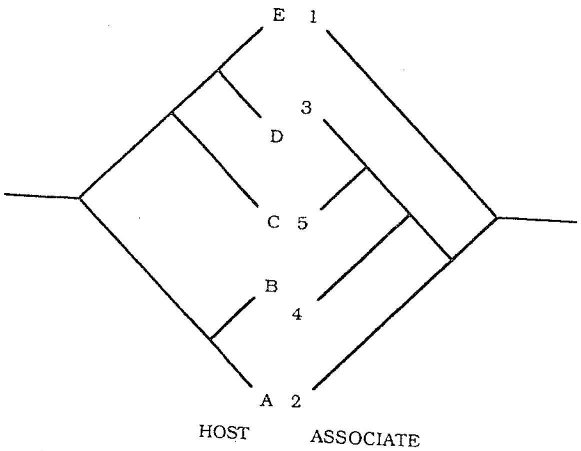
From the perspective of resource-tracking models, the explanation for *congruence between portions of host and associate phylogenies* is that the associates are specialized on a host resource that is restricted to the host clade and has evolved in a manner congruent with the phylogenetic diversification of the host clade. This model differs from sequential colonization because it proposes that the resources are distributed in an apomorphic, rather than a plesiomorphic or convergent, fashion. It differs from allopatric cospeciation by assuming that hosts and associates do not speciate simultaneously (association by descent); rather, the hosts evolve first and then associates colonize



(a) RESOURCE IS PLESIOMORPHIC



(b) RESOURCE IS CONVERGENT



(c) LACK OF CONGRUENCE BETWEEN PHYLOGENIES

Fig. 8.5. Sequential colonization model. (*a*) Target area for colonization sequences (*box*) if the resource being used is plesiomorphic and widespread. (*b*) Target area for colonization sequences if the resource being used is convergent and widespread. (*c*) Predicted lack of congruence between the host and associate phylogenies.

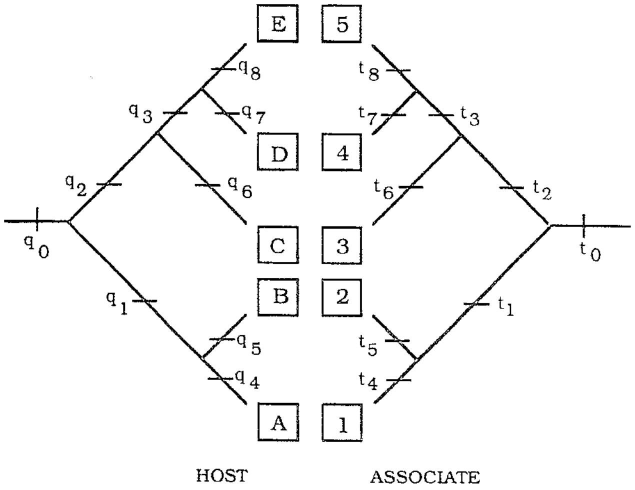


Fig. 8.6. Phylogenetic tracking model. Every speciation event in the host lineage is accompanied by a modification of the resource (changes in q). Members from the ancestral associate colonize the new hosts, adapt to the new resource (changes in "tracking ability," t), and eventually produce a new associate species responsive to that resource.

them. The evolutionary sequence of events is as follows (fig. 8.6): A new host species evolves, characterized, in part, by an evolutionarily modified form of the required resource. This new species of host is then colonized by individuals from the species associated with the ancestral host. Some of these individuals adapt to the new form of the resource, eventually producing, in their turn, a new species of associate. And so the cycle continues.

In order for this evolutionary scenario to occur, the ancestral host ~~species~~ resource ! *must* persist after the speciation event that produces descendants bearing the modified resource; otherwise, the ancestral associate species would have no resource base to support the population through the colonization phase. As we discussed in chapter 4, ancestral species can persist following sympatric, parapatric, and peripheral isolates allopatric speciation. So, in order to distinguish "phylogenetic tracking" from allopatric cospeciation (fig. 8.4b) we require (1) an understanding of the manner in which the host group speciated (see chapter 4), (2) a method for distinguishing persistent ancestors on a phylogenetic tree (see chapters 2 and 4), and (3) a detailed mapping of the host-resource and associate tracking characters (if present) on the appropriate phylogenetic trees.

Evolutionary Arms Race

This is the classical coevolution model (Mode 1958; Ehrlich and Raven 1964; Feeny 1976; Berenbaum 1983), sometimes termed the **exclusion** model, and originally proposed for insect-plant systems. It may be summarized as follows: phytophagous insects reduce the fitness of their hosts. Plants that, by chance, acquire traits (defense mechanisms) that make them unpalatable to these insects will increase their fitness relative to their undefended brethren, and the new defense mechanism will spread throughout the plant population (new host species). Eventually some mutant insects will, in their turn, overcome the new defense mechanism and be able to feed on the previously protected plant group. If this confers a fitness advantage on the mutants (e.g., through reduction of inter- or intraspecific competition for food), the counterdefense mechanism will spread throughout the insect population (new associate species). This new species of insect will be able to specialize on the previously protected plant group, and the cycle will begin anew.

The primary assumption in "arms race" models of coevolution is that coevolving ecological associations are maintained by mutual adaptive responses. For example, it is possible that during the course of evolution novel traits arise that "protect" the host from the effects of the associate. It is also possible that traits countering such "defense mechanisms" may evolve in the associate lineage. The macroevolutionary patterns that result depend upon the time scale on which the adaptive responses occur. In systems for which the "defense" and "counterdefense" traits arise on a microevolutionary scale, we would expect *fully congruent host and associate phylogenies, with appropriate "defense" and "counterdefense" traits appearing at the same point in the common phylogeny* (fig. 8.7). In such cases, the coevolutionary arms race would not affect the patterns of macroevolutionary associations between host and associate clades, leading us to expect phylogenetic congruence. This type of evolutionary arms race can be differentiated from allopatric cospeciation by the presence in both lineages of co-originating, mutually adaptive traits.

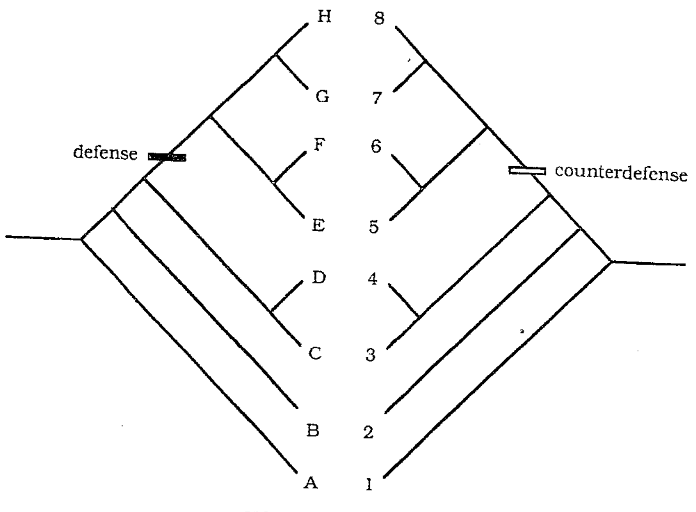


Fig. 8.7. Evolutionary arms race, type I. Host and associate phylogenies are congruent. Defense and counterdefense traits appear at the same point in the common phylogenies.

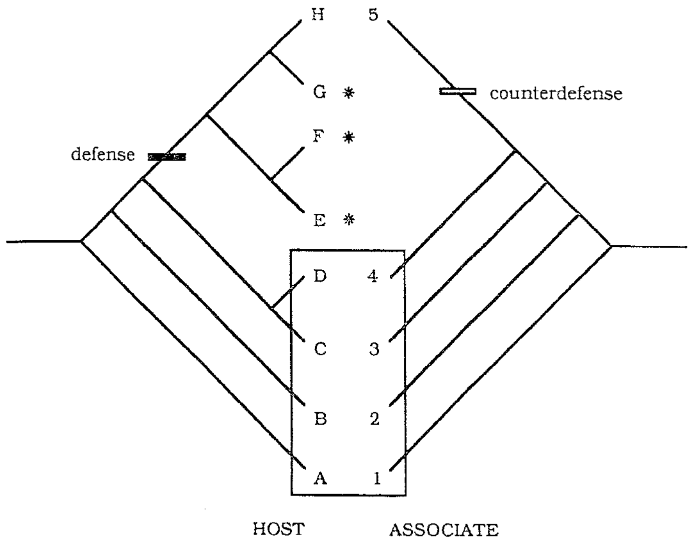


Fig. 8.8. Evolutionary arms race, type II. The host and associate phylogenies are congruent (*box*) up to the point at which the defense trait appears. If the origination of a counterdefense lags behind this, and if the hosts continue to speciate, associate species will be prohibited from interacting with any of the new host species (*asterisk*). Once a counterdefense appears, the host and associate phylogenies rejoin, and the cycle continues.

Evolutionary arms-race models generally assume that, in many cases, the time scale on which the "defense" and "counterdefense" traits originate in response to reciprocal selection pressure is longer than the time between speciation events. Given this, we might expect to find macroevolutionary patterns similar to those shown in figure 8.8, in which *the associate group is missing from most members of the host clade characterized by possession of the "defense" trait.*

A third possible macroevolutionary pattern results when one or more relatively plesiomorphic members of a host clade are colonized by more recently derived members of the associate group bearing the "counterdefense" trait. In this case, *host and associate phylogenies will demonstrate some degree of incongruence, and we would expect to find evidence that some associates*

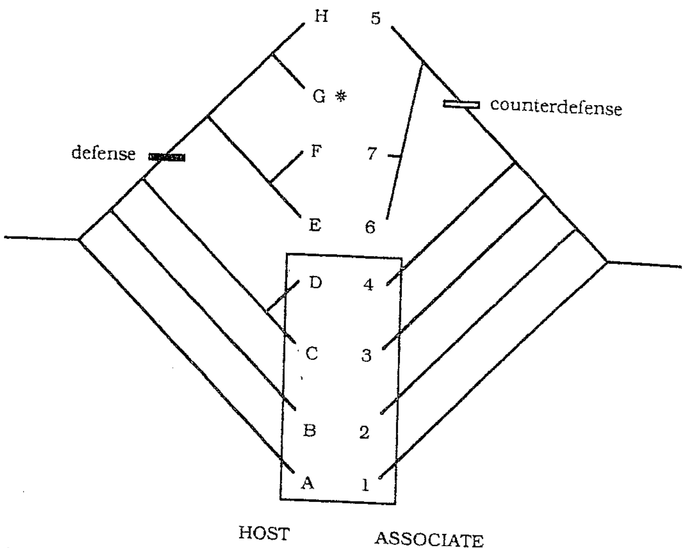


Fig. 8.9. Evolutionary arms race, type III. Once the counterdefense trait has appeared in the associate lineage, continued speciation will produce new species capable of colonizing host species bearing only the old defense. The situation depicted here is an intermediate version of the large number of possible patterns that may be produced, ranging from all associates that bear the counterdefense (species 5, 6, and 7) back-colonizing on all members of the host lineage, to no back-colonization.

have "back-colonized" hosts in the clade diagnosed by the presence of the "defense" trait (fig. 8.9).

And finally, Ehrlich and Raven (1964) postulated that coevolutionary patterns similar to ones expected for the sequential colonization resource-tracking model depicted in figure 8.5b would result when host shifts by insects with a counterdefense trait occurred between plants that had **convergently** evolved similar secondary metabolites in response to insect attack. In both cases, there is a departure from phylogenetic congruence between hosts and associates; however, the resource-tracking model requires only that the associates be opportunistic. The host resource can be widespread due to either plesiomorphic occurrence or convergence, but its evolutionary patterns are not affected by the presence or absence of the associates. In contrast, the mechanism by which the host resource evolves in the Ehrlich and Raven case requires a high degree of convergent mutual modification on the part of the host and associate groups. Differentiation between the two models requires information about the evolutionary elaboration of putative defense and counterdefense traits.

Case Studies

Birches and the midges that gall them

Dipteran insects of the genus *Semudobia* (family Cecidomyiidae, subfamily Cecidomyiinae) are commonly called gall midges. The association between gall midges and their hosts is more intimate than a simple dinner/diner relationship. Females lay their eggs in bracts or fruits of various species of birches (genus *Betula*), and the larvae develop in situ, drawing both sustenance and shelter from their host, inducing a thickening in the plant tissue (gall formation) in return. Research on members of other gall midge tribes indicates that characteristics of the host plant have considerable influence on larval development (Åhman 1981, 1985; Skuhravy, Skuhrava, and Brewer 1983). This, in turn, may provide a barrier to speciation via host switches in these insects (Roskam 1985). Although as many as three species of *Semudobia* may co-occur in the same host, none of the five species composing the genus is found on plants other than birches. This specificity led Roskam (1985) to investigate the coevolutionary aspects of the association between birches and their gall midges.

The birch genus *Betula* comprises four sections, *Costatae, Humiles, Acuminatae,* and *Exelsae* (fig. 8.11b). Members of the sections *Costatae* and *Humiles* bear erect pendulous flowers, called catkins, and retain their fruits over the winter, while their relatives, the *Acuminatae* and *Exelsae,* display pendulous catkins and drop their fruits in the autumn. *Semudobia skuhravae,* the sister species of the rest of the gall midges (fig. 8.10a), induces galls in the bracts of *Costatae, Humiles,* and *Exelsae* birches. The remaining gall midge species all lay their eggs in the fruits of various members within the *Exelsae* section. Since these birches drop their fruits in the fall, the fruit-galling *Semudobia* develop and overwinter in the soil. Gall midges are never found on birches in the section *Acuminatae.*

There are pronounced differences in host preferences among the gall midges. *S. skuhravae* occurs commonly in association with members of sections *Costatae* and *Humiles,* and less so with members of *Exelsae.* Within the Palearctic *Exelsae, S. betulae* is regularly found on species in the series *Verrucosae* and only occasionally associated with the series *Pubescentes.* The reverse situation occurs for *S. tarda,* a gall midge displaying a marked preference for *Pubescentes* and a secondary preference for *Verrucosae.* Relationships between the insects and their host plants produce a similar pattern of preferences in the Nearctic *Exelsae,* where *S. steenisi* and *S. brevipalpis* occur commonly in association with birches within the *Verrucosae* and less commonly with *Pubescentes.* Mapping the host preferences of the five contemporaneous species of *Semudobia* onto the host phylogeny (fig. 8.11a) re-

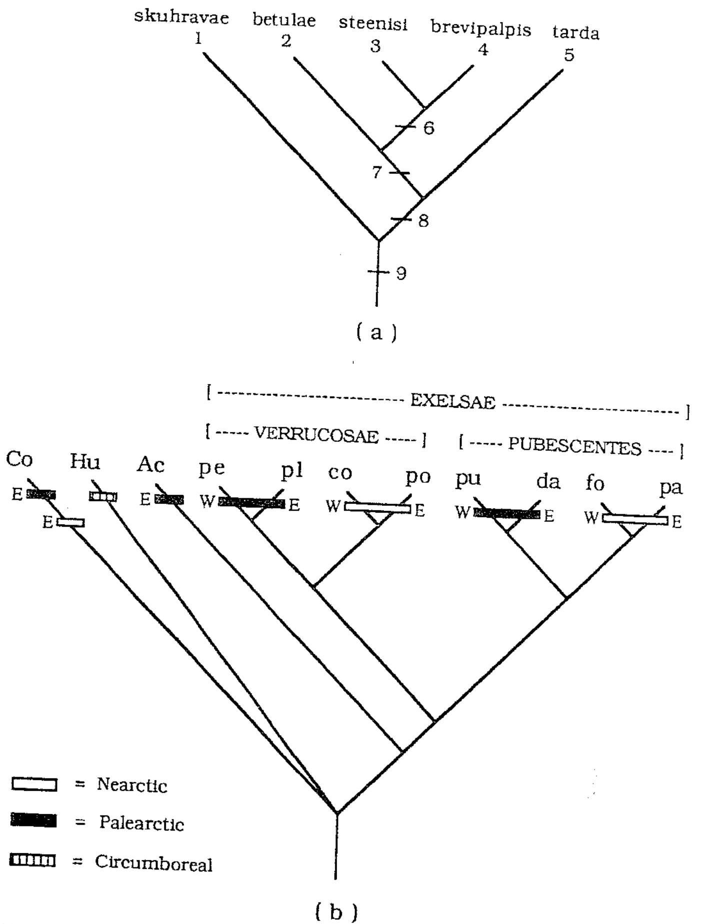


Fig. 8.10. Phylogenetic trees for the birches and their gall midges. (*a*) The gall midges, genus *Semudobia*, coded for coevolutionary analysis. (*b*) The host birches, genus *Betula*. Sections: *Co = Costatae; Hu = Humiles; Ac = Acuminatae*. Species: *pe = Verrucosae pendula; pl = V. platyphylla; co = V. coerulea; po = V. populifolia; pu = Pubescentes pubescens; da = P. davurica; fo = P. fontinalis; pa = P. papyrifera*. The distributions of the birches are mapped onto their phylogenetic tree: *W* = west; *E* = east.

veals that no two species of *Semudobia* show their greatest preference for the same birches. Based on these distributions, and the assumption that the associations of greatest preference are those of longest evolutionary duration, Roskam postulated that the majority of the birch–gall midge associations could be explained by allopatric cospeciation (fig. 8.10b).

