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PROCESS AND PATTERN IN THE EVOLUTION OF SPECIES ASSOCIATIONS

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Abstract.—We discuss the use of phylogenetic patterns in testing the predictions of coevolutionary scenarios or process models. For this purpose we develop a general method for reconstructing the coevolutionary history of an association from the phylogenies of the component groups and an association matrix describing the associations between the species. We focus on the evolution of the traits that determine which species are associated, and therefore set up a null model with no change in these traits. Furthermore, we distinguish among three different processes that change association patterns: (1) colonization, whereby new associations are created; (2) exclusion, whereby old associations disappear; and (3) successive specialization, through which ancestral associations split into two or more descendant associations. In contrast to earlier methods for coevolutionary analysis, the method we propose explicitly includes all these processes as possible explanations of observed deviations from the null model. The parsimony principle can be used to choose between alternative reconstructions of the history of an association if successive specialization, colonization, and exclusion events are given weights relative to the probability of each of these events occurring. However, it is often possible to take advantage of the distribution of traits in the phylogenies of the associated groups to choose between alternative reconstructions; then, the weights need not be specified. Although the method we propose is explicitly developed for coevolutionary analysis, it should also be applicable to biogeographical problems with suitable modifications. The method is compared to parsimony mapping (Brooks parsimony analysis) and found to be superior in several respects. To illustrate the potential of the method, we first discuss different coevolutionary process models for insect-host plant associations with emphasis on the patterns they predict and how reconstructions of the coevolutionary history of an association can be used to test these predictions. We then use the method to analyze the evolution of an association between gall midges (*Semudobia* spp.) and birches (*Betula* spp.). [Species associations; coevolution; parsimony mapping; Brooks parsimony analysis; insect-host plant relations.]

Species that interact closely with each other form species associations. Examples include parasite-host, pollinator-plant, and herbivore-plant associations; in fact, most species are members of several species associations. Species change over time, and so do species associations. When such changes are carried over a number of speciation events, they create phylogenetic or historical patterns in the associated groups. These patterns have two components, namely (1) the phylogeny of the species in each of the associated groups and (2) the changes in the traits affecting the association in each of the associated groups. Both these components may be reconstructed using phylogenetic systematics and parsimony analysis (Hennig, 1950, 1966; Wiley, 1981):

Hypotheses describing how species associations change over time in terms of the traits of the species and the species associated may be called coevolutionary scenarios or process models. Several different coevolutionary models have been proposed (e.g., Ehrlich and Raven, 1964; Jermy, 1976, 1984; Smiley, 1978). It is the purpose of this paper to investigate the connections between coevolutionary processes and the phylogenetic patterns they create. More specifically, we want to show how phylogenetic patterns can be used to test coevolutionary process models.

As pointed out by O'Hara (1988), the relationship between evolutionary scenarios and phylogenetic patterns is analogous to that between narratives and chronicles in historical sciences. The phylogenetic pat-

		host plants		
		A	B	C
insects	1	x	-	-
	2	-	x	-
	3	x	-	x

FIG. 1. Association matrix for an insect-host plant association. Insects 1 and 2 occur on plants A and B, respectively, whereas insect 3 occurs on both plants A and C.

terns, as they are revealed by phylogenetic analysis, are the chronicles of evolutionary biology. They can be used to test evolutionary scenarios in the sense that scenarios that are not consistent with patterns are falsified. Our goal is to devise a test of this kind. To this end, we develop a general method for reconstructing the coevolutionary history of an association. The method is somewhat similar to parsimony mapping (Brooks parsimony analysis; Brooks, 1981, 1988, 1990; Wiley, 1988), but differs in several important respects. To illustrate the potential of the method, we first discuss different models for the evolution of insect-host plant associations with emphasis on the patterns they predict and how the reconstruction of the coevolutionary history of an association can be used to test these predictions. Finally, we use the method to analyze the evolution of an association between birches and gall midges.

RECONSTRUCTING THE COEVOLUTIONARY HISTORY OF AN ASSOCIATION

Terminology

Before discussing the problem of reconstructing the coevolutionary history of an association, it will be useful to introduce some new terms and define terms that otherwise might be ambiguous. Throughout the paper we use "ancestral species" to refer to specific interior branches in the trees under discussion. In other words, ancestral species are considered to go extinct when they speciate. It is important to note that this methodological convention does not

preclude the possibility that a descendant species may sometimes be identical to its ancestor.

Species associations can be described in terms of an *association matrix*. For instance, assume that we are studying an insect-host plant association where insect species 1 and 2 are associated with host plants A and B, respectively, whereas insect 3 occurs on both host plants A and C. The association matrix would then be as illustrated in Figure 1.

It is useful to distinguish between two sets of factors that determine which species are associated. First are the *intrinsic factors*, namely the traits of the associated species. For instance, in phytophagous insects the ovipositional preferences of the female and the survival of the larva on different host plants might be two important traits restricting the range of host plant species used by the insect. The traits that are important in determining the members of an association may be called the *defining traits* of the association. In addition to the intrinsic factors, the members of an association are also determined by *extrinsic factors*. Of chief importance among them is the distribution area of the species; two species that do not occur in the same area cannot be associated.

Association matrices may change over time and the changes may take three different forms: *colonization*, *exclusion*, and *successive specialization*. Colonization events create new associations (Fig. 2a), whereas exclusion events terminate old associations (Fig. 2b). In terms of insect-host plant associations, colonization involves changes that permit an insect to utilize a new host plant, whereas exclusion is a process whereby a host plant escapes from attack by an insect that it previously hosted. In biogeography, colonization is equivalent to dispersal and exclusion is equivalent to local extinction. In addition to colonization and exclusion, an association matrix may change through modification of old associations. This can occur when one or more of the component lineages of an association speciate. The effect of a successive modification event is to divide an ancestral

association into two or more descendant associations. In the example given in Figure 2c, the ancestral association between species 1 and A is divided into two descendant associations, namely between species 2 and B and 3 and C. In a biogeographical context, species assemblages undergo successive modification through allopatric cospeciation (Brooks, 1979), whereas coevolving species associations are modified through successive specialization. In terms of insect-host plant associations, successive specialization involves a tendency in separate insect and plant lineages to diverge with respect to the defining traits of the association.

Successive specialization is an irreversible process because it involves speciation, a process which by itself is irreversible. Once an association has split into a number of descendant associations, the ancestral association cannot reappear because the relevant species no longer exist. Furthermore, successive specialization events are historically constrained in the sense that they do not break ancestor-descendant lineages of species associations. In other words, the possible future associations that can be created by successive specialization events are limited by the associations that exist at present. Colonization and exclusion events, on the other hand, are not constrained in this way. It is always possible to go from one association matrix to any other by a combination of colonization and exclusion events.