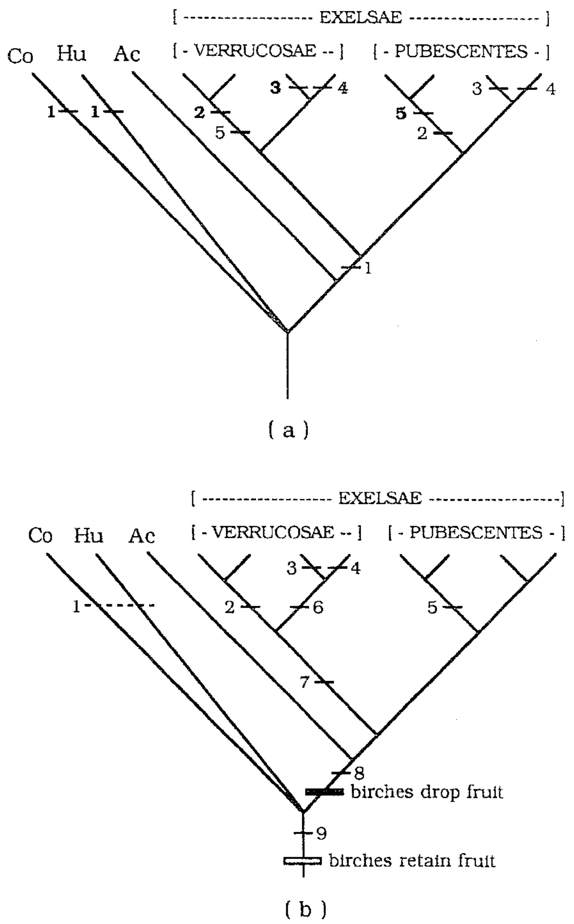


Fig. 8.11. Of birches and gall midges. *Co = Costatae; Hu = Humiles; Ac = Acuminatae. 1 = Semudobia skuhravae; 2 = S. betulae; 3 = S. steenisi; 4 = S. brevipalpis; 5 = S. tarda.* (*a*) Host preferences of the five gall midge species mapped onto the host phylogeny. *Bold numbers* = preferred birch host; *nonbold numbers* = secondarily preferred hosts. (*b*) Phylogeny for the gall midges, mapped onto the phylogeny for the host birches.

In brief, Roskam proposed that the initial speciation event producing *S. skuhravae* and the ancestor of the remaining gall midges (ancestor 8; fig. 8.11b) represented a host shift from the fruit-retaining birches, *Costatae* and *Humiles*, to the fruit-dropping birches, *Exelsae*. This change in host preference was accompanied by a shift from the old resource (retained bracts) to the new resource (dropped fruit), and was reinforced by a selective advantage to individuals overwintering in the soil, compared to midges that remained within the birch tree itself (Möhn 1961). The congruence of this portion of the host and associate phylogenies, coupled with the associate's response to an apomorphic resource, appears to be an example of phylogenetic resource tracking. However, it is also possible that the ancestor of *Semudobia* (ancestor 9) cospeciated with the ancestor of *Betula*. According to this second interpretation, one of the descendant gall midge species, *S. skuhravae*, retained the ancestral (plesiomorphic) "bract present/lay eggs in bracts" association with the new birch species. In the sister lineage, the evolutionary appearance of the character "drop fruit" in the new host species was accompanied by the evolutionary appearance of the character "lay eggs in fruit" in the ancestor of the remaining gall midges (ancestor 8). Resolution of this problematical event requires more details about the manner in which the host group speciated.

The remaining speciation events occurred within a common ecological context (eggs laid in dropped fruit). The second speciation event, producing *S. tarda* and the ancestor of the remaining three midge species (ancestor 7; fig. 8.11b), was associated with the allopatric speciation of the *Exelsae* series *Verrucosae* and *Pubescentes* (Roskam and van Uffelen 1981). Finally, two vicariance events occurred. The first isolated *S. betulae* in the Palearctic and the ancestor of *S. steenisi* and *S. brevipalpis* in the Nearctic (ancestor 6), and the second isolated *S. steenisi* and *S. brevipalpis* in the west and east Nearctic, respectively. Although allopatric cospeciation appears to be the predominant mode underlying the pattern of insect-host associations in this system, gall midges were able to incorporate additional hosts into their preference repertoire under circumstances of secondary host sympatry. The biogeographic distributions shown in figure 8.10b support apparent convergent sympatry of Palearctic and Nearctic birches within the series *Verrucosae* and *Pubescentes*, and of members of *Costatae* and *Humiles* with members of *Exelsae*. Overall, then, the combination of biogeographical evidence supporting convergent sympatry, the patterns of phylogenetic association, and the differences in host preference tend to support Roskam's explanation. Additional research is required to explain the absence of gall midges from any member of *Betula* section *Acuminatae*. This appears to be an excellent test case for an evolutionary arms race, or exclusion, explanation, that is, one in which the plants appear to have "won" the arms race, at least for the moment. If this is true, members of *Acuminatae* may produce an unrecognizable cue, a substance that repels *Semudobia*, or a substance that affects development of gall midge larvae adversely.

Gyrocotylids and ratfish revisited

In chapter 7 we discovered that the evolutionary association between the leaflike gyrocotylid flatworms and their ratfish hosts has involved a large

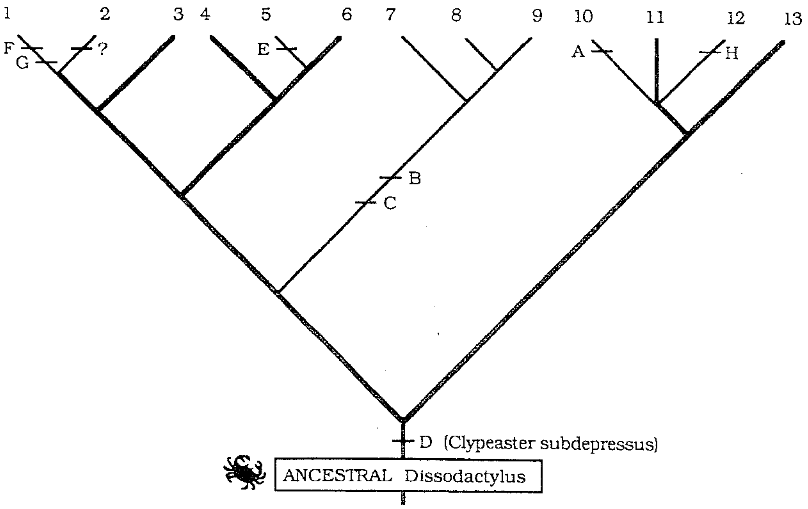


Fig. 8.17. Phylogenetic tree for species of pinnotherid crabs composing the genus *Dissodactylus*, with hosts optimized onto it. Crabs: *1 = D. primitivus; 2 = D. schmitti; 3 = D. latus; 4 = D. glasselli; 5 = D. mellitae; 6 = D. crinitichelis; 7 = D. lockingtoni; 8 = D. nitidus; 9 = D. xantusi; 10 = D. rugatus; 11 = D. juvenilis; 12 = D. usufructus; 13 = D. stebbingi*. Hosts: *A = Clypeaster rosaceus; b = Encope* spp.; *C = Mellita* spp.; *D = C. subdepressus; E = Mellita longifissa; F = Meoma* spp.; *G = Plagiobrissus* spp.; *H = C. speciosus; ? =* unknown.

decided they were tasty morsels. If so, this is an example of sequential colonization analogous to some models of the colonization of plants by insects (Jermy 1976, 1984; Mitter, Farrel, and Wiegemann 1988).

Of butterflies, magnolids, and rosids

The Papilionidae is a relatively small (for insects) group of exotic, widespread, swallowtailed butterflies which feed upon a variety of plants within the subclasses Magnoliidae and Rosidae. Miller (1987) examined the phylogenetic relationships of the papilionids on three different levels in his search for macroevolutionary patterns of butterfly-plant associations. Figure 8.18 depicts his phylogenetic tree, based on forty-four morphological characters with a consistency index of 70%, for the six tribes of swallowtails. Unfortunately, there is a paucity of phylogenetic information about the relationships among the major plant groups upon which these butterflies feed (table 8.1). Hickey and Wolfe (1975) suggested that the Magnoliidae is a paraphyletic group; postulating that the Magnoliales are the sister group of the Aristolochiales + Laurales + Rosidae, and the Aristolochiales are the sister group of the Laurales + Rosidae. Dahlgren and Bremer (1985) reexamined the

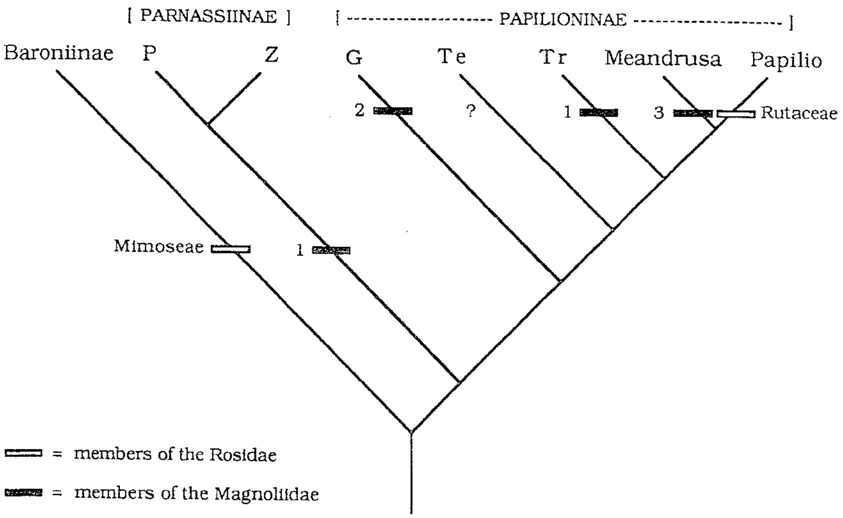


Fig. 8.18. Phylogenetic relationships within the butterfly family Papilionidae. The Baroniinae, Parnassiinae, and Papilioninae are subfamilies. Tribes: *P* = Parnassiini; *Z* = Zerynthiini; *G* = Graphiini; *Te* = Teinopalpini; *Tr* = Troidini. *Meandrusa* and *Papilio* are genera within the tribe Papilionini. The host-plant preferences, at the family level, have been mapped onto this cladogram. *1* = Aristolochiales; *2* = Magnoliales; *3* = Laurales; *?* = dietary data missing.

relationships phylogenetically and found a number of equally parsimonious trees. They agreed, however, with the previous authors' conclusions that the Magnoliidae are paraphyletic, adding that three orders within this "subclass," the Annonales, Magnoliales, and Laurales, are also probably paraphyletic. Without an adequate phylogeny for the host plants, studies of coevolutionary relationships between swallowtails and their preferred foodstuffs are at best preliminary; but nonetheless, they are interesting.

Table 8.1 Classification of the two major plant subclasses of interest to swallowtail butterflies.

Subclass Magnoliidae		Subclass Rosidae	
Magnoliales	**Laurales**	**Rosales**	**Fabales**
Winteraceae	Monimiaceae	Crassulaceae	Mimoseae
Magnoliaceae	Lauraceae	Saxifragaceae	
Annonaceae	Hernandiaceae	Rosaceae	
Piperales	**Aristolochiales**	**Saphindales**	**Apiales**
Piperaceae	Aristolochiaceae	Rutaceae	Araliaceae
		Zygophyllaceae	Apiaceae

Source: Classification based on Cronquist 1981; redrawn and modified from Miller 1987.
Note: Bold type denotes orders, regular type, families.

The monotypic *Baronia*, the sister group of the rest of the papilionids, inhabits west-central Mexico, where it feeds on plants of the genus *Acacia*, (family Mimoseae, subclass Rosidae; fig. 8.18). The rest of the papilionids appear to feed primarily on plants within the subclass Magnoliidae. The swallowtail tribes Parnassiini, Zerynthiini, and Troidini, with exceptions in two genera, dine on Aristolochiaceae (order Aristolochiales). Interestingly, the exceptions to this preference for magnoliids are two highly derived genera within the Parnassiini whose members are primarily restricted to rosids. Most of the 147 Graphiini species specialize on plants of the family Annonaceae (order Magnoliales). Host plants are unknown for the two species composing the rather modest Teinopalpini tribe. The tribe Papilionini is comprised of two genera. *Meandrusa* (two species) feeds on Lauraceae (order Laurales) while the extremely species-rich *Papilio* (220 species strong) prefers the culinary delights offered by plants in the family Rutaceae (order Sapindales, subclass Rosidae).

Examining the relationships between the butterflies and their preferred food sources at this phylogenetic level clearly indicates that the specialization of *Papilio* species on rosids represents a colonization event. In addition, it appears that some degree of host switching among three of the magnoliid "orders" (Magnoliales, Laurales, and Aristolochiales) accounts for much of the diversification within the subfamilies Parnassiinae and Papilioninae. However, this host switching has not been random, and the patterns depicted in figure 8.18 suggest a certain amount of host specificity at the tribal level in swallowtail butterflies. Although the Parnassiinae and the Troidini are not sister groups, their species feed primarily on members of the Aristolochiaceae. Ehrlich and Raven (1964) argued that this similarity was the result of maintenance of the plesiomorphic host preference in these butterflies, while Miller proposed that preference for Aristolochiaceae evolved twice (convergence). In light of the questionable monophyletic status of the Magnoliales and Laurales (host switches 2 and 3 in fig. 8.18), resolution of this problem awaits a detailed phylogeny for the host plants, as well as information about food preferences in the Teinopalpini.

Miller moved next to the second level of his analysis: examination of the phylogenetic relationships among the five genera within the tribe Graphiini. The species within this tribe are predominantly distributed throughout tropical and neotropical African/Indo-Australian regions. *Iphiclides* provides the exception; both species inhabit the Palearctic. *Graphium* is the largest genus (eighty-nine species), with *Eurytides* (fifty-three species) a close second and the remaining genera, *Iphiclides* and *Lamproptera* (two species) and *Protographium* (one species) out of the running. Miller's phylogenetic tree for this group (fig. 8.19) is based on fifty-six morphological characters and has a consistency index of 89%. Mapping the distribution of food preferences on this tree suggests that a fair amount of host switching has occurred at this level. With the exception of *Iphiclides,* who feed on rosids (family Rosaceae, order Rosales), all members of this tribe prefer some type of magnoliid plant. Three of the genera feed primarily on Annonaceae (order Magnoliales); however, although these are the only swallowtail butterflies to use this resource, it is impossible to determine whether this is a primitive or derived preference within the group because the sister group to the Graphiinae, the Parnassiinae, do not eat any of the plants eaten by the Graphiini. Past this point a number of explanations for the patterns within the remaining genera are possible, and as many as ten sequential colonizations can be postulated by this analysis. Of these, only the *Iphiclides* preference for rosids is a concrete example of host switching. The remaining putative cases of sequential colonization cannot be further evaluated without resolution of the phylogenetic relationships among the host plants, since the suspect "groups" Annonaceae, Magnoliales, and Laurales are included in this analysis.

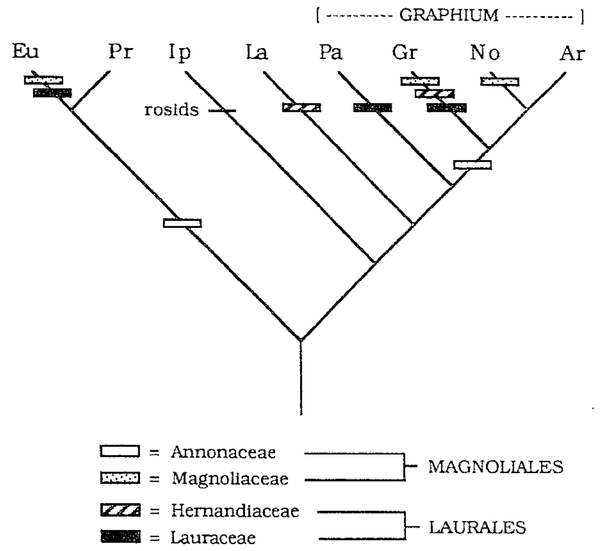


Fig. 8.19. Dietary preferences mapped onto the phylogenetic tree for the swallowtail butterfly tribe Graphiini. Genera: *Eu = Eurytides; Pr = Protographium; Ip = Iphiclides; La = Lamproptera.* Subgenera within the genus *Graphium: Pa = Pazala; Gr = Graphium; No = Nomius; Ar = Arisbe. Bars =* host preferences.

A different pattern is found when host preferences are optimized on the phylogenetic tree (fig. 8.20). This analysis suggests that these butterfly genera appear to be primitively associated with plants of the family Annonaceae. Two speciation events on the phylogenetic tree are associated with host

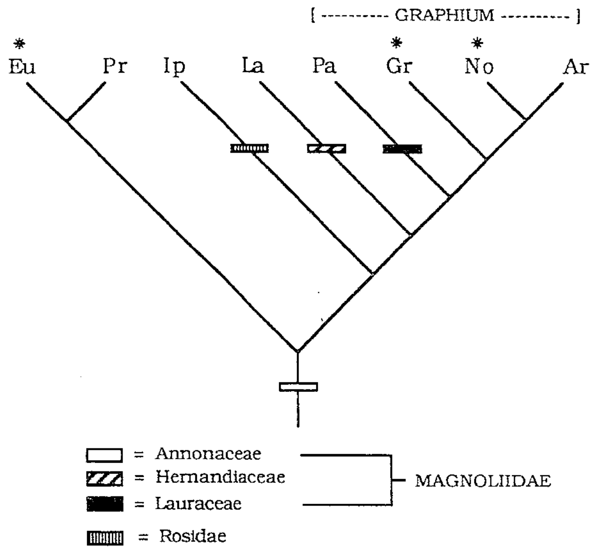


Fig. 8.20. Dietary preferences optimized onto the phylogenetic tree for the swallowtail butterfly tribe Graphiini. Genera: *Eu = Eurytides; Pr = Protographium; Ip = Iphiclides; La = Lamproptera.* Subgenera within the genus *Graphium: Pa = Pazala; Gr = Graphium; No = Nomius; Ar = Arisbe. Bars* = host preferences; * = generalist on many hosts.

switches from Annonaceae to one other Magnoliidae order (the Laurales), and one speciation event is associated with a switch from Magnoliidae to Rosidae. The widespread host preferences displayed by three of the subgenera (denoted by an asterisk in fig. 8.20: *Graphium, Nomius,* and *Eurytides*) are postulated to represent colonization events subsequent to the original point of cladogenesis. This scenario thus proposes that the initial diversification within the Graphiini resulted from a combination of three instances of host switching and four speciation events associated with retention of the plesiomorphic food type.

Evidence bearing on the second scenario can be sought by investigating the food preferences within a phylogenetic context for each Graphiini genus. If this scenario is correct, primitive members of each genus should display a preference for Annonaceae plants. Miller undertook just such an analysis of the genus *Graphium.* The relative phylogenetic relationships for the species within this genus whose host plants have been identified is depicted in figure 8.21 (see Saigusa et al. 1982, cited in Miller 1987). Once again, mapping the distribution of plant preferences on this tree suggests that a fair amount of host switching has occurred within this genus. However, as was the situation at the generic level, the butterfly-plant association pattern portrayed in the preceding figure is only one of several potential representations of these data. Optimization of host types on the phylogenetic tree suggests that the species in this genus are primitively associated with plants of the family Annonaceae (fig. 8.22).

Two speciation events on the tree are associated with host switches from Annonaceae to other Magnoliidae orders (the Laurales and the Piperales), and one speciation event is associated with a switch within the order Laurales from Lauraceae to Hernandiaceae. The remaining speciation patterns are congruent with these initial three host switches across magnoliid orders. The widespread host preferences displayed by five of the butterfly taxa (denoted

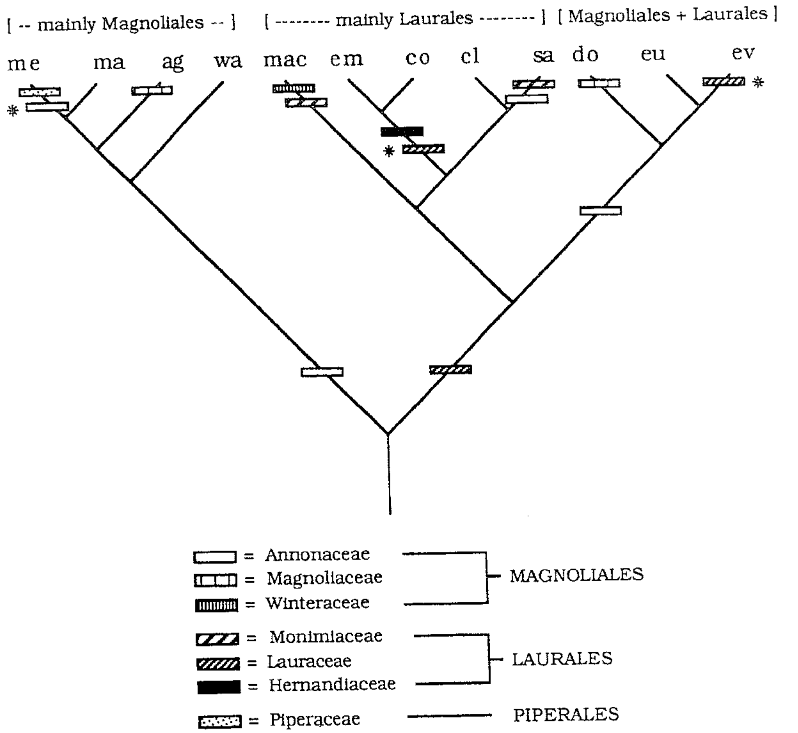


Fig. 8.21. Dietary preferences mapped onto the phylogenetic tree for the swallowtail butterfly subgenus *Graphium.* All the host plants depicted on this cladogram are members of the Magnoliidae; however, *G. macleayanum* and *G. sarpedon* also feed on rosids. Species: *me = G. mendana; ma = G. macfarlanei; ag = G. agamemnon; wa = G. wallacei; mac = G. macleayanum; em = G. empedovana; co = G. codrus; cl = G. cloanthus; sa = G. sarpedon; do = G. doson; eu = G. euryplus; ev = G. evemon. Bars* = host preferences; * = generalist on many hosts.

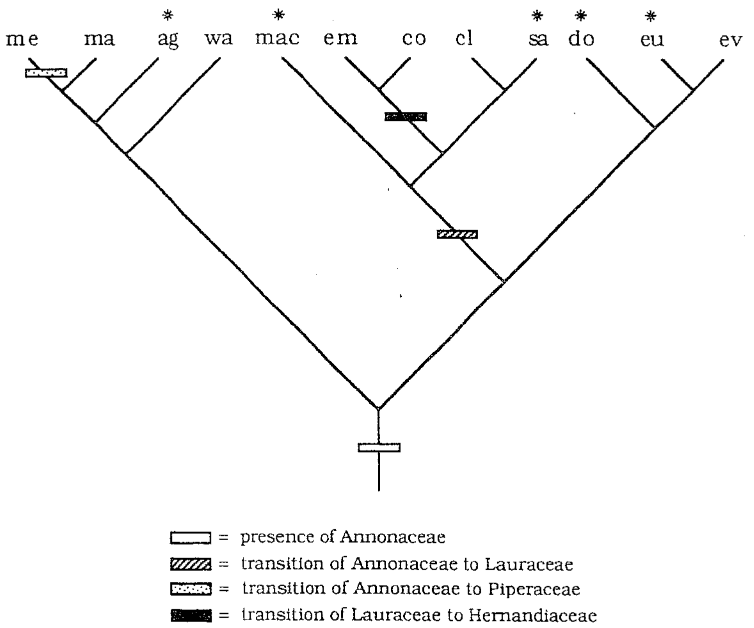


Fig. 8.22. Optimization of the host preferences on the phylogenetic tree for the swallowtail subgenus *Graphium*. Species: *me = G. mendana; ma = G. macfarlanei; ag = G. agamemnon; wa = G. wallacei; mac = G. macleayanum; em = G. empedovana; co = G. codrus; cl = G. cloanthus; sa = g. sarpedon; do = G. doson; eu = G. euryplus; ev = G. evemon. Bars =* host preferences; * = generalist on many hosts.

by an asterisk in fig. 8.22: *G. agamemnon, G. macleayanum, G. sarpedon, G. doson,* and *G. euryplus*) are postulated to represent colonization events subsequent to the origin of these species. Overall, then, this scenario paints a dramatically different picture from the ebullient portrait of widespread sequential colonization depicted in figure 8.21.

There is a recurring pattern at all three phylogenetic levels investigated in this study. The earliest phylogenetic split in the swallowtail butterfly group separates a species feeding on rosids from species feeding primarily on magnoliids (fig. 8.18). Because the magnoliids as a whole are not the sister group of the rosids, this would appear to be evidence of association between the plants and insects subsequent to the evolution of the plant groups. However, if we consider the Baroniinae and Parnassiinae to be numerical relict groups and examine only the Papilioninae, the relationships of the butterfly tribes and the plant families are potentially congruent, depending upon the details of the relationships within the Magnoliidae: the Graphiini feed mostly on members of the Magnoliales, the Troidini mostly on members of the Aristolochiales, *Meandrusa* feeds on members of the Laurales, and *Papilio* is specialized on rosids.

Diversification at the generic level within the Graphiini occurs primarily in association with members of the magnoliid family Annonaceae, with colonization occurring through switching to either other magnoliid species or to rosids. In this case, there is evidence of a correlation between cladogenesis and host switching to rosids in *Iphiclides,* the only Nearctic member of the group, followed by at least two colonization events from Annonaceae to Laurales. This pattern is repeated within the genus *Graphium,* where most of the phylogenetic diversification has also occurred in association with members of the Annonaceae, and three speciation events are correlated with colonization of different magnoliid orders.

Analyses at the generic and specific levels provide evidence of substantial phylogenetic diversification in some of the insect groups feeding on the members of a single family of plants. We do not have detailed phylogenetic hypotheses for the plant groups, so it is not possible to tell if there are any congruent portions of the host and butterfly phylogenies, or if these represent cases of "phylogenetic tracking." For example, the association between the *Graphium* species and members of the Annonaceae may be similar to the case of dissodactylid crabs and their echinoderm hosts discussed previously. If so, the butterflies speciated while the plants did not, which could be construed as evidence that the plants evolved before the association with the butterflies began. In addition, the relatively restricted range of hosts inhabited suggests some degree of resource tracking, while the high degree of host switching within that context suggests that the resource is widespread (and hence presumably plesiomorphic rather than convergent) among members of the magnoliids. This latter point is corroborated by two observations: (1) major instances of host switching occurring outside the magnoliids involve members of the Rosidae, which contains the hosts of the sister group of the Papilionidae, and (2) the Magnoliidae is a paraphyletic group, and paraphyletic taxa are grouped by shared plesiomorphic characters. Miller (1987) suggested that these data supported a resource-tracking model of sequential colonization more than a coevolutionary arms-race model. We agree that this is the best explanation for those episodes of phylogenetic diversification involving host switching. However, this study must be considered preliminary because of its lack of species-level information concerning host plant and butterfly phylogenetic relationships, and because the episodes of phylogenetic diversification that apparently did not involve host switching have not been identified as episodes of either phylogenetic tracking or of allopatric cospeciation.

Summary

The current data base for phylogenetic analyses of potentially coevolved or coevolving systems is sparse and weighted towards the interests of a few authors. Since the majority of empirical phylogenetic studies involve metazoan endoparasites of vertebrates, while most of the dynamical models of coevolution were developed for insect-plant systems, it is inappropriate at this time to form generalizations about the relative merits of particular models. However, it appears that there is considerable overlap in the macroevolutionary patterns associated with each coevolutionary model. For example, one outcome of a resource-tracking dynamic produces patterns of host and associate phylogenetic congruence that look like allopatric cospeciation patterns, while another outcome produces patterns that resemble the results of a coevolutionary arms race. Outcomes of the arms-race model range from strict cospeciation patterns to widespread host-switching patterns. Thus, the macroevolutionary effects of coevolutionary processes tend to blur the distinctions among the models (table 8.2).