The Pattern Approach

The central idea of the pattern approach is to use the phylogenies of associated groups to reconstruct the coevolutionary history of the association. To date, most of the work has been concentrated on finding congruence between the phylogenies of associated groups (e.g., Roskam, 1984, 1985; Miller, 1987; Brooks, 1988; Wanntorp et al., 1990). The most powerful technique available at present for detecting congruence between phylogenies is the parsimony mapping technique proposed by Brooks (1981). This technique involves treating the associated groups as multistate characters

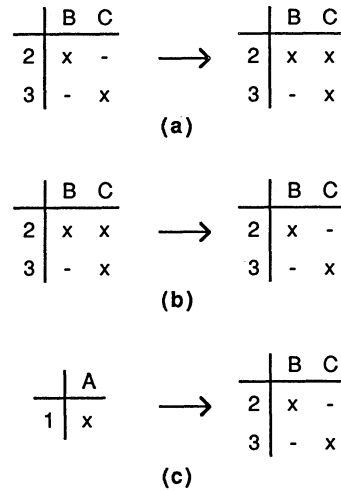


FIG. 2. Three different processes that change association matrices. (a) Colonization, whereby a new association is created. (b) Exclusion, whereby an old association is terminated. (c) Successive specialization, through which ancestral associations split into two or more descendant associations. Species 1 and A are ancestors of 2 and 3 and B and C, respectively.

of each other or of the associations and then performing a parsimony analysis. A simple example is given in Figure 3. Parsimony mapping has been used both in historical biogeography (Wiley, 1988; Brooks, 1990) and in the study of species associations (Brooks, 1988).

If we are interested in testing coevolutionary models, there are four major problems with the parsimony mapping technique. First, it is not sufficient to investigate the congruence between phylogenies of associated groups. This is because coevolutionary process models are concerned with changes in the intrinsic factors and not in the extrinsic factors, whereas congruence is determined by both intrinsic and extrinsic factors. Thus, to test coevolutionary process models we need a technique that corrects for the influence of extrinsic factors.

Second, parsimony mapping uses allopatric cospeciation as the null model, but allopatric cospeciation can occur with or without changes in the defining traits of species associations. Therefore, allopatric cospeciation is not a suitable null model for coevolutionary analysis. Furthermore,

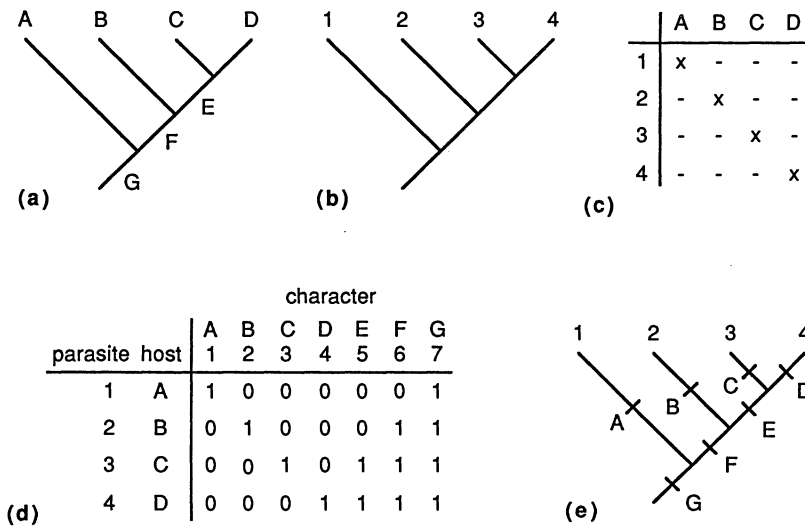


FIG. 3. Parsimony mapping used to map a host phylogeny onto a parasite phylogeny. (a) Host phylogeny. E, F, and G are ancestral species. (b) Parasite phylogeny. (c) Association matrix. (d) Character matrix. Each of the extant host species (A–D, column) is transformed to a set of binary characters (1–7, row) by additive binary coding. Each binary character denotes the presence (1) or absence (0) of a particular host species (A–G, row) in the ancestry of one of the extant species. Each parasite is assigned the states of its particular host, and then the binary characters (A–G) are mapped onto the parasite phylogeny using ordinary (Fitch–Wagner or reversible) parsimony. (e) The host phylogeny mapped onto the parasite phylogeny. The absence of homoplasy indicates perfect congruence between host and parasite phylogenies.

using a null model implying some sort of successive modification of associations makes it difficult to recognize cases where there is a lack of such events. This occurs, for instance, when a lineage fails to respond to a vicariance event by speciating. In a general method for coevolutionary analysis, we need a null model with no changes in the defining traits of species associations and with no implications of successive modification events.

The third problem with parsimony mapping is the evolutionary interpretation of the resultant cladogram. This problem arises because in parsimony mapping there is no clear distinction between historically constrained and unconstrained changes. Parsimony mapping is essentially a method for detecting patterns that are consistent with historically constrained changes (i.e., successive modifications of an old association) and does not give plausible reconstructions of historically unconstrained events like colonization and exclusion (Wiley, 1988). Furthermore, reversibility is often assumed for the mul-

tistate host or parasite characters, whereas historically constrained changes in their nature are irreversible. This means that parsimony mapping sometimes will produce inconsistent results in that a reversal in a host or parasite multistate character would imply a reversal in time flow if interpreted as a successive specialization event. At the same time, the reversals cannot be easily interpreted as exclusion events because an exclusion event is historically unconstrained and breaks an ancestor–descendant sequence of species associations, whereas a reversal does not break the sequence but simply reverts it. On the other hand, if irreversibility is assumed, then exclusion or extinction events are not taken into account at all, and surely such events do occur (Brooks, 1990). To solve this problem it is necessary to distinguish clearly between historically constrained and unconstrained changes and include both as possible explanations of observed deviations from the null model.

The final problem with parsimony mapping is the treatment of taxa occurring in

more than one association. In historical biogeography, this is equivalent to the problem of widespread taxa (Nelson and Platnick, 1981; Wiley, 1988). The usual way of solving this problem is by "inclusive OR-ing" (Cressey et al., 1983; O'Grady and Deets, 1987; Brooks, 1990). This procedure is equivalent to interpreting the occurrence of species in more than one association as the result of multiple parallel successive modification events. We believe that a general method for reconstructing the history of species associations must also consider the possibility that species may obtain wide host ranges through colonization events, lack of successive specialization, or a combination of these with exclusion events.

Below we propose solutions to the first three problems and discuss a strategy for solving the fourth. These findings are incorporated in a general method for reconstructing the coevolutionary history of an association. With suitable modifications, the method should be applicable also to problems in historical biogeography.

Correcting for the Influence of Extrinsic Factors

The effect of extrinsic factors is that they preclude some species associations that would otherwise be possible. Thus, to correct for extrinsic factors, we must examine combinations of species that are not associated. Consider a phytophagous insect species that is absent from a particular plant species. If the insect and plant occur together, intrinsic factors must be responsible for precluding the association. However, if they occur in different areas, we do not know if the absence of the insect from the plant is due solely to the fact that they occur in different areas, or if the traits of the insect and the plant would not allow them to be associated if they had occurred in the same area. Thus, this instance represents a potential association. A similar problem occurs if the only means of dispersal of individuals of a particular species is from parent to offspring of individuals of the species with which it is associated. In this case, virtually every nonexistent

species association represents a potential association.

In a method for reconstructing the evolution of the defining traits of associations, potential associations represent missing data. We can treat these data in two ways. One way is to treat them as missing data and then choose the interpretation that best fits the other data and the null model. This means that we stand some risk of detecting fewer deviations from the null model than are really there, but this seems a reasonable compromise in the face of missing data. Alternatively, we might test the potential associations experimentally. An important disadvantage of this approach, however, is the difficulty of extrapolating from experimental data to natural conditions.