Table 8.2 Comparative summary of models of coevolution.

	Model Class		
		Host Switching	
Phylogenetic Pattern	Allopatric Cospeciation[a]	Resource Tracking[b]	Coevolutionary Arms Race[c]
Congruence	**null model**	apomorphic resource **phylogenetic tracking**	defense/counterdefense traits co-orginate
Incongruence	*	plesiomorphic resource OR convergent resource **sequential colonization**	hosts with no associates OR associates back-colonize hosts defense/counterdefense traits do not co-originate

[a] Adaptive response need not be present in either host or associate.

* = broad host range and selective extinction (this is dangerous to invoke because all incongruences could be "explained" this way, reducing all coevolutionary explanations to cospeciation).

[b] Adaptive response may be present or absent in host, is present in associate.

[c] Adaptive response is present in both host and associate.

Virtually every association analyzed to date includes some departures from cospeciation, each of which, by definition, must involve some form of host switching. The majority of examples discussed in chapter 7 appear to be combinations of allopatric cospeciation and sequential colonization, the latter identified as such because the wide range of associate specificity indicates that these species are tracking a plesiomorphic resource (e.g., gyrocotylids and almost any ratfish, *Taenia* and almost any carnivore, *Ligictaluridus* and

ictalurid catfish from two different subgenera). It is thus likely that apparently discrete "models" of coevolution at the microevolutionary level are influencing coevolving systems in a variety of ways at the macroevolutionary level. If this is true, we should not expect a priori that the coevolutionary history of a given clade will conform completely, or even predominantly, to a single model. Rather, like speciation, each system may represent an aggregate of the differential effects of allopatric cospeciation, resource tracking, and the evolutionary arms race. Unfortunately, at the moment the data base is not large enough to investigate the relative frequencies of these modes in a manner analogous to Lynch's (1989) study of speciation modes (see chapter 4).

Coevolution and Evolutionary Specialization

Having discussed the models and patterns of coevolution in a general sense, we will now turn our attention to some of the characters involved in such interactions. It is possible that differences in the biological attributes of diverse associations may bias evolutionary outcomes. For example, phytophagous insects, by their very behavior, decrease the fitness of their host plants. From the plant's perspective the relationship is straightforward; characters that contribute to foiling insect diners are selectively advantageous. On the other hand, the relationship between insect pollinators and their host plants is founded on a delicate balance between opposing selection pressures. Again from the plant's perspective, the decrease in fitness caused by the pollinator's role as herbivore is balanced against the increased fitness that results from the dissemination of gametes. Some associations track broadly through a single trophic level (e.g., polyphagous phytophagous insects), whereas others track narrowly through several levels (e.g., digenetic trematodes, which use molluscs as first intermediate hosts; plants, invertebrates, or vertebrates as second intermediate hosts; and vertebrates as final hosts). Of all the biological attributes, the degree of specificity, or specialization, exhibited by the members of any given association has consistently been assigned a prominent role in explanations of coevolutionary systems.

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Resource Specificity

Concepts of evolutionary specialization and resource ("host") specificity play major roles in all of the coevolutionary models because the extent to which an associate can be expected to colonize new hosts is dependant upon its degree of specialization on the original host resource, and upon the evolutionary diversification of the hosts (see Futuyma and Moreno 1988, and Humphery-Smith 1989 for recent reviews of theories about the evolution of specialization and host specificity). Examination of evolutionary specialization, host specificity, and host switching within a macroevolutionary context produces a vexing paradox (cf. the discussion in chapter 4 concerning models of sympatric speciation; also Futuyma and Mayer 1980). On one hand, it seems reasonable to propose that the possibilities for successful sequential colonization are enhanced in inverse proportion to the degree of host specificity. That is, species that respond to a more general, widespread type of cue or a large number of different cues are afforded a greater opportunity to colonize a variety of hosts than their narrowly focussed counterparts. But on the other hand, if colonization of a new host leads to speciation and the establishment of a unique association, then the host must have acted as a strong directional selection force. The chances of this occurring should be higher for species with pronounced host specificity, because they are theoretically more sensitive to changes in the host component of their environments than their more tolerant, generalist relatives.

Necessary ?

The mechanisms underlying patterns of resource specialization depend upon whether the specificity originates from the biology of the associate or the biology of the host. If the association is maintained by the host group's possession of a particular resource that is necessary for the survival of the associate, then the specificity may reflect the resource's distribution among sympatric or parapatric host species and the opportunistic behavior of the associate. Specificity due to some attribute of the associate might result from a general macroevolutionary trend toward ecological specialization in the group, which could be manifested as increasing host specificity (Smiley 1978). Alternatively, it could be due to some characteristic of the associate's deme structure that increases the likelihood that host switching will lead to speciation. For example, groups that are capable of producing a viable deme from a single colonization event would be (1) more likely to speciate as a result of colonization than those requiring a larger founding population and (2) more likely to be members of a clade comprising many host-specific species than of a clade comprising a few generalists. The monogenean parasitic flatworms are excellent examples of both these points. Monogeneans exhibit direct development and have generation times much shorter than those of their vertebrate hosts; hence, it is possible for a single monogenean to establish a viable deme, and produce colonizing offspring, while residing on one host. As predicted, the evolutionary diversification of this species-rich group has been driven by a great deal of host switching (chapter 7), even though individual monogenean species are highly host-specific.

Of course, as in any biological system we expect attributes of both hosts and associates to play roles in determining specificity patterns. For example, in the relationship between ancyrocephalid monogeneans and centrarchid fishes, the hosts exhibit high rates of hybridization. The characteristics of monogenean biology that make them such good colonizers are thus coupled with an increased opportunity for colonization, since, as different species of centrarchid fishes assemble on the fields of courtship, more than just gametes are exchanged. Once again, the result has been the evolutionary diversification of many highly host-specific species, most of which have evolved as a result of host switching.

In the following section, we will consider two types of questions about host specificity and macroevolution: Is there a relationship between host specificity and the degree of cospeciation for a given clade? Are there any macroevolutionary trends in host specificity within clades? A preliminary answer to the first question can be sought among the examples presented in this book. In chapter 7 we discussed numerous studies in which pronounced host specificity was coupled with substantial phylogenetic congruence between hosts and associates. We also presented cases in which pronounced host specificity was coupled with substantial incongruence between host and associate phylogenies (monogenean flatworms and centrarchid fishes, gyrocotylid flatworms and ratfish, tapeworms and alcid birds, and tapeworms and carnivorous mammals). The relationship between *Homo sapiens* and some of their roundworm parasites is an interesting example of this second category. Of the two nematode groups inhabiting the great apes, one (*Enterobius*, the pinworms) is more host-specific than the other (*Oesophagostomum*, hookworms). And yet, host relationships implied by the pinworms place *Homo* between *Hylobates* (gibbons) and *Pongo* (orangutans), whereas host relationships implied by the less-specialized hookworms unite *Homo* with *Pan* (chimpanzees) and *Gorilla*, the consensus view of hominoid relationships. Finally, if the example of the gall midges (Roskam 1985) represents a case of allopatric cospeciation followed by an expansion of the host repertoire through secondary colonization, then differences in host preference provide an essential indicator of the coevolutionary dynamics in this system. Overall, then, it appears that pronounced host specificity may be a necessary, but not sufficient, component of cospeciation. If this is true, then low degrees of host specificity should be correlated with limited phylogenetic congruence, while substantial host specificity will be associated with a wide range of phylogenetic patterns. This may be the reason for all the exceptions to the various "parasitological rules" that have been formulated over the past century (see Brooks 1979b, 1985).

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The second question requires that we search for regularities in patterns of host specificity emerging over the evolutionary diversification of a group. There are three possibilities here. First, host specificity can increase during phylogenesis as historical effects progressively constrain host preferences (fig. 8.23a). This is consistent with hypotheses of progressive specialization in coevolving lineages (see, e.g., Smiley 1978). The second possibility involves the reverse process; host specificity decreases during phylogenesis (fig. 8.23b). This is consistent with hypotheses about the evolution of ex-

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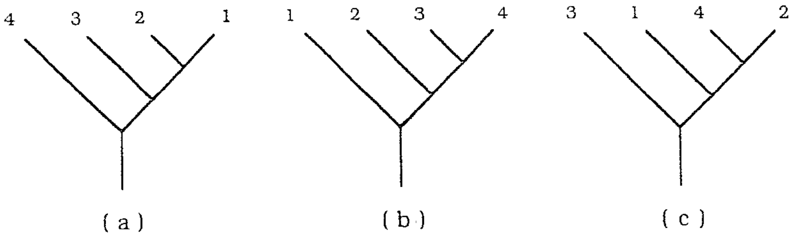


Fig. 8.23. Three potential macroevolutionary trends in host specificity within a clade. *Numbers* = the number of host species inhabited by each species of the associate clade. (*a*) Specificity increases. (*b*) Specificity decreases. (*c*) No patterns in specificity emerge.

treme opportunists, in which traits that facilitate opportunistic behavior are ③ optimized during evolution. Finally, it is possible that no macroevolutionary regularities will emerge during the course of phylogenetic diversification (fig. 8.23c).

According to the current data base, the predominant macroevolutionary trend in changes in host specificity within a clade corresponds to the pattern shown in figure 8.23c. While some members of any given clade of associates are highly host-specific, others are not, and the distribution of these two types of associates within the clade appears to be random. The only example that we have discovered that demonstrates increasing host specificity within an entire clade (fig. 8.23a) is provided by the relationship between telorchiid trematodes and North American turtles (Macdonald and Brooks 1989). To date, there are no phylogenetically based studies that show the pattern depicted in figure 8.23b.

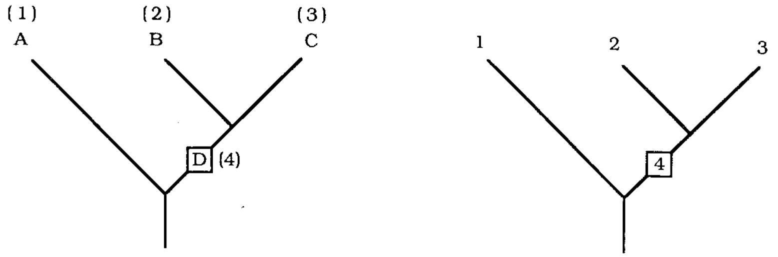
Genetic Diversification

A newly emerging approach to studying coevolution involves attempts to determine the influence that members of an association might have on each other's rate of genetic divergence. A complete investigation of coevolutionary changes in genetic characters must include both phylogenetic and genetic information. Examination of the sister-group relationships within each study group and the degree of phylogenetic congruence (cospeciation) among the study groups allows us to determine whether each association is a historical one. *Once the historical framework has been established, studies of genetic differentiation among members of each clade involved in the association will allow us to determine the degree of correlation between the putative genetic changes.* There are many methods for assessing the degree of genetic differentiation within and among species, the most common of which is the calculation of "genetic distances" based on molecular data. There is currently a great controversy raging around the use of genetic distance data for building phylogenetic trees (if you are interested in this particular issue, see, e.g., Farris 1981, 1985; Avise and Aquadro 1982; Felsenstein 1982; Avise 1983; Buth 1984). For the purposes of this chapter, however, all you need to remember is that if you construct phylogenetic trees using genetic distance data, you cannot then use genetic distance data to study the relationship between host and associate genetic divergence without introducing circularity. Although there are numerous studies investigating either the phylogenetic or the genetic relationships between species, very few authors have attempted to combine the two to produce a more robust investigation of coevolution. Therefore, our discussion of the genetic correlates of coevolutionary associations must, at the moment, be based primarily on hypothetical examples and preliminary studies.

Before proceeding with this discussion, we would like to offer two caveats for those who are interested in expanding this promising area of research. First, always remember that estimates of the relationship between host and associate genetic divergence are highly susceptible to sampling errors. For example, it is often difficult to draw a statistically adequate sample of the entire genome for members of either host or associate clade. Second, recall that population biologists have compiled a substantial data base demonstrating that degrees of genetic variability often differ between groups of organisms (see, e.g., Ayala 1982b). Because of this, if we only have access to genetic distance data, we can never be sure if correlations (or their absence) between species are a reflection of a coadaptive interaction (or lack of it) or an artifact of the species genetic structure. *In order to have stronger grounds for postulating coadaptation we need to compare the genetic distances among members of both groups involved in the association with the genetic distances among members of their nonassociated sister groups.* A complete coevolutionary analysis thus incorporates information about (1) the differences in genetic distance between associated species and (2) the macroevolutionary relationship between changes in genetic distances among members of a clade and the appearance of an ecological association between those species. Four potential patterns are produced by the interaction between phylogenetic and genetic processes in coevolving systems (table 8.3).

Table 8.3 Interactions between phylogenetic and genetic factors in coevolving systems.

	Genetic Divergence	
	Equal Rates	Different Rates
Cospeciation	reciprocal coadaptation (fig. 8.24) I	no coadaptation (fig. 8.27) II
Host switch	directional coadaptation (fig. 8.26) III	no coadaptation (fig. 8.25) IV



PHYLOGENETIC CONGRUENCE BETWEEN THE TWO GROUPS

MEASURE:
distance (B, C) and distance (2, 3)
distance (A, D) and distance (1, 4)

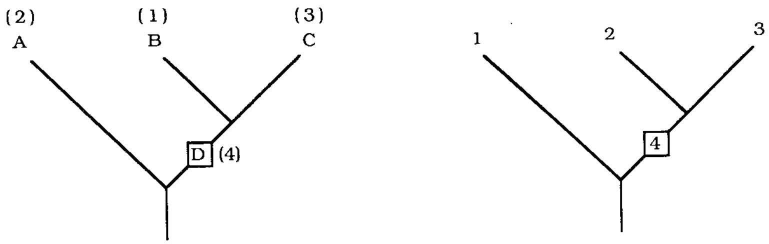
DISCOVER:
distance (B, C) = distance (2, 3)
distance (A, D) = distance (1, 4)

Fig. 8.24. Interaction type I. Total congruence between the host and associate phylogenies and similarity between the genetic distance measurements for the appropriate host-to-host/associate-to-associate comparisons. *Letters* = host taxa; *numbers* = associate taxa. The distributions of the associates in each host are listed in parentheses above the host tree.

In the first pattern we find phylogenetic association between hosts and associates (cospeciation) coupled with a similar amount of genetic divergence in both clades (fig. 8.24). There are two possible explanations for these observed patterns: 1. interactions between the organisms produces **reciprocal coadaptation** which, in turn, reinforces the association, or, what appears to 2. be reciprocal coadaptation could simply be a manifestation of equivalent evolutionary rates in the host and associate lineage, independent of any interactions between the associated species. In order to distinguish between these alternatives we need information about the rates of genetic divergence in the nonassociated sister groups of both the clades. If we find a macroevolutionary type correlation between a change in the rate of genetic divergence and the origin of the association, we have strong support for a coadaptational hypothesis that the associated species have mutually modified each other's genetic structure.

The next example demonstrates the opposite situation: here there is an absence of phylogenetic association (association by colonization: host switching), coupled with a lack of similarity in degrees of genetic divergence (fig. 8.25). Once again, there are two possible explanations for this observation: the hosts and associates have had relatively independent histories of association and show no indication that their genetic structure has been affected by their relatively recent association with each other, or, the rate of genetic change has in fact been modified, but the interaction was not strong enough

This whole approach is too



LACK OF PHYLOGENETIC CONGRUENCE BETWEEN THE TWO GROUPS

MEASURE:
distance (B, C) and distance (1, 3)
distance (A, D) and distance (2, 4)

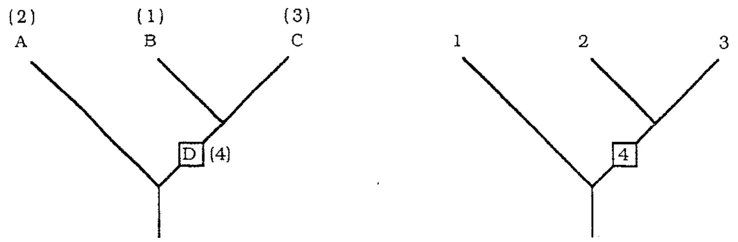
DISCOVER:
distance (B, C) ≠ distance (1, 3)
distance (A, D) ≠ distance (2, 4)

Fig. 8.25. Interaction type IV. Little congruence between the host and associate phylogenies and no similarity between the genetic distance measurements for the appropriate host-to-host/associate-to-associate comparisons. *Letters* = host taxa; *numbers* = associate taxa. The distributions of the associates in each host are listed in parentheses above the host tree.

or has not persisted for long enough to be detected as equivalent degrees of divergence. If we find no macroevolutionary correlation between a rate No, change in genetic divergence and the origin of the host switch, we have a strong refutation of a hypothesis of coadaptation.

A third possibility falls between the two preceding examples. In this case, there is an absence of phylogenetic association coupled with a similarity in degree of genetic divergence in the host and associate groups (fig. 8.26). It is possible to hypothesize that the new host acquired through colonization exerted such strong directional selection pressure on the colonizing associate that the degree of genetic divergence between the two associate species approached the degree of divergence between their hosts. We have called this type of outcome **directional coadaptation.** Alternatively, what might appear to be directional coadaptation might simply reflect inherent similarities between the associated groups (i.e., the two groups possessed equivalent rates of genetic divergence before the evolutionary origin of their association). Investigation of genetic divergence rates within the clades before and after the host switch will help to distinguish between these two alternatives.

Finally, there is the possible case of hosts and associates that show cospeciation patterns yet also have different degrees of genetic divergence (fig. 8.27). Such systems would imply that it is possible for ecological associates to maintain independent genetic divergence patterns despite a long-standing association; that is, mutual descent without mutual modification, at least at



LACK OF PHYLOGENETIC CONGRUENCE BETWEEN THE TWO GROUPS

MEASURE:
distance (B, C) and distance (1, 3)
distance (A, D) and distance (2, 4)

DISCOVER:
distance (B, C) = distance (1, 3)
distance (A, D) = distance (2, 4)

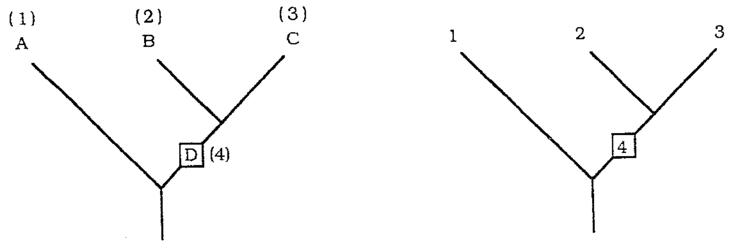
Fig. 8.26. Interaction type III. Little congruence between the host and associate phylogenies and similarity between the genetic distance measurements for the appropriate host-to-host/associate-to-associate comparisons. *Letters* = host taxa; *numbers* = associate taxa. The distributions of the associates in each host are listed in parentheses above the host tree.

the genetic level. This is the case in which cospeciation is due to a casual, rather than causal, phylogenetic association.

Having discussed the theoretical possibilities, let us turn our attention to some examples of this research. Bear in mind that none of the following authors have attempted the second stage of a genetic coevolutionary analysis; tracing the macroevolutionary interactions between changes in genetic divergence rates and the evolutionary origin of the association. Since these studies are based solely upon comparisons of genetic distance data between associated species, the results are preliminary, but interesting nonetheless.

Rodents and mites (type I)

Hafner and Nadler (1988) presented a coevolutionary study of geomyid rodents and their trichodectid mite ectoparasites. They reported that (1) their host and parasite trees indicated a considerable amount of congruence (i.e., a long historical association) between the rodents and the mites, and that (2) the relative genetic distances between related hosts and between their associated parasites were roughly equal. The authors interpreted the high degree of phylogenetic association coupled with the similarity in rates of genetic divergence in host and parasite lineages to indicate a strong coevolutionary coupling of genetic change between the two clades. However, the allozyme data used to calculate the genetic distances between species were also used to construct the phylogenetic trees. Formulating evolutionary hypotheses about relationships between characters using a phylogenetic reconstruction based upon those characters introduces a degree of circularity, and thus weakens the resulting evolutionary hypothesis. In addition, the authors used phenetic rather than phylogenetic methods to generate their trees. Phenetic analyses cluster taxa to maximize the fit of the data to a model of homogeneity of evolutionary rates. Since they incorporate this a priori assumption of homogeneity, phenograms are not good independent tests of similarity in coevolutionary rates of genetic divergence, even if based on data other than those used to infer the rates of divergence in the first place. What is needed here, then, is an independent phylogenetic assessment based, for example, on morphological characters, of the phylogenetic association between the rodents and the mites. Examination of Hafner and Nadler's allozyme data to determine the relative degree of genetic divergence between the hosts and parasites within this phylogenetic context would avoid the problem of circularity, thus providing a strong test of the putative coevolutionary relationships between the two groups.



PHYLOGENETIC CONGRUENCE BETWEEN THE TWO GROUPS

MEASURE:
distance (B, C) and distance (2, 3)
distance (A, D) and distance (1, 4)

DISCOVER:
distance (B, C) ≠ distance (2, 3)
distance (A, D) ≠ distance (1, 4)

Fig. 8.27. Interaction type II. Total congruence between the host and associate phylogenies and no similarity between the genetic distance measurements for the appropriate host-to-host/associate-to-associate comparisons. *Letters* = host taxa; *numbers* = associate taxa. The distributions of the associates in each host are listed in parentheses above the host tree.

Marsupials and tapeworms (type IV)

Baverstock, Adams, and Beveridge (1985) studied a group of tapeworms inhabiting Australian marsupials. In contrast to Hafner and Nadler's results, they found that (1) there was little congruence between host and parasite trees and that (2) the genetic distances between tapeworm species differed markedly from the genetic distances between their associated host species. The authors interpreted these results as indicating independent genetic histories for the host and parasite group, consistent with a limited amount of phylogenetic association between the lineages. However, their host tree (a "distance Wagner" tree constructed using genetic distances) and their parasite tree (a phenogram) were constructed using different methods of analysis, neither of which was a phylogenetic systematic approach. Based on the reanalysis of Hafner and Nadler's data, we suspect that the trees of Baverstock et al. show at least some incongruence because they were constructed by different methods.

Trematodes and frogs (type III)

Four species of parasitic flatworms, all members of the trematode genus *Glypthelmins,* inhabit the upper small intestines of North American ranid frogs. Hills, Frost, and Wright (1983), Hillis and Davis (1986), and Hillis (1988) presented a phylogenetic tree for these ranids based on a variety of morphological and molecular data. O'Grady (1987), investigating the relationships within *Glypthelmins* using morphological and ontogenetic characters, produced one tree with a consistency index of 76%. Since both host and parasite cladograms were available, O'Grady extended his study to include a cospeciation analysis using the methods described in chapter 7. He concluded that *G. intestinalis* inhabits *Rana pretiosa* as a result of cospeciation, whereas *G. californiensis* inhabits *R. aurora* as a result of a host switch. Thus the two frog hosts, *R. aurora* and *R. pretiosa,* are more closely related to each other than their associated parasites, *G. intestinalis* and *G. californiensis,* are to each other (fig. 8.28).

The first prerequisite for a coevolutionary study—the existence of phylogenetic trees, based on characters other than those used to determine genetic distances, and an analysis of the historical context of the association between the two clades—is thus met for these flatworm-frog interactions. Rannala (in press) calculated Nei's genetic distances from electrophoretic data and compared the degree of genetic divergence between the trematodes *G. californiensis* and *G. intestinalis,* and between their hosts, *R. aurora* and *R. pretiosa.* Surprisingly, the degree of genetic divergence between the frogs was statistically indistinguishable from the degree of genetic divergence between the parasites, even though the two frog species are more closely related to each other than the two parasite species are to each other. This is a possible case of directional coadaptation.

Unfortunately, few of the studies published thus far address the issue of rates of genetic divergence in associated lineages, and of those, different methods have been used to construct the phylogenetic trees. Thus the results

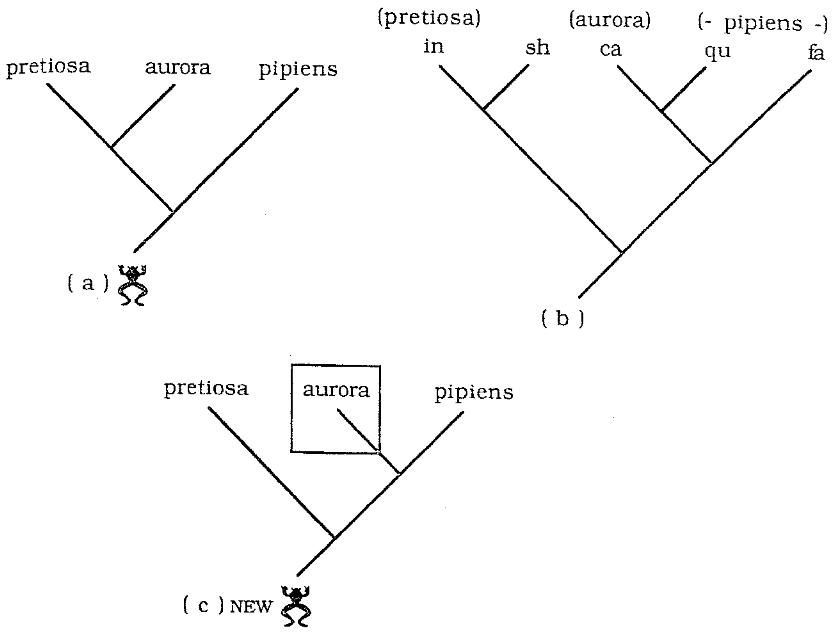


Fig. 8.28. Phylogenetic analyses of the relationships between ranid frogs and their flatworm parasites. (*a*) Simplified phylogenetic tree for the ranids based on rDNA restriction sequence data. Only three hosts are shown: *Rana pretiosa, R. aurora,* and *R. pipiens* (species complex). (Modified and redrawn from Hillis and Davis 1986.) (*b*) Simplified phylogenetic tree encompassing five species of *Glypthelmins,* based on morphological and ontogenetic characters. *in* = *G. intestinalis; sh* = *G. shastai; ca* = *G. californiensis; qu* = *G. quieta; fa* = *G. facioi.* The hosts inhabited by each species of flatworm are listed in parentheses above the species names. (Modified and redrawn from O'Grady 1987.) (*c*) New host cladogram derived from the phylogenetic relationships of the parasite taxa (see chapter 7 for methods). Note that *R. aurora* (*box*) is now misplaced on the cladogram; therefore, this is interpreted as a case of host switching by *G. californiensis.*

to date cannot be directly compared, and results from future investigations will continue to be incompatible until a standardized approach to coevolutionary studies is adopted. Perhaps the most important conclusion to be drawn from the three preceding examples is that similarity in degrees of genetic divergence between ecological associates does not necessarily indicate phylogenetic association, and phylogenetic congruence does not necessarily indicate similar genetic divergence between biological associates. We think this area of investigation holds exciting promise for the future, because the combination of phylogenetic, ecological, and genetic information permits both detailed reconstructions of coevolutionary pathways and an examination of the interaction between macroevolutionary patterns and microevolutionary changes.

Community Evolution: Composition and Structure of Multispecies Ecological Associations

One of the most difficult aspects of studying the evolution of communities is that biologists hold widely divergent views about just what exactly is a community. For example, some researchers view communities as associations of species so strongly tied together by their ecological and behavioral interactions (synecological attributes) that they are almost "superorganisms" (e.g., Wilson 1980, 1983). Others feel that communities are arbitrary assemblages of species that happen to be in the same place at the same time. A recent statement (Strong et al. 1984) summarizes this perspective.

> One possibility that we expect to obtain fairly commonly is the community with so few strong interactions that organization arises primarily from mutually independent autecological processes rather than synecological ones. Such communities would not be holistic entities, but rather just collections of relatively autonomous populations in the same place at the same time.

In many ways, the discussion of this question resembles the discussion among systematists about the definition of the term "species"! Ricklefs (1990:656) stated that "the term *community* has been given a variety of meanings by ecologists." As a consequence, we are not going to champion one community concept over another, nor are we going to summarize and categorize all of the literature in this area. Rather, we will assume that a variety of community types exist on this planet, and thus almost all concepts of community will be valid for particular cases.

Given this, we should be able to uncover both historical and nonhistorical components in community structure. The interesting question then becomes, Are all communities influenced to the same degree by the interaction of these two components, or has each travelled along a unique, evolutionary pathway? Phylogenetic history may confound our attempts to identify the type of community with which we are working, if species occur together due to common episodes of vicariant speciation. This historical component of the community will appear to represent a "holistic entity"; however, it does not necessarily follow that members of this "holistic entity" will exhibit strong synecological interactions. Because of this, cospeciation studies such as those outlined in chapter 7 are a useful starting point for coadaptation studies in community evolution. Needless to say, such studies are apt to be difficult because they require that we examine the members of more than one community in order to draw robust explanations for the evolution of any single community.

There is a marked similarity in many ecological associations, especially of specialized species, around the world that suggest phylogenetic influences in interaction structure as well as species composition. For example, McCoy and Heck (1976) examined the communities of corals, seagrasses, and mangroves throughout the tropics of the world, and concluded that these ecological associations all had a common origin. Hill and Smith (1984) discovered similar roosting patterns between six species of bats in a Tanzanian cave and fourteen species of bats in a cave on New Ireland Island off the northeastern coast of New Guinea. In both communities, species of the genus *Hipposideros* lived near the rear of the cave in association with species of *Rhinolophus*, while species of *Rousettus* roosted just inside the first major overhang (fig. 8.29).