A Coevolutionary Null Model

Coevolutionary process models describe how traits that affect species associations change over time. Therefore, to test coevolutionary models we need a null model with no change in these traits. The pattern produced by the null model in macroevolutionary time (i.e., time scales larger than that between speciation events) is illustrated in Figure 4. Consider a species association consisting of an insect species (1) specialized on a single host plant (A), the association being defined by traits present in the insect (x) and in the plant (y). Now, assume that both the insect and the plant lineages speciate, giving rise to the descendant species 2 and 3 and B and C, respectively. Because the null model predicts no change in the traits that define the species association, we expect the insect species 2 and 3 to have traits x and the plant species B and C to have traits y. Given that the association is not influenced by extrinsic factors, both insect species should be present on both plant species (Fig. 4). Thus, under the null model we expect the association to include more and more species as the component lineages speciate.

Deviations from the Null Model and Reconstruction of the Coevolutionary History of Associations

Confronted with phylogenetic and association patterns that are not consistent

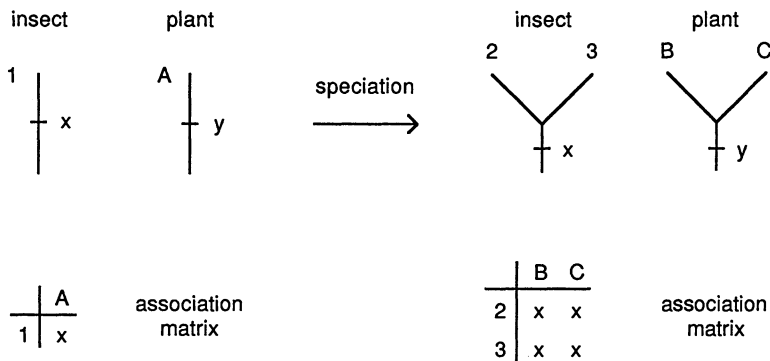


FIG. 4. Pattern expected under the coevolutionary null model. The insect species 1 is specialized on the plant species A, the association being defined by the traits x in the insect and y in the plant. After speciation in the insect and plant lineages, we expect the association to include all of the descendant species unless the defining traits of the association have changed.

with the null model, we want to make a reconstruction of the evolution of the defining traits of the associations that involves as few pattern-affecting changes as possible. In other words, we are searching for the most parsimonious explanation of the data.

Deviations from the null model may take three different forms: successive specialization, colonization, and exclusion. Typically, any deviation from the null model can be explained by invoking either successive specialization or a combination of colonization and exclusion. Therefore, the task of finding the most parsimonious reconstruction of the coevolutionary history of an association will be very difficult. For simplicity, we will first treat parasite-host associations under the assumption that each parasite species (including ancestral species) at any one time is restricted to a single host species. We will then discuss how this assumption might be relaxed.

To find a reconstruction of the coevolutionary history of an association that involves only successive specialization events, we can use parsimony mapping. For instance, in an insect-host plant association we can treat the host plants as multistate characters of the insects. The host plant phylogeny defines the transformation series of the host plant "characters." The host plant "characters" are then

mapped onto the insect phylogeny, using parsimony, to produce a successive specialization scenario explaining the evolution of the association. Because successive specialization can only proceed from ancestral to descendant species, it is necessary to use irreversible (Camin-Sokal) parsimony, that is, the host plant "characters" must be considered to proceed irreversibly from ancestral to descendant plant species (cf. Wiley, 1988). Examples of successive specialization explanations are given in Figure 5.

The above procedure works only if we map hosts onto the parasite phylogeny. This is because the restriction that any one parasite may have only one host gives a situation where parsimony mapping will always work. If we do it the other way around, several parasites may be present on a single host, and parsimony mapping will not be able to handle this without invoking inclusive OR-ing. However, for each reconstruction with hosts mapped onto the parasite phylogeny, there is always one and only one corresponding reconstruction with the parasites mapped onto the host phylogeny. Thus, a parasite phylogeny with hosts mapped on that has been produced by parsimony mapping can easily be converted to a host phylogeny with parasites mapped on, even if the latter could not have been produced directly by parsimony mapping.

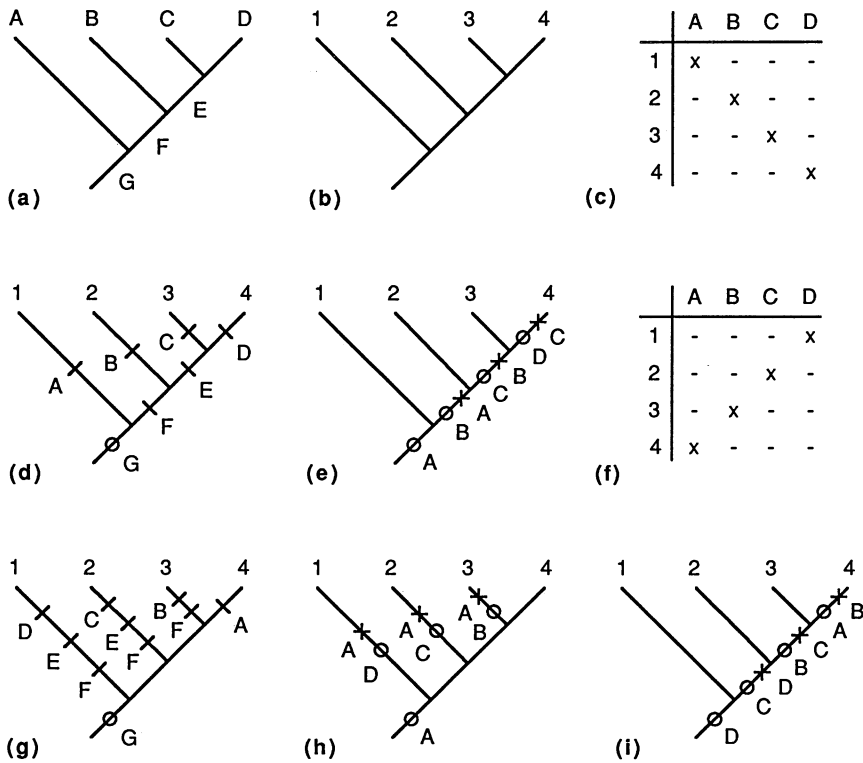


FIG. 5. Pure successive specialization and colonization/exclusion scenarios explaining the evolution of an insect-host plant association. (a) Plant phylogeny. (b) Insect phylogeny. (c) Association matrix for pattern 1. (d) Most parsimonious successive specialization explanation of pattern 1. (e) One of several equally parsimonious colonization/exclusion explanations of pattern 1. (f) Association matrix for pattern 2. (g) Most parsimonious successive specialization explanation of pattern 2. (h, i) Two of several equally parsimonious colonization/exclusion explanations of pattern 2. ○, colonization; x, exclusion; -, successive specialization.

To find a reconstruction of the coevolutionary history of an association involving only colonization and exclusion events, it is necessary to use a different procedure. In an insect-host plant association, we might again treat the host plants as multistate characters of the insects. However, this time the host plant phylogeny is not used to define the transformation series of the host plant "characters." Instead, the extant host plants are mapped onto the insect phylogeny by using Fitch optimization. Each evolutionary transformation between plant species in the insect phylogeny inferred by this method is equivalent to one colonization and one exclusion event. Examples of colonization and exclusion explanations are given in Figure 5. If several parasites occur on the same host, Fitch op-

timization will work only if the hosts are mapped on the parasite phylogeny. However, as pointed out above, the solution obtained can easily be converted to a host phylogeny with the parasites mapped on.

Under the assumption that parasites never have more than one host, colonization and exclusion events will always be coupled. Such a sequence of one colonization and one exclusion event may be called a host shift. However, it is still important to keep exclusion and colonization events separate for several reasons. First, a host shift must necessarily consist of a colonization and an exclusion event—it is difficult to imagine a parasite momentarily shifting to a new host. Second, if colonization and exclusion events are separated, a parasite phylogeny with the hosts

mapped on can easily be converted to a host phylogeny with parasites mapped on. This is not the case if only host shifts are indicated—each host shift in the parasite phylogeny refers to two different branches in the host phylogeny. Third, and most important, colonization and exclusion events may occur independently if we consider the possibility that a parasite occurs on several host species. If colonization and exclusion events are lumped together, it becomes impossible to detect such cases of independent colonization or exclusion events.

To use parsimony to make comparisons between pure successive specialization and pure colonization/exclusion scenarios, we must know how to weight a combined colonization and exclusion event (a host shift) relative to a successive specialization event. There are two independent lines of evidence suggesting that a successive specialization event should not be weighted as heavily as a host shift. First of all, it seems reasonable to assume that a host shift involves a more substantial change of the traits that define a species association than a successive specialization event—it should be more difficult to establish a new association and terminate an old one than to modify the defining traits of an existing association. Second, successive specialization produces particular patterns, whereas colonization and exclusion events are basically insensitive to patterns. This is because colonization and exclusion events are largely independent of phylogeny. Note that the specialization explanation of pattern 1 (Fig. 5c) involves six successive modifications of the ancestral species association (Fig. 5d), whereas the specialization explanation of pattern 2 (Fig. 5f) requires as many as nine modifications (Fig. 5g). The colonization and exclusion explanations, on the other hand, involve only three colonization and three exclusion events for both patterns (Fig. 5e and h, i, respectively). Furthermore, successive specialization explanations are always consistent with an old association, whereas colonization and exclusion explanations often are not. In none of the colonization and ex-

clusion explanations given in Figure 5 can the ancestor of the insects have speciated before the appearance of plant species A; in one of the explanations (Fig. 5i), the first speciation in the insect phylogeny could not have taken place until the appearance of plant species D.

Thus, if we observe a pattern that is consistent with successive specialization, it seems reasonable to prefer such an explanation over one involving colonization and exclusion. Parsimony will not produce this result unless a combined colonization and exclusion event is weighted more than twice as heavily as a successive specialization event (e.g., compare Fig. 5d and e).

Note that the type of weighting we propose is different from ordinary character weighting. In ordinary character weighting, characters are given different weights. Then, in comparisons between trees, parsimony tends to favor trees that are consistent with heavily weighted characters. However, given a certain tree, the weights do not influence the reconstruction of ancestral states of a character. The weighting procedure we propose is different in that it implies differential weighting of character transformations. For a binary character with states 0 and 1, differential weighting of character transformations means that a 0 → 1 transformation is counted differently from a 1 → 0 transformation. In contrast to ordinary character weighting, transformation weighting *will* affect the reconstruction of ancestral states. A reconstruction involving few heavily weighted transformations will be favored over one implying many such transformations.

Camin-Sokal parsimony can be viewed as an extreme form of transformation weighting in which reversals are given infinite weight. Thus, no matter how many forward changes can be substituted with one reversal, the reconstruction with only forward changes will be favored by Camin-Sokal parsimony. Fitch parsimony of course represents the special case where all transformations are given equal weight.

In transformation weighting, the weights can be said to represent the probability of

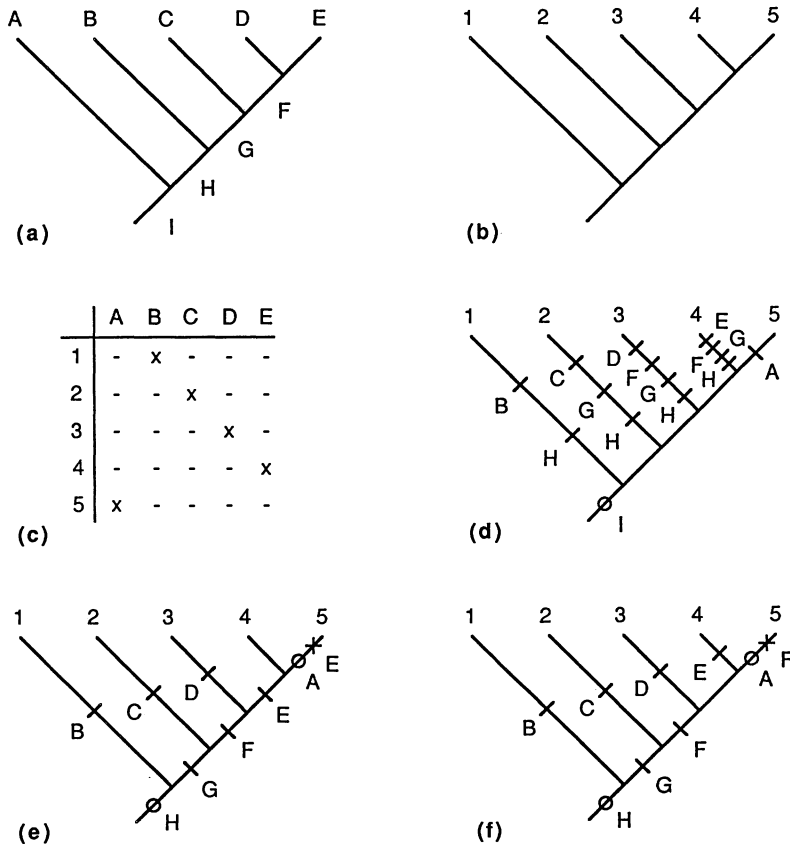


FIG. 6. Combination of successive specialization and colonization/exclusion in a single scenario. (a) Plant phylogeny. (b) Insect phylogeny. (c) Association matrix. (d) Initial, pure successive specialization explanation involving 14 successive specialization events. (e, f) Two alternative, equally parsimonious, refined explanations involving six successive specializations, one colonization, and one exclusion.

a certain event: the more unlikely an event is to occur, the more heavily it is weighted. The weighting procedure we propose is thus equivalent to weighting colonization, exclusion, and successive specialization events relative to the probability of each of these events occurring.

None of the existing parsimony methods can be used to produce an explanation that mixes successive specialization with colonization and exclusion. A simple way of approaching this problem is to search empirically for a solution as follows. First, a successive specialization explanation is produced. Then, any cases of extensive parallel specializations are replaced by colonizations and exclusions as appropriate, with the aim of reducing the total number

of pattern-affecting changes. This method is illustrated in Figure 6. By assuming that insect species 5 escaped from host plant E and colonized plant A, we can reduce the total number of assumed changes from 14 successive specializations (Fig. 6d) to 6 successive specializations, 1 colonization, and 1 exclusion event (Fig. 6e). An alternative, equally parsimonious explanation is that insect 5 escaped from host plant F (Fig. 6f).