On the parasitological side, Benz (cited in O'Grady 1989) examined the

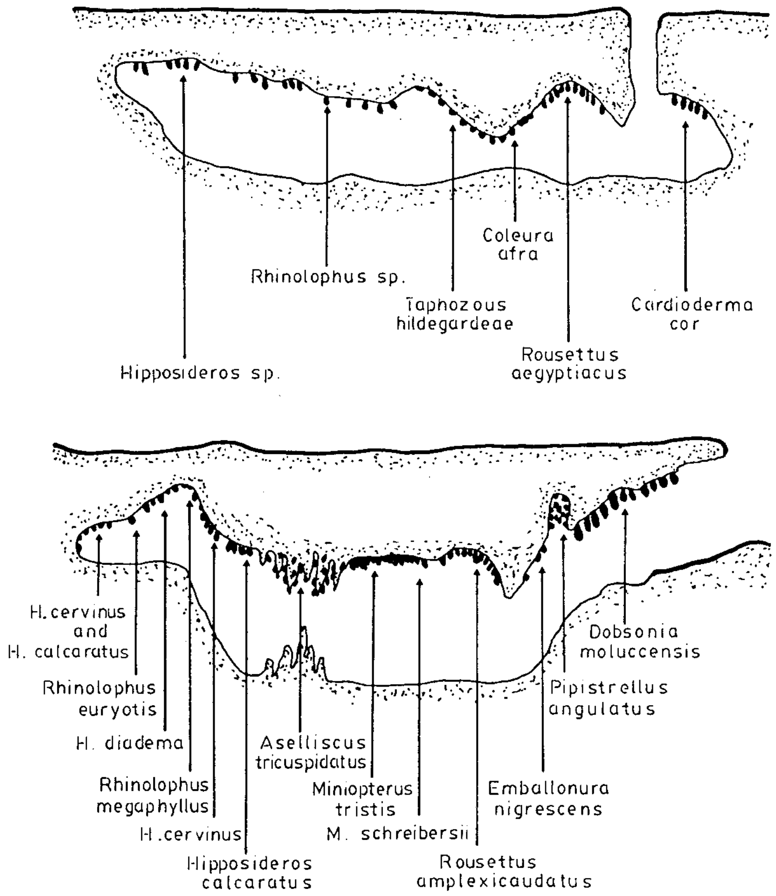


Fig. 8.29. Roosting positions of several bats species in Tanzanian (*top*) and New Ireland Island (*bottom*) caves. (From Brooks and Wiley 1988; redrawn and modified from Hill and Smith 1984.)

distribution of copepods living on sharks' gills. He discovered substantial diversification in habitat preference (site selection) within these copepod communities. Interestingly, the phylogenetic structure of these gill niches was retained even though the specific shark and copepod species varied from community to community. In almost every case, species of *Pandarus* inhabit the gill arch, *Eudactylinodes* and *Gangliopus* attach themselves to the secondary lamellae, *Nemesis* burrow into the efferent arterioles, *Phyllothyreus* inhabit the superficial portions of the interbranchial septum, *Paeon* embed in the interbranchial septum, and *Kroyeria* are found in the water channels of the secondary lamellae or embedded in the interbranchial septum (fig. 8.30).

Price (1984, 1986) outlined four models for the evolution of communities of specialists, including communities of parasites. These models, based on the differential contributions of competition, niche availability, rates of colonization and extinction, and phylogeny to molding extant patterns of com-
1. munity structure, may be summarized as follows: (1) **Nonasymptotic model**
(Southwood 1961): the community never reaches a saturation point because
its member species are too specialized to fill all the available niches. (2)
2. **Asymptotic equilibrium model** (MacArthur and Wilson 1967; Wilson
1969): the balance between colonization and extinction rates holds the com-
munity at equilibrium. Extinctions are postulated to be driven by biological
3. factors such as interspecific competition and predation. (3) **Asymptotic non-**
equilibrium model (Connor and McCoy 1979; Lawton and Strong 1981):
"vacant niches" are present in the community because colonization rates are
4. not sufficient to fill them up. (4) **Cospeciation model** (Brooks 1980a):
"niches" are duplicated by allopatric cospeciation of community members,
so extant community structure is due to the persistence of historical associa-
tions.

If we use Price's "models" to represent macroevolutionary influences on the evolution of ecological associations, Price's discussion can be extended to encompass all multispecies ecological associations, be they called associations, guilds, communities, biotas, or ecosystems. Just as we believe that coevolving lineages may represent the interaction of different "models of coevolution," we think it likely that any given multispecies association may be characterized by an interaction of any, or all, of these influences. These models can be further enhanced by incorporating concepts of spatial and resource allocation among co-occurring species (Brown 1981, 1984; Brown and Maurer 1987, 1989). For example, all species within a community contain information about (1) their origin with respect to the biota (spatial allocation), and (2) the origin of traits relevant to the association, that is, traits that characterize a species' interactions with other species and with the environment (resource allocation). The occurrence of a given species in a community may be due to either phylogenetic association (its ancestor was associated with the

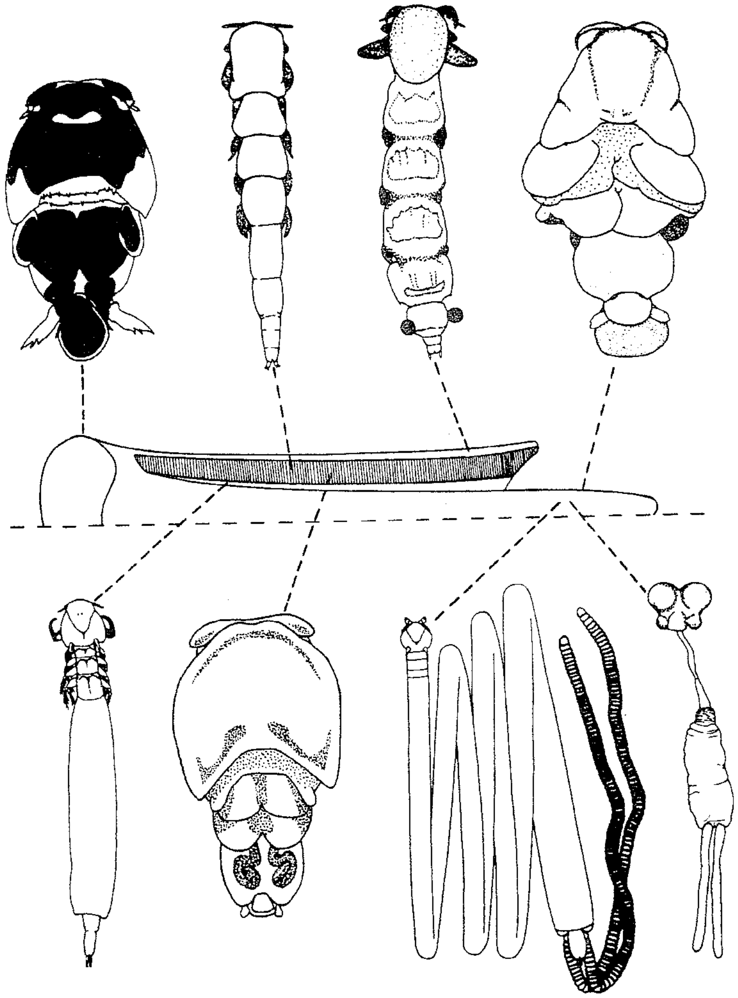


Fig. 8.30. Distribution of eight species of copepods on the gill of a shark. The copepods in this guild are (*clockwise, from the top left*) *Pandarus cranchii, Eudactylinodes uncinata, Nemesis lamna, Phyllothyreus cornutus, Paeon vaissieri, Kroyeria caseyi, Gangliopus pyriformis*, and *K. lineata*. (From O'Grady 1989.)

resident R-
colonizing C

ancestors of other community members), in which case we refer to it as a resident species, or to colonization, in which case, not surprisingly, the taxon is termed a colonizing species. Similarly, the ecology of any given species in a community may reflect the presence of persistent ancestral traits or of recently evolved, autapomorphic traits. Starting to sound familiar? Under the guise of spatial and resource allocation, colonization, extinction, and competition, we have returned full circle to the evolutionary processes of speciation and adaptation discussed for individual clades in chapters 4 and 5. The combinations of species occurrence (speciation processes) and interactions (adaptation processes) are depicted in table 8.4. Brown and Zeng (1989) recently suggested that communities should be considered mosaics of all four of these types of historical and ecological influences.

Is this OK?

Table 8.4 Heuristic depiction of four classes of species contributing to community structure.

Species Occurrence	Species Interactions	
	Ancestral	Derived
Ancestral	historically constrained residents I	? stochastically changed residents II
Derived	noncompetitive colonizers III	competitive colonizers IV

Note: There are two components to ecological associations: Species composition: the occurrence of each species in an association is either ancestral or derived. Species interactions: the characters involved in interactions among members of the association are either ancestral or derived.

Phylogenetic history (table 8.4, type I): The conservative homeostatic portion of any community is composed of species that evolved in situ through the persistence of an ancestral association (congruent portions of phylogenies in a cospeciation analysis). Such species display the plesiomorphic condition for characters involved in interactions with other community members and with the environment (fig. 8.31). Since this section of the community is characterized by a stable relationship across evolutionary time, it may act as a stabilizing selection force on other members of the community by resisting the colonization of competing species. Macroevolutionary patterns of this nature correspond to an allopatric cospeciation model.

Why?
Always?

Ross (1986) reported a high degree of phylogenetic constraints in the structuring of contemporaneous reef-fish communities. Boucot (1982, 1983) concluded that the fossil record demonstrates the conservative nature of community structure throughout evolutionary history. He further suggested that when evolutionary changes do occur, they tend to reverberate through most

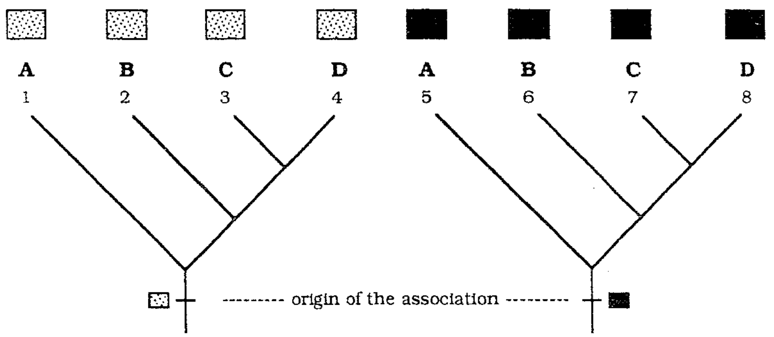


Fig. 8.31. Phylogenetic effects in community structure in area D. *Letters* = areas; *numbers* = species. Species 1 + 5 occur together in area A, species 2 + 6 occur in area B, species 3 + 7 occur in area C, and species 4 + 8 occur in area D. The state of a particular character involved in the interaction between these community members is depicted by the *boxes*. In this situation, both the origins of the traits and the origins of the association between community members are old. Extant community structure in area D thus represents *the persistence of an ancestral association, coupled with the persistence of ancestral interaction traits in both members of the community.*

of the community structure. Historical ecological methods can provide a complementary approach to this study. Consider the hypothetical case depicted in figure 8.32. Five areas (A–E) contain biotas composed of a member from each of three clades (1–5, 6–10, 11–15). Communities A, B, and C are characterized by plesiomorphic interactions among their component species (1, 6, 11; 2, 7, 12; and 3, 8, 13, respectively), whereas communities D and E are characterized by apomorphic interactions among species (4, 9, 14 and 5, 10, 15, respectively). The phylogenetic explanation for this pattern is as follows: The correlation among the plesiomorphic interaction traits is the result of historical conservatism in the evolution of these communities. Novel ecological interactions evolved in the common ancestor of species 4 + 5, the common ancestor of species 9 + 10, and the common ancestor of species 14 + 15. These clades show a pattern of historical congruence; therefore, the evolutionary changes in ecological interactions co-originated in co-occurring species in the same (ancestral) biota. We can thus hypothesize that a common cause is responsible for this suite of ecological changes.

Maybe b/c environ. might have changed too.

Colonization by "preadapted species" (table 8.4, type III): This portion of the community contains species that have been added by colonization. Such species can be recognized in part because their phylogenetic history is incongruent with the histories of other community members. In addition, the term "preadapted" implies that these individuals are able to colonize the area because they already possess traits that do not conflict with the existing community structure (fig. 8.33). This scenario postulates that there is no compe-

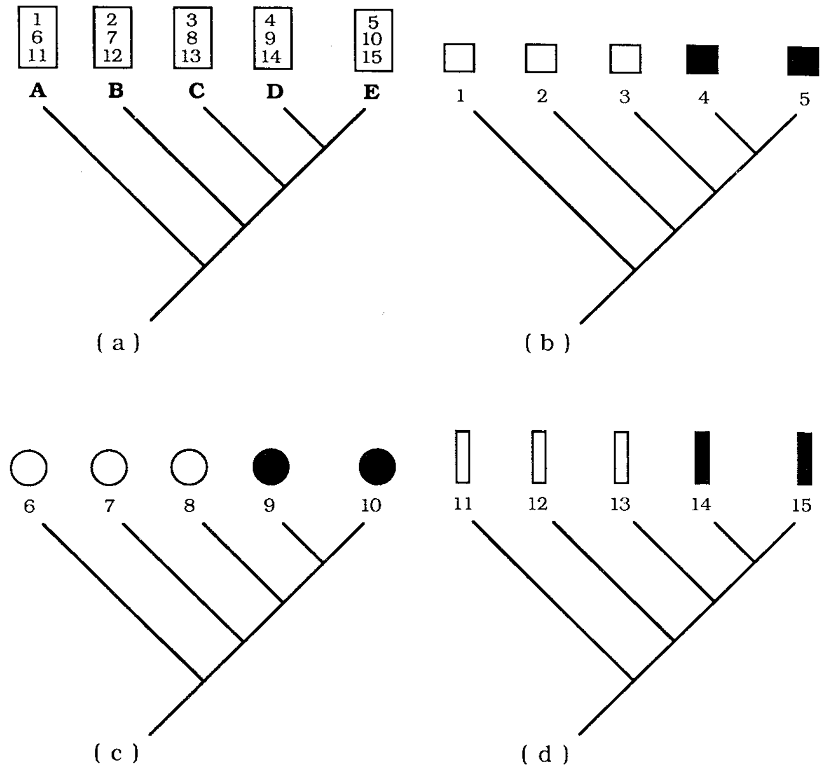


Fig. 8.32. Correlated evolutionary changes in the evolution of communities. *Letters* = five communities; *numbers* = members of three different clades that inhabit those communities. (*a*) Area cladogram of the historical relationships among the communities, based on the phylogenetic relationships of the species that occur in them. (*b–d*) The phylogenetic trees for the members of the three clades. Superimposed above each species number is a symbol indicating a particular resource utilization character. *White symbols* = plesiomorphic trait; *black symbols* = apomorphic trait. Note that the shift from plesiomorphic to apomorphic traits in each clade occurred in the common ancestor of the two most recently differentiated species, leading to the emergence of an ecological structure in communities D and E that differs from the ecological structure in communities A–C.

tition between colonizing individuals and established (resident) members of the community. On the one hand, if the appearance of these species reduces the possibilities for the subsequent addition of species into the community, then this type of macroevolutionary pattern corresponds to the asymptotic equilibrium model of MacArthur and Wilson (1967). On the other hand, if the rates of colonization are low enough, the community may persist below expected equilibrium numbers (corresponding to the asymptotic nonequilibrium model). Similarly, if the colonizers are so specialized ecologically that

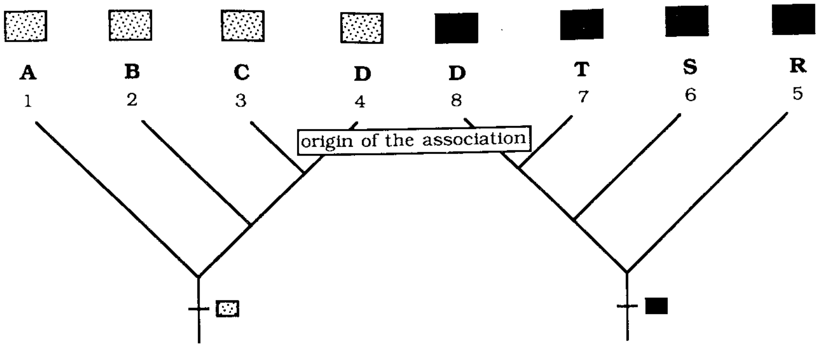


Fig. 8.33. Community structure of area D influenced by colonization of "preadapted species." *Letters* = areas; *numbers* = species. The state of a particular character involved in the interaction between these community members is depicted by the *boxes*. Species 8 has colonized area D and is now interacting with species 4. In this situation, the origins of the traits are old (plesiomorphic) while the origins of the association between community members are relatively recent (apomorphic). Extant community structure in area D thus represents *the appearance of a colonizing species, coupled with the persistence of plesiomorphic interaction traits in both members of the community.*

they do not affect other members of the community or preexisting potential niche space, community diversity may increase without approaching an apparent equilibrium (corresponding to the nonasymptotic model).