A more rigorous method that will always produce the most parsimonious reconstruction is as follows. First, produce a series of empty association matrices for each possible sequence of speciation events in the associated groups. For instance, if we consider two parasite and two host species, there are three possible sequences of spe-

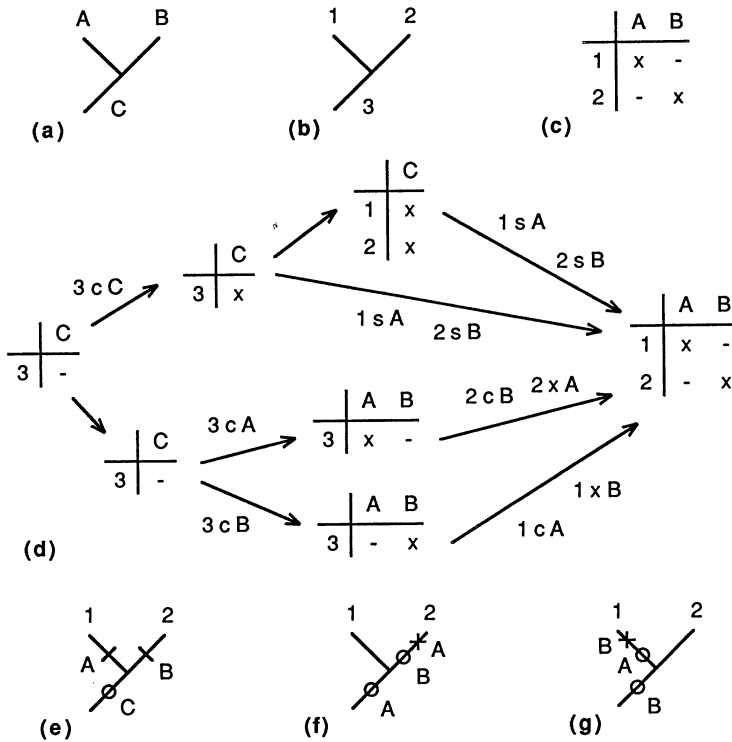


FIG. 7. A rigorous method for producing the most parsimonious reconstruction of the history of an association. (a) Host phylogeny. (b) Parasite phylogeny. (c) Observed association matrix. (d) All possible series of association matrix patterns with the minimum number of required changes indicated on each transition between matrices. c, colonization; x, exclusion; s, successive specialization. (e-g) The three alternative reconstructions of the coevolutionary history of the association produced by the method. If a combined colonization and exclusion event is weighted more than twice as heavily as a successive specialization event, the reconstruction in (e) will be favored by parsimony.

ciation events: the parasites may have speciated first, the hosts may have speciated first, or both lineages may have speciated simultaneously. Then, for each association matrix, produce all possible association patterns with the restriction that each parasite species must occur on a single host. However, the stem species of the parasites should be absent from hosts until immediately before it speciates. Each of these association matrix patterns is taken to be the state immediately before the next speciation event. All possible series of association matrix patterns start with the ancestor of the hosts and the ancestor of the parasites not being associated with each other, and end with the observed association matrix. The length of a given series of association matrix patterns may now be

calculated by separately optimizing each time sequence between association matrix patterns. Parsimony can then be used to choose between alternative reconstructions given that the weight of a combined colonization and exclusion event is specified relative to that of a successive specialization event.

The length of a given time sequence between two consecutive association matrix patterns can be optimized relatively easily. Let $H_i(X)$ be the host of parasite X at the beginning of the time sequence and $H_f(X)$ the host at the end. Call a species persistent if it does not speciate during the time sequence. For lineages that do speciate, call species present at the beginning ancestors and species present at the end descendants, and let $Anc(X)$ be the ancestor of a descen-

dant species X. The most parsimonious reconstruction of pattern-affecting changes can now be calculated according to the following rules:

For each parasite species X that is persistent:

1. If X is the stem species of the parasites, and $H_i(X) = 0$ and $H_j(X) \neq 0$, colonization of $H_j(X)$ is implied.
2. If $H_i(X) = H_j(X)$, no change is required.
3. If $H_i(X) = \text{Anc}(H_j(X))$, successive specialization of X on $H_j(X)$ is implied.
4. If $H_i(X) \neq H_j(X)$ and $H_i(X) \neq \text{Anc}(H_j(X))$ and $H_i(X)$ is persistent, a host shift from $H_i(X)$ to $H_j(X)$ is implied.
5. If $H_i(X) \neq H_j(X)$ and $H_i(X) \neq \text{Anc}(H_j(X))$ and $H_i(X)$ is not persistent, successive specialization on a descendant of $H_i(X)$ plus a host shift to $H_j(X)$ is required.

For each descendant parasite species X, calculate the minimum number of required changes as above, but substitute $H_i(X)$ with $H_i(\text{Anc}(X))$.

The entire procedure is illustrated in Figure 7. Three alternative reconstructions emerge (Fig. 7e-g). Of these, the successive specialization explanation (Fig. 7e) is favored by parsimony provided that a combined colonization and exclusion event is weighted more than twice as heavily as a successive specialization event.

A more complicated transition is illustrated in Figure 8. Species 5 and D are assumed to speciate simultaneously to give rise to species 1 and 2 and B and C, respectively. Parasite species 1 occurs on the same host (A) as its ancestor. Therefore, no change is required for this species. Species 2 does not live on the same host as its ancestor, nor is its host a descendant of the host of the ancestor. Because the ancestor lived on a persistent host species (A), the occurrence of species 2 on host B can be explained by a host shift from A to B. Species 3 shifts from an ancestral host species (D) to a descendant of that species (C). This can be explained by successive specialization on C. The shift in species 4 from an ancestral host species (D) to a host (A) that is not a descendant of the former must be explained by successive specialization on

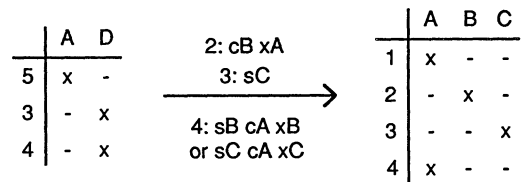


FIG. 8. Transition between two association matrices. Species 1-5 are parasites; species A-D are hosts. Species 5 and D are assumed to speciate simultaneously to give rise to species 1 and 2 and B and C, respectively. The changes implied by the transition are indicated in the figure. c, colonization; x, exclusion; s, successive specialization.

one of the descendants of D, and then a host shift to A (Fig. 8).

The method presented above is inefficient in that several alternative series of association matrix patterns will often give the same result when the required changes are mapped onto host and parasite phylogenies. An important task for future investigations will be to develop a more efficient algorithm.

Species Occurring in More than One Association

For many species associations, it is not reasonable to assume that a particular species in one of the component groups at any one time is always restricted to being associated with one species of the other group. Therefore, a general method for coevolutionary analysis must also be capable of handling problems with species of both component groups occurring in more than one association, e.g., when a parasite occurs on more than one host and a host harbors more than one parasite. In this case, it will be much more difficult to reconstruct the coevolutionary history of the association. This is because, in addition to successive specialization and host shifts, we now also have to consider the possibility that colonization and exclusion events occur independently of each other and that the associations may be broadened to include more species according to the null model. Furthermore, to use parsimony to distinguish between alternative reconstructions, we have to define weights sep-

arately for colonization, exclusion, and successive specialization events.

In principle, it should be possible to provide a rigorous method that will always find the most parsimonious solution along the same lines as suggested previously. However, the rules for optimizing each time sequence will now be more complicated, and we will not attempt to provide an exact algorithm here. We simply observe that in many cases it will be possible to find a reconstruction by trying different alternatives, guided by intuition, until a tenable solution is found. In simple cases, e.g., an insect associated with a monophyletic group of host plant species, the insect species can simply be assigned the ancestral state, i.e., present on the ancestor of the plant group. The presence of the insect on each of the extant descendants of the ancestral plant species then does not need a special explanation. In more complicated cases, several different explanations have to be tried and the explanation most consistent with the pattern of associations in the rest of the species chosen.

So far in our discussion, the choice between alternative reconstructions has been based on a parsimony method where colonization, exclusion, and successive specialization events are weighted relative to the probability of each of these events occurring. However, often one has a relatively good idea about the kinds of traits that are important in defining associations. If this is the case, it is possible to take advantage of the distribution of these traits in the phylogenies of the associated groups to choose between alternative reconstructions of the coevolutionary history of the association. An event that can be explained by the distribution of traits must be considered a more plausible explanation of a pattern than an event that cannot be so explained. This principle forms a complement to the strict parsimony criterion discussed previously and is particularly useful in complicated cases such as problems with species occurring in more than one association.

Two examples involving insect-host plant associations will illustrate the treat-

ment of species occurring in more than one association and the possibility of examining the distribution of traits in the phylogenies of the associated groups to complement parsimony. For the first example, phylogenies of insects and plants and an association matrix describing the associations between them are given in Figure 9a-c. Three alternative explanations that could explain how these associations arose are presented (Fig. 9d-f). The most parsimonious reconstruction involves an exclusion event, where plant species C is postulated to have escaped from attack by insect species 2 (Fig. 9d). The two colonization explanations (Fig. 9e, f) are slightly longer, involving one successive specialization event more than the exclusion explanation. In this case, it would be appropriate to investigate the distribution of defining traits in the plant and insect phylogenies. The exclusion explanation would be supported if it could be demonstrated that plant C acquired a trait that made insect 2 incapable of feeding on it, or if insect 2 acquired a trait that made it impossible for it to feed on plant C. The colonization explanations would be supported if it was found that insect 2 acquired traits enabling it to feed on either plant B or D. Alternatively, the colonization explanation would be supported if it was found that insect 2 demonstrates a marked preference for or a better performance on one of the plant species it feeds on. This could indicate a more ancient association with that plant species.

For the pattern given by the association matrix in Figure 9g, two alternative explanations are presented. The colonization explanation (Fig. 9h) is the most parsimonious one, involving only one colonization event; the alternative explanation (Fig. 9i) includes two exclusion events. Thus, the colonization explanation should be the favored reconstruction of the coevolutionary history of the group unless there is evidence against it in the distribution of traits in the insect and plant phylogenies.

Comparison with Parsimony Mapping

Because of the superficial similarity between the technique proposed by us and

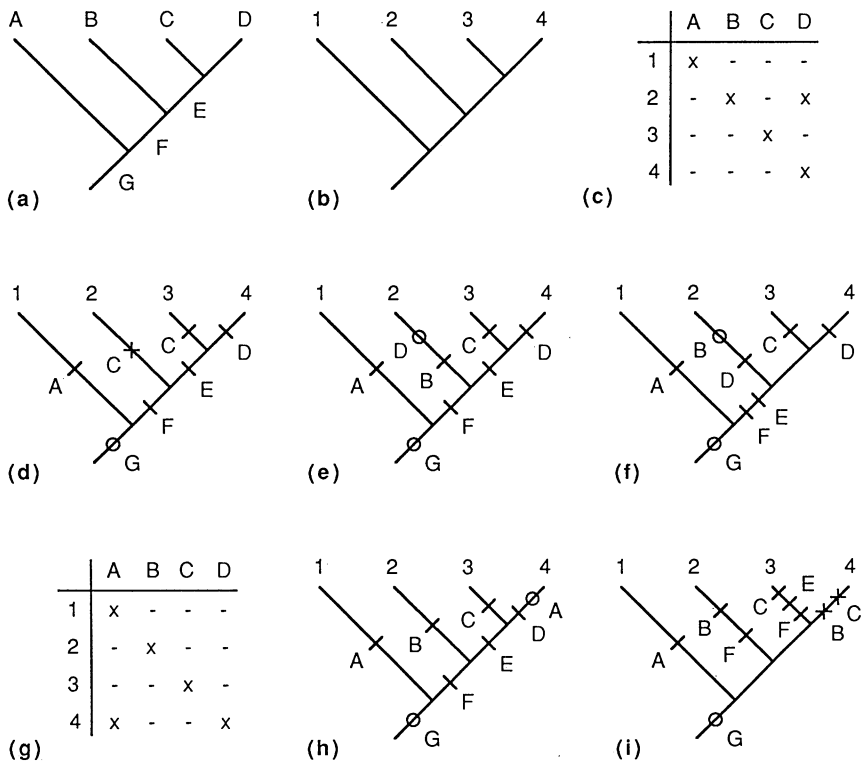


FIG. 9. Treatment of taxa occurring in more than one association. (a) Plant phylogeny. (b) Insect phylogeny. (c) Association matrix for pattern 1. (d-f) Three alternative explanations of pattern 1. (g) Association matrix for pattern 2. (h, i) Two alternative explanations of pattern 2.

ordinary parsimony mapping; we present the following example to illustrate some important differences (from Brooks, 1990: his Figs. 18, 19 and his Table 11). Two groups of species (1-5 [Fig. 10a] and 10-13 [Fig. 10b]) occur in the areas A-E as indicated in the matrix in Figure 10c. Figure 11a and b and c and d illustrates two alternative relationships between the areas A-E with the species mapped onto the cladograms. In Figure 11a and c, ordinary parsimony mapping has been used, whereas the reconstructions in Figure 11b and d have been obtained using the technique proposed in the present paper.

In Figure 11a, the reconstruction produced by parsimony mapping indicates that species 16, 15, and 14 became extinct in area E. However, this is not a very plausible reconstruction of the history of the species assemblage. For instance, if species 16 became extinct in area E, then species 15

would not have originated in that area. Hence, species 15 could not have gone extinct in area E unless it colonized it separately after the extinction of species 16, something that is not suggested either by the data or by the cladogram. Similarly, if species 14 became extinct in area E, it must have been present in the area first, and this is most easily explained by not assuming that species 15 or 16 became extinct in that area. A single extinction event in area E is enough to explain the data, and this is directly evident from one of several equally parsimonious reconstructions produced by our method (Fig. 11b).