Erwin's (1985) "taxon pulse" model is an example of this kind of influence in the evolution of biotic diversity. As outlined in chapter 5, according to this model, a group of species might begin with an ancestor that displays a certain ecological propensity. As time passes, the ancestor and its descendants spread over a larger and larger geographical area, with descendant species fulfilling the same or very similar ecological roles in different locations. Subsequent to this first wave of dispersal, a new ecological trait arises in one of the descendant species in one of the localities. The species bearing this novel trait then undergoes widespread dissemination, and a new "pulse" of diversity occurs, producing a new set of descendant species, all performing similar functions in different locations. Diverse and highly structured communities could be formed in many different areas in this manner, with every community containing a member of each of the "pulses." The number of occupied "niches" within each community would thus correspond to the number of pulses represented by the species that were present. Roughgarden and Pacala (1989) presented a similar argument (using the term "taxon cycle") to explain the species composition and size structure of anoline lizard communities on Caribbean islands.

Colonization by competing species (table 8.4, type IV): All species that colonize a community will exhibit incongruence in a cospeciation analysis. However, unlike the conservative situation depicted for preadapted species (fig. 8.33), varying patterns of character evolution will be traced upon this phylogenetic framework if colonizing individuals compete with resident species. In this situation, at least one of three things must happen in order for the colonizer to become established: the colonizing species will change (fig. 8.34a), the resident species competing with the colonizer will change (fig. 8.34b), or both the resident and the colonizer will change (fig. 8.34c). This will produce a pattern in which the colonizer, the resident, or both exhibit an apomorphic condition of the traits relevant to the competitive interaction. Replacement of the resident by the colonizer would be indicated on a cospeciation analysis if (1) the extinction event is coupled with the colonization event and (2) other members of the "extinct" species' clade have similar resource requirements to the colonizer. These macroevolutionary patterns correspond most closely with the asymptotic equilibrium model of MacArthur and Wilson (1967).

Stochastic ("nonequilibrium") effects (table 8.4, type II): If there is unoccupied "niche space" in a community over extended periods of time, stochastic evolutionary processes operating on resident species may produce changes resulting in the use of some of that previously unoccupied space. In this scenario, evolutionary changes in ecological characters occur within a cospeciation framework. Species contributing to this portion of the community structure can be recognized by their historical congruence with other community members, coupled with the presence of apomorphic traits characterizing their interactions with other species and with the environment (fig. 8.35). Since these changes do not affect other community members, they may represent a type of stochastic wandering through modifications "allowed" by the existing community structure. Such species appear to diverge ecologically for no apparent reason, although care must be taken to rule out the effects of previous competition. The longer a community exists below equilibrium numbers, through any of the processes described under "colonization by preadapted species," the greater the possibility that resident species will experience these sorts of evolutionary changes.

Preliminary Examples

Communities of specialists: Neotropical stingrays and their helminth parasites

Price (1986) stated that

> one major advantage of parasite communities over others is that the habitat they live in, the host, has such a well defined structure. . . . The host microcosm is replicated through time and space much more so than habitats for most other organisms. Therefore, the study of comparative community structure is very powerful.

And possibly misleading for other
types of habitats + associations

untapped resources in colonizing the new host. No resident species are displaced; the colonizers simply increase the community's diversity. Finally, one community, in the stingrays of the Orinoco Delta, has been assembled according to variety of influences (three type I, two type II, four type III, and three type IV influences). The structure of this community is therefore the end product of a complex interaction among history, host switching into unfilled resource space, host switching by potential competitors (see legend in table 8.5), and stochastic effects.

A more familiar type of community: Some North American freshwater fishes

Biologists have been studying North American freshwater fishes for more than a century. Because of this fascination, a vast data base has been accumulated; and because of this data base, we are now beginning to catch tantalizing glimpses of historical, geographical, and ecological interactions during the evolution of these animals. Gorman (in press) built his study of freshwater fish communities upon this foundation. He was interested in uncovering the relative role of historical constraints on (1) the species composition or "structure" of communities (cospeciation) and (2) the species associations or "functions" within those communities (coadaptation).

Gorman's research centered on three rivers in the extensive Central Highland Mississippi drainage system, the White, the Gasconade, and the Wisconsin driftless. The White and the Gasconade are both part of the Ozark drainage, closer together and more similar ecologically than either is to the Wisconsin; therefore, it is not untoward to predict that the communities in these two rivers should show a closer affinity. Gorman tested this ecological prediction by examining distribution patterns for twenty-nine species of fish at two levels of analysis: the rivers and specific habitats within these rivers. We will present a step-by-step discussion of this analysis because it highlights the differences between a historical and a nonhistorical approach to the study of community structure.

COMMUNITY STRUCTURE ON A LARGE SPATIAL SCALE: COMPARISONS AMONG RIVER SYSTEMS

1. The nonhistorical approach: Map the distribution of the twenty-nine species onto an unresolved diagram for the drainages (fig. 8.38). Now, reconstruct the relationships of the river drainages by clustering according to the presence/absence of species (fig. 8.39). Clustering river systems according to the raw similarity of their community structure (presence/absence of species) places the Gasconade with the Wisconsin driftless drainage. Notice that the occurrence of *Notropis boops* and *N. greenei* in the Gasconade and White rivers is unresolved; either these species are primitively present for all drainages and have become extinct in the Wisconsin (fig. 8.39a) or they originated in one of the Ozark rivers and dispersed into the other (fig. 8.39b). Ambiguity aside, the results of this analysis do not support the ecological expectation that the two Ozark drainages should display a more-similar community composition.

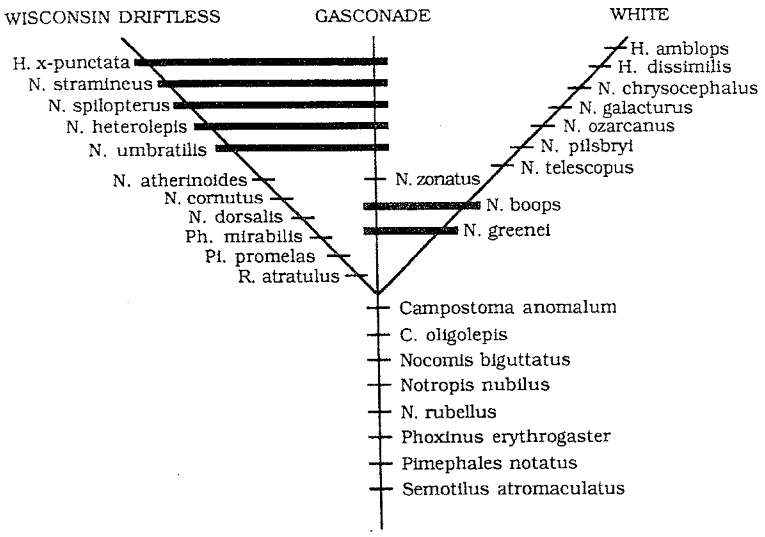


Fig. 8.38. Distribution of twenty-nine North American freshwater fish. *H.* = *Hybopsis; N.* = *Notropis; R.* = *Rhinichthys; Ph.* = *Phoxinus; Pi.* = *Pimephales; C.* = *Campostoma.*

2. The phylogenetic approach: Mayden (1988) reconstructed the historical relationships among the rivers of the Mississippi drainage, based upon comparing information from two sources: the geological relationships of the river drainages *and* the phylogenetic relationships of fishes living in those drainages. (Sound familiar? See chapter 7 for a discussion of this study.) According to this analysis, the three rivers of interest to us are associated in the manner shown in figure 8.40.

This phylogenetic analysis supports the intuitive expectations of community ecologists; the two Ozark drainages are more closely related to each other than either is to the Wisconsin driftless system. Now, how can we explain the anomalous results from the nonhistorical analysis? On the surface, the Wisconsin and the Gasconade drainages appear to have a more similar community structure because they share five species in common, whereas the Gasconade shares only two species with the White River (fig. 8.39). Since this conflicts with the phylogenetic hypothesis (fig. 8.40), we would have to conclude that

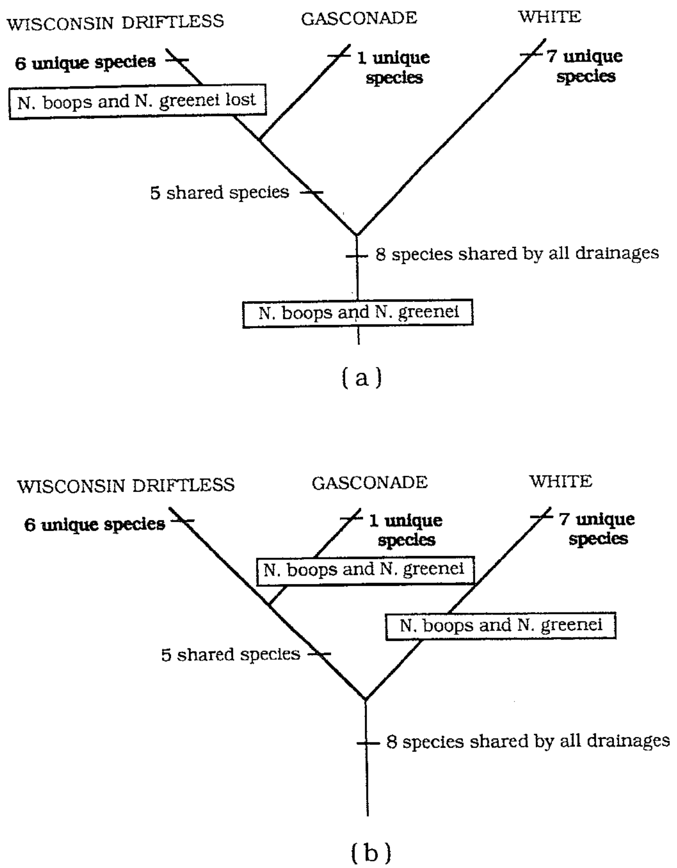


Fig. 8.39. Relationships among drainages, based upon shared species. This is a **phenetic** analysis of these relationships: drainages are grouped according to raw similarity (presence/absence of species).

history is a poor predictor of community composition at this level of investigation. However, there are two types of similarities in community structure based upon the presence of shared common species and **sister species.** A nonhistorical approach paints an incomplete picture because it does not examine the entire community; only the "shared species" are investigated, the endemic or "unique species" are disregarded (fig. 8.39). By contrast, a phylogenetic analysis incorporates both historical and nonhistorical information from all species within the community.

Bearing this in mind, let us reexamine the distribution of these fishes (fig. 8.41). With an eye to history (i.e., the Ozark drainages are more closely related), we can say that, of the twenty-nine species,

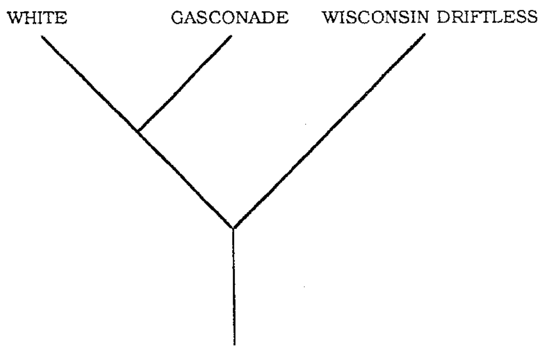


Fig. 8.40. Mayden's (1988) consensus cladogram for the three river drainages, based on an analysis of forty fish species. This cladogram indicates that *the White and Gasconade are more closely related to each other than either is to the Wisconsin.*

1. We can predict the distribution patterns for twelve species on the basis of history—*Campostoma anomalum, C. oligolepis, Nocomis biguttatus, Notropis nubilus, Notropis rubellus, Notropis boops, Notropis greenei, Phoxinus erythrogaster, Pimephales notatus,* and *Semotilus atromaculatus. Notropis zonatus* and *Notropis pilsbryi* also represent a historical component of the community structure because they are sister species (Mayden 1988) in sister river systems.
2. We cannot predict the distribution patterns for the five species shared between the Gasconade and Wisconsin driftless systems (*Hybopsis x-punctata, Notropis stramineus, N. spilopterus, N. heterolepis, and N. umbratilis*) on the basis of the historical relationships of the drainages or their current proximity. These species are assumed to be where they are because of dispersal, but, in the absence of phylogenies for the fishes, we don't know whether they dispersed from the Wisconsin into the Gasconade or vice versa. For example, a member of both the *H. x-punctata* (*H. dissimilis:* Wiley and Mayden 1985) and *N. heterolepis* (*N. ozarcanus:* Mayden 1989) clades is found in the White River. If these pairs of relatives are sister species, their presence in the White and Gasconade rivers is explained by common history (predictable), followed by the dispersal of *H. x-punctata* and *N. heterolepis* from the Gasconade into the Wisconsin. Once we have identified the existence and direction of dispersal events, we can begin to investigate the environmental variables in common between the two river systems and the impact of dispersing species on an established community.
3. We do not have enough information about the phylogenetic relationships

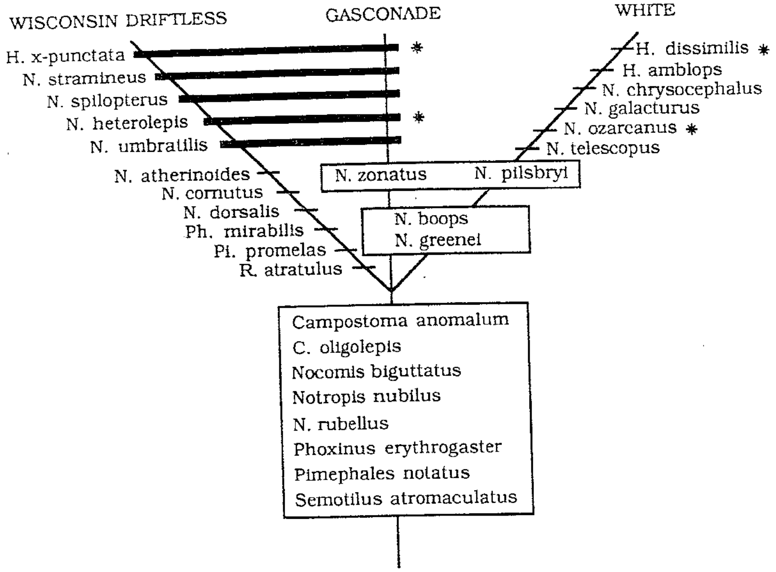


Fig. 8.41. Distribution of fishes (ecological data) examined from a phylogenetic perspective. Historical components of community structure are enclosed within *boxes*. * = putative members of the same clade. *H.* = *Hybopsis; N.* = *Notropis; R* = *Rhinichthys; Ph.* = *Phoxinus; Pi.* = *Pimephales; C.* = *Campostoma.*

of the remaining endemic species to determine how many are present due to dispersal (unpredictable) and how many are present due to common speciation patterns (predictable; i.e., sister species in sister drainages like *N. zonatus* and *N. pilsbryi*). In order to resolve this problem we need a phylogeny for the problematical *Notropis* group (groups?).