One could say that the a posteriori interpretation of the cladogram necessary when using parsimony mapping is only a slight inconvenience and not a serious disadvantage of the method. However, in this particular example there is a special danger involved, because the explanation in Fig-

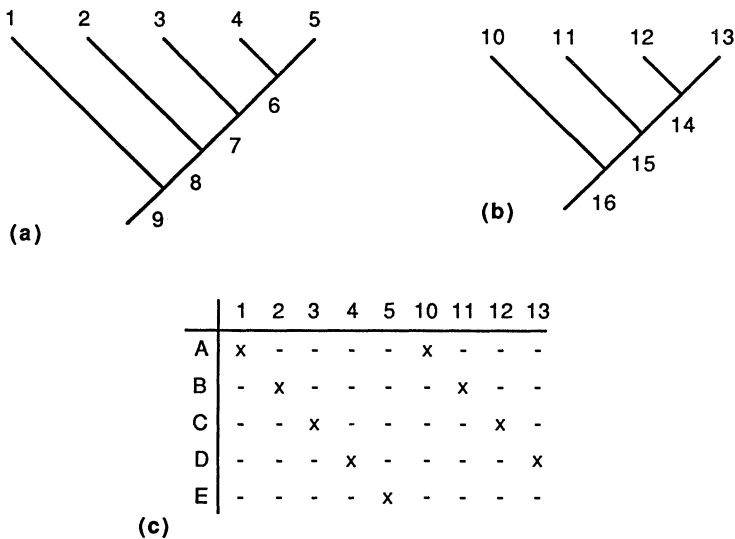


FIG. 10. A problem in historical biogeography. (a) Phylogeny of species 1-5. (b) Phylogeny of species 10-13. (c) Matrix describing the distribution of species 1-5 and 10-13 in areas A-E.

ure 11b might go undetected by parsimony mapping. This is because that particular explanation requires one step more than the optimal parsimony mapping solution (Fig. 11a), whereas there is nothing in the data to suggest that extinction of species 13 in area E is more unlikely than extinction of species 14, 15, or 16. Using our method, we get four equally parsimonious solutions indicating extinction in area E of species 13, 14, 15, or 16, respectively.

Some readers might respond that extinction of species 15 or 16 in area E involves a paradox because the other data suggest that species 15 and 16 became extinct before area E separated from area D. Our method could easily be constrained so that these solutions were not obtained. However, there are reasonable interpretations of these solutions. For instance, if species 16 was distributed over the land mass once formed by areas A + B + C + D + E, but was absent from the part later to become area E, this would correspond to an apparent extinction of species 16 in area E. Such absence of stem species from particular areas might be considered a more likely explanation of a distribution pattern than a subsequent extinction event. We do not hold this view, but if one wishes to

make that assumption, it is easily incorporated into our method.

There is a further problem with parsimony mapping in the above example, in that parsimony mapping produces an alternative, equally parsimonious solution to that presented in Figure 11a. In this solution, the distribution of species 14 is not explained by origin in area C + D + E and subsequent extinction in area D, but by parallel occurrence in areas C and D. However, parallel occurrence of species 14 in areas C and D amounts to an extra assumption that is not warranted by the data. Using our method, parallel occurrence of species 14 would require one more step than the most parsimonious solutions.

For the pattern in Figure 11c, parsimony mapping produces extensive parallelisms. These parallelisms are concentrated in area E, indicating an instance of dispersal to that area. After consulting the data, we may conclude that species 6 colonized area E from area D and later gave rise to species 5 in that area. Alternatively, species 5 might have shifted from area D to area E. These two alternative scenarios are directly evident from the cladograms produced by our method. The relative weighting used determines which of the two alternatives will

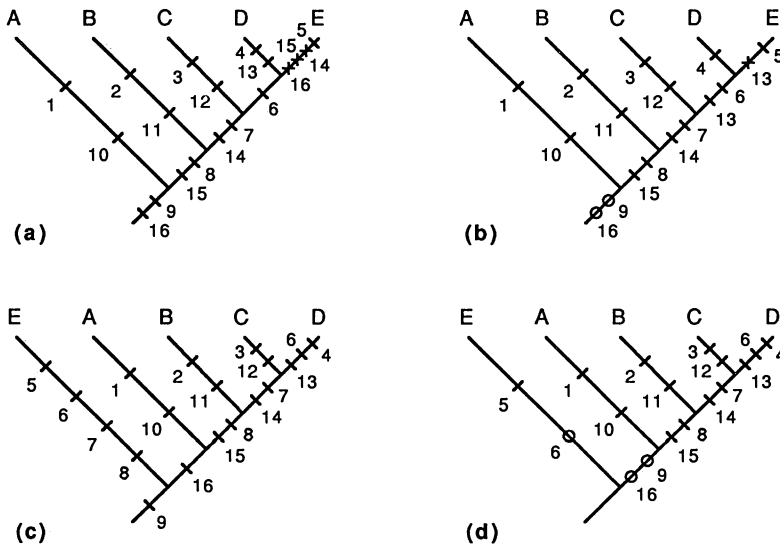


FIG. 11. Alternative reconstructions of the history of the species assemblage described in Figure 10. (a) and (c) were produced by parsimony mapping; (b) and (d) were produced by the technique proposed in this paper.

be the most parsimonious one. In Figure 11d, the cladogram consistent with the first scenario is presented.

Also in this case parsimony mapping produces a spurious alternative solution to that in Figure 11c. In this solution, species 8 is indicated to have gone extinct in area A. Using our method, there are several reconstructions that are more parsimonious than this one.

Notice that in each of the cases discussed above, the history of the assemblage can be read directly from the reconstructions produced by our method, but the parsimony mapping solutions require careful a posteriori interpretation. This problem with parsimony mapping is not cured by coding the absence of a group from a particular area as missing data as suggested by Wiley (1988). In the problem discussed above, the absence of species 10-13 from area E would be recoded as missing data. If this is done, the taxa can be mapped onto the area cladogram in Figure 11a with complete congruence. However, the absence of species 10-13 from area E still needs a special explanation; the absence cannot be explained simply by vicariance. This fact is

directly evident from the reconstructions produced by our method (Fig. 11b). Using recoding, one must remember that the procedure requires an a posteriori explanation (Brooks, 1990).

Brooks (1990) has suggested that some of the problems with parsimony mapping in historical biogeography be solved by duplicating areas that appear to have a composite history. We will not attempt to discuss the advantages and disadvantages of this technique here. We simply observe that species do not have composite histories, and this fact might complicate the application of the duplicating technique to problems with species associations. We also note that, when feasible, the duplicating technique further complicates the interpretation of the resultant cladograms.

The weighting required in our method might be considered by some readers as a serious disadvantage compared to parsimony mapping. However, historically constrained and historically unconstrained events are produced by completely different processes, and equal weighting must be justified just as well as unequal weighting. As discussed above, there are

several reasons for believing that unequal weighting is biologically more sound than equal weighting.

Limits to the Approach

There are mainly two limits to the pattern approach to the study of the evolution of species associations. First of all, coevolutionary changes that do not affect the pattern created cannot be detected because they do not violate the null model. Second, associations that are characterized by numerous colonization and exclusion events will produce numerous equally or nearly equally parsimonious interpretations of the evolution of the association, and, in such cases, the patterns themselves will not provide a sufficient clue to the coevolutionary history of the association.

COEVOLUTIONARY PROCESS MODELS

In one of the earliest papers on coevolution, Ehrlich and Raven (1964) developed a coevolutionary scenario for insect-host plant associations that subsequently became very popular. The scenario is an arms race between insects and plants, with a continuously escalating series of defense and counterdefense traits in the two groups. In the original formulation, the insect and plant groups were assumed to radiate between the origin of defense and counterdefense traits, and, furthermore, the defense traits were assumed to be so drastic that they excluded insects from the plants that acquired them (arms race model type II). Later, many authors considered the evolutionary changes to occur on a much shorter time scale and the effects of the defense and counterdefense traits to be less drastic (arms race model type I). Several authors have criticized the arms race view and pointed out that there may be a general trend toward specialization in the insects independent of evolutionary changes in the plants (Jermy, 1976; Smiley, 1978; Bernays and Graham, 1988). These ideas can be used to formulate an alternative to the arms race scenario, the "specialization model." Jermy (1984) suggested that many insect groups may be much younger than the plant groups on which they live, a sce-

nario that could be called the "late colonization model." Finally, it is possible that insects have switched to new, unrelated host plants so frequently throughout their evolution that the historical pattern is lost. This scenario may be termed the "opportunistic model."