In summary, examination of the species presence/absence from a phylogenetic perspective has uncovered a by now familiar pattern: communities comprise both historical (cospeciation) and nonhistorical (dispersal) elements. This, in turn, highlights the need for researchers interested in investigating community structure to examine their ecological data within a phylogenetic context.

COMMUNITY STRUCTURE ON A SMALL SPATIAL SCALE: COMPARISONS AMONG HABITATS WITHIN THE RIVERS

In this section we will turn our attention to fish communities inhabiting pools and slow raceways of third- and fourth-order streams in the White, Gasconade, and Wisconsin driftless river systems. Since the presence/absence of rare fishes may be strongly affected by sampling errors, we will base this analysis upon the predominant species in these habitats.

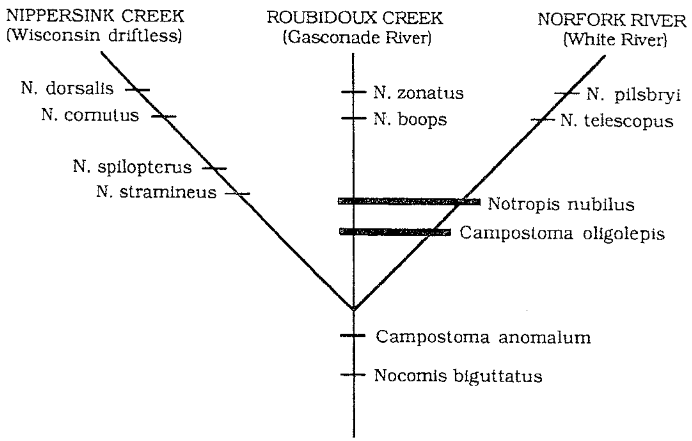


Fig. 8.42. Distribution of predominant species (> 5% of all individuals) collected in pool and slow raceway habitat of third- and fourth-order streams from three river drainages. *N.* = *Notropis*.

1. The ecological data: Let us begin by mapping the distributions of predominant species onto an unresolved diagram for the creeks (fig. 8.42).
2. The phylogenetic perspective: Now, let us reexamine these distributions in light of the historical relationships of the river (creek) systems (fig. 8.43).

The distribution of species in these headwater communities indicates that Roubidoux Creek (Gasconade River drainage) and Norfork River (White River drainage) are more closely related to each other than either is to the Nippersink Creek (Wisconsin driftless drainage). Since this *agrees* with Mayden's phylogenetic analysis, it appears that **the effects of historical constraints on community structure can be detected at both the large spatial scale of river drainages and the small spatial scale of individual habitats within those drainages.** The incorporation of additional phylogenetic information into this study uncovers even more interesting aspects of the evolution of community structure. For example, the relationships depicted in figure 8.41 indicate that *Notropis nubilus* and *Campostoma oligolepis* are primitively present in all three drainages, while *N. boops* is shared between the Gasconade and White rivers. Based upon this we can see that,

1. Roubidoux Creek community structure is completely predicted by history (six out of six species): four species are primitively present in all these river drainages (*Nocomis biguttatus, C. anomalum, Notropis nubilus, C. oli-*

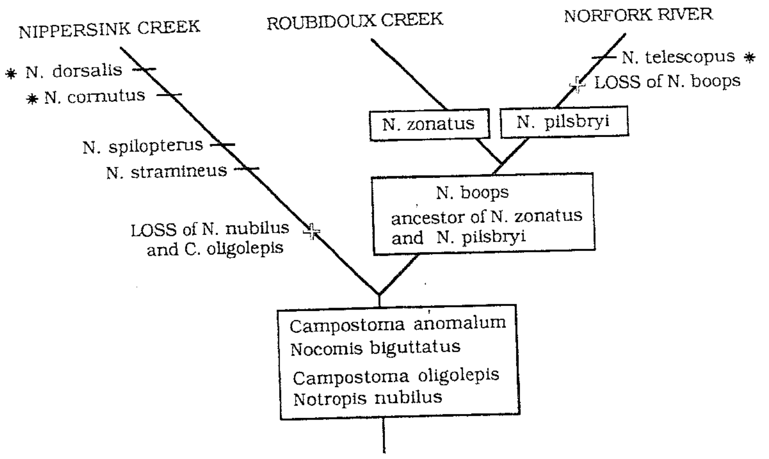


Fig. 8.43. Analysis of data within the phylogenetic framework presented by Mayden (1988) and incorporating additional information from the drainage-level analysis (fig. 8.41). * = endemic species.

golepis), one species is shared with its sister system the White River (*Notropis boops*), and one species, *Notropis zonatus*, occurs due to a shared speciation event with the White River—remember, *N. zonatus* and *N. pilsbryi* are sister species.

2. Norfork River community structure is almost completely predicted by history (five out of six species): four species are primitively present in all these river drainages (*Nocomis biguttatus, C. anomalum, Notropis nubilus, C. oligolepis*), and one species, *Notropis pilsbryi*, occurs due to a shared speciation event with the Gasconade River. The remaining species, *Notropis telescopus*, is endemic to the White River drainage so we would have expected to find it based upon our analysis at the drainage level. However, this does not tell us where that species came from originally (see discussion for endemics in the preceding section).

3. Nippersink Creek community structure is only weakly predicted by history (two out of six species): two species are primitively present (*Nocomis biguttatus, C. anomalum*), and two species are endemics, *Notropis dorsalis* and *Notropis cornutus*. The presence of *Notropis spilopterus* and *Notropis stramineus* is problematical; as discussed in the previous section, these species may have dispersed into the area.

Overall, then, thirteen out of eighteen of the predominant species in these pool and slow raceway habitats represent the presence of historical constraints on community structure. This, in turn, raises the following questions: (1) Why is *Notropis boops* absent in the Norfork River? (2) Why are *N. nubilus* and *C. oligolepis* absent in Nippersink Creek? (3) Why are *N. spilopterus* and *N. stramineus* absent in Roubidoux Creek? The answers to these questions might be found by examining the ecological interactions among species within these communities.

ANALYSIS BASED UPON CATEGORIES OF ECOLOGICAL INTERACTIONS

Let us begin by adding the ecological profiles to the information discussed in the previous section (fig. 8.44). There are some fascinating patterns here.

1. The oldest component of all these creek communities is the near-benthic forager. In the Ozark systems, the upper and midpelagic species may have been added next if the ancestor of *Notropis zonatus* and *N. pilsbryi* was a midpelagic forager. If not, the upper-pelagic forager was added to the community first, and the midpelagic species second.

2. Both the Ozark communities have the same functional structure: three near-benthic species, one lower-pelagic species, one midpelagic species, and one upper-pelagic species. This agrees with both the historical relationship of the areas and the similar environmental parameters found in the creeks.

3. Nippersink Creek has a radically different ecological composition from the Ozark creeks: one near-benthic species, three lower-pelagic species, and two midpelagic species. We need to resolve the phylogenetic relationships for the four most recent additions to this community in order to determine which, if any, of them are present because they evolved there (perhaps the endemics

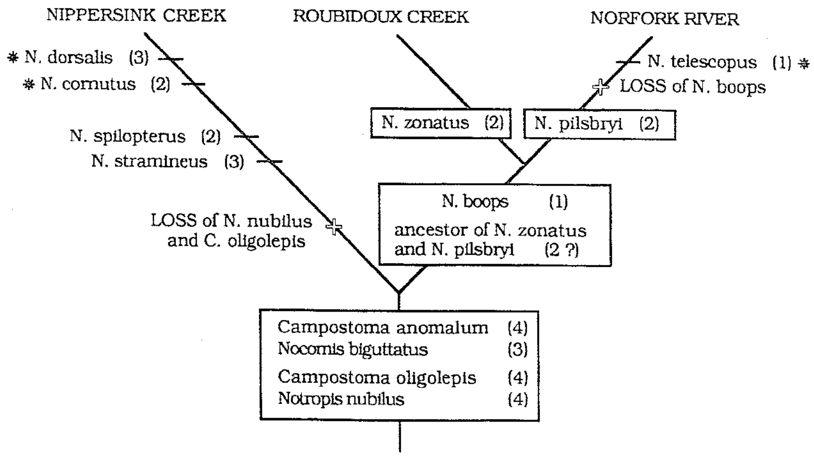


Fig. 8.44. Ecological profiles of dominant species mapped onto the cladogram for the river systems. Foraging categories: *1* = upper pelagic; *2* = midpelagic; *3* = lower pelagic; *4* = near benthic.

Notropis dorsalis and *N. cornutus*) or because they dispersed in (perhaps *N. spilopterus* and *N. stramineus*). If we can find historical evidence for dispersal, then the phylogenies can be used to determine whether the current interactions among the residents and colonizers is ancestral (type III, table 8.4) or derived (type IV). This, in turn, will tell us where to look for interspecific competition in this community.

4. "Why is *N. boops* absent in the Norfork?" The macroevolutionary patterns indicate that *N. boops* was potentially replaced by its ecological equivalent *N. telescopus*. Is there any way to move from a hypothesis based upon patterns to an experiment designed to test processes? In this case the answer to this question is definitely yes. Although rare, *N. boops* is present in the Norfork. Given this, we need to collect further information about the history of *N. telescopus* (i.e., what is its sister species, and did it evolve in the Norfork or disperse into that area?). If it dispersed into the Norfork, and if experiments reveal that it is currently out-competing *N. boops* in that river, then we have convincing evidence for competitive exclusion *without having to invoke the ghost of competition past.*

5. "Why are *N. nubilus* and *C. oligolepis* absent in Nippersink Creek?" Contrary to the *N. boops* example, these species have not been replaced with ecological equivalents. The answer to this probably lies in the structure of the substrate in Nippersink Creek (i.e., it is more sandy than in the Ozark streams, and both these species are near-benthic foragers). If so, habitat- and food-preference experiments should help resolve this problem.

ANALYSIS BASED UPON A SPECIFIC ECOLOGICAL INTERACTION

In the final section of his study, Gorman performed a series of experiments designed to investigate the role of preferred habitat use in the assemblage of the Roubidoux Creek community. The experimental protocol was simple and elegant. Preferred vertical distributions were determined for *Nocomis biguttatus, Notropis nubilus, C. anomalum, C. oligolepis, Notropis zonatus, and Notropis boops*, by observing isolated individuals in the laboratory. These patterns were then compared with distributions observed in the field and obtained in the laboratory in a mixed-species group, with stunning results. The fishes that demonstrate the same distributions in the lab (both alone and in mixed-species groups) and in the field are the four oldest members of the communities, *Nocomis biguttatus, Notropis nubilus,* and the two *Campostoma* species. Additionally, the overlap in preferred habitats among these species is low. So, as would be expected for the oldest part of an ecological association, this component has reached, and is being maintained in, a stable state. On the other hand, the more recently derived members of the community (*Notropis zonatus* and *Notropis boops*) still show evidence of interspecific interactions, that is, they are displaced from their preferred position in the field and in the mixed-species group. As discussed in the previous section, evidence of competitive interactions should be sought in two places within the community: between an older member of the community and its functional replacement (*Notropis boops* and *Notropis telescopus*) or between the most recently derived member of the community and the original residents (*Notropis zonatus*).

Overall, three generalizations about the evolution of these freshwater fish communities can be drawn from this extensive study: communities are composites of both historical and nonhistorical components; this pattern can be detected on both large and small spatial scales; and historical ecological analysis can provide a framework for experimental investigations of the impact of ecological interactions on community assemblage.

Summary

Although the preceding two studies are preliminary, we have presented them to illustrate two points. First, it is possible to combine phylogenetic, biogeographic, ecological, and behavioral data to ask questions about the relative contributions of historical and nonhistorical influences on the spatial and resource allocation patterns in biotas. Second, **patterns of evolution in communities are generally not the result of a single influence.** This is a familiar result. We discovered a similar generalization in the speciation dynamics involved in producing clades, and the coevolutionary processes involved in producing tight ecological associations. Paleontological studies (e.g., Boucot 1975a,b, 1978, 1982, 1983) tend to support this view.

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Adaptive changes in community structure involve both species composition and interactions. They tend to be evolutionarily conservative today, and the paleontological evidence suggests that they have been conservative in the past. Thus the conservative nature of adaptive changes and adaptive radiations in individual clades (chapter 5) is carried through into biotic structure. Type III and IV influences in community evolution encompass the two components of the MacArthur-Wilson (1967) equilibrium model of island biogeography, colonization by preadapted species when biotas are below equilibrium numbers, and colonization by competing species when biotas are at or near equilibrium numbers. Type I and II influences are nonequilibrium phenomena, which also must be taken into account when attempting to explain biotic structure and diversity. If these nonequilibrium influences are as pervasive as we (and others—see, e.g., Wiens 1984) think, and as the examples we have presented in this book suggest, much of the structure found in communities could be due to historical association. This structure, in turn, could

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be misinterpreted to indicate the influence of proximal factors (e.g., strong synecological interactions) if the evolutionary interactions within the community are not investigated within a historical framework.

At the moment, it is impossible to draw any meaningful generalizations about the relative contributions of historical constraints and adaptive change to the evolution of either closely interacting species (coevolutionary studies) or interacting communities (community evolution studies). Traditionally there has been very little interaction between biologists who study these two aspects of coadaptation. We hope we have demonstrated that there is so much common ground between these research programs, at least from a macroevolutionary perspective, that any cross-fertilization will be mutually beneficial. Indeed, some researchers are already discovering the benefits of examining complex systems within a cooperative atmosphere (see, e.g., Futuyma and Slatkin 1983 and Strong et al. 1984).