Below we outline the different coevolutionary process models, with emphasis on the patterns they predict and on how reconstructions of the coevolutionary history of the association can be used to test these predictions. It is important to point out that the models are not mutually exclusive, that is, several processes may be acting simultaneously in the evolution of an association.

Arms Race Model Type I

This is an arms race model with reciprocal adaptations occurring in microevolutionary time (i.e., time scales shorter than that between speciation events). Phytophagous insects are assumed to lower the fitness of their plant hosts. Therefore, the plants tend to develop defense traits that reduce the fitness of the insects they host. However, because of a strong selection pressure acting on them, the insects will continuously evolve counterdefense traits that allow them to overcome the negative effects of the defense traits of the plants. When a host plant speciates, the descendant lineages will tend to evolve different defense traits. This will, in turn, promote divergence in the phytophagous insects.

The pattern predicted by this model is one of extensive successive specialization, where the specialization events are associated with defense traits in the plants and counterdefense traits in the insects (Fig. 12).

Arms Race Model Type II

This is essentially the same scenario as in the arms race model type I, but with the changes occurring in macroevolutionary time. In other words, we expect several speciation events in insects and plants to occur between the origin of defense and counterdefense traits. Plants are assumed to develop defense traits that are so drastic

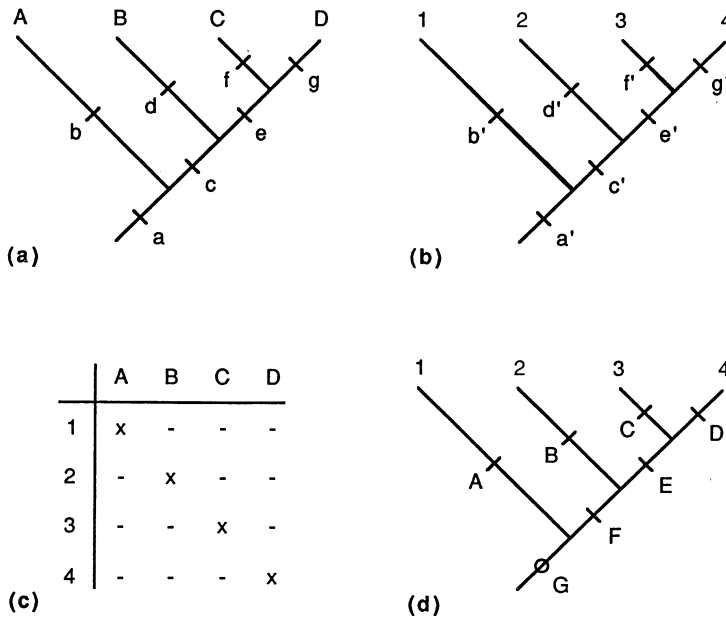


FIG. 12. Pattern predicted by the arms race model type I and the specialization model. (a) Plant phylogeny. In the case of the arms race model, a-g represent the origins of defense traits in the plants, whereas for the specialization model, a-g represent the origins of diverse traits in the plants usually not directly related to the presence of insects on the plants. (b) Insect phylogeny. In the case of the arms race model, a'-g' denote the origins of counterdefense traits in the insects, whereas for the specialization model, a'-g' denote the origins of traits associated with specialization in the insects. (c) Expected association matrix. (d) Correct reconstruction of the coevolutionary history of the association.

that they will exclude phytophagous insects from them. Then, in the absence of phytophagous insects, the plants may radiate. However, some insects will eventually evolve a counterdefense trait that will allow them to colonize the previously protected plant group. In the absence of competitors, the insects may then radiate.

Under this model, we expect exclusion events associated with the origin of defense traits in the plants and colonization events associated with the origin of counterdefense traits in the insects (Fig. 13). On intermediate time scales, the arms race model type II grades into type I. We then expect to see some successive specialization and some colonization and exclusion, but in all cases the changes should be associated with the origin of defense and counterdefense traits.

Specialization Model

In contrast to the arms race models, the specialization model does not involve re-

ciprocal adaptations. Instead, it involves a general trend toward specialization in the insects independent of evolutionary changes in the plants (sequential evolution; Jermy, 1976). This trend may be generated by intraspecific competition (Smiley, 1978), interspecific competition, predation (Bernays and Graham, 1988), or other factors.

As for the arms race model type I, the specialization model should generate patterns with extensive successive specialization (Fig. 12). However, in this case the successive specialization events should be associated with changes in the insects restricting the range of host plants used by them, instead of being associated with the origin of defense and counterdefense traits.

If the selection pressure that favors specialization in the insects is very strong, so that it is important for the insects to be monophagous, we should see very few colonization and exclusion events. If the selection pressure is weaker, there could be

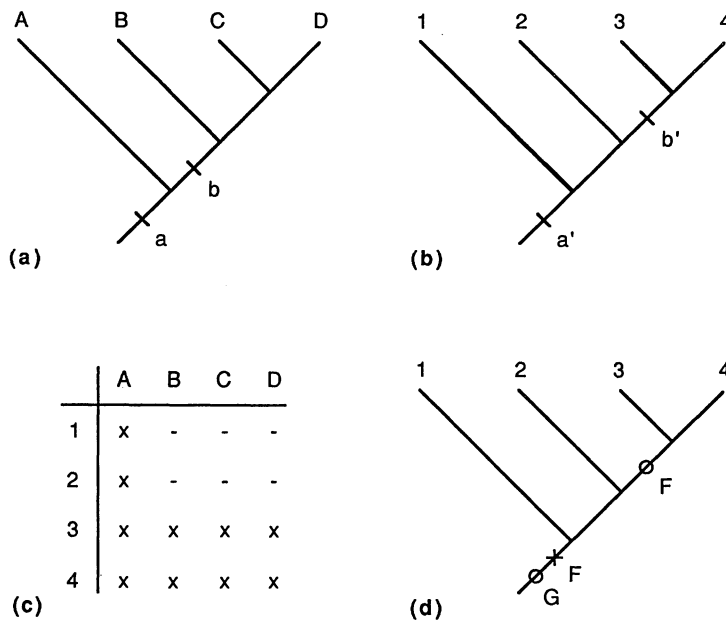


FIG. 13. Pattern predicted by the arms race model type II. (a) Plant phylogeny. a and b denote the origins of defense traits. (b) Insect phylogeny. a' and b' denote the origins of counterdefense traits. (c) Expected association matrix. (d) Correct reconstruction of the coevolutionary history of the association.

some colonizations and exclusions, but if specialization is important in shaping the evolution of insect-host plant associations, there should be a limit to the number of such events.

Late Colonization Model

In contrast to the earlier models, the late colonization model does not assume that the insects and plants have been evolving together. Instead, the insect group is assumed to have colonized the host plants only recently and to have radiated onto already existing plant species.

The pattern expected under this model is one of colonization and exclusion. Colonization should be associated with the origin of a particular resource in the plant phylogeny and an adaptation in the insects that allows them to exploit this resource. Exclusion should be associated with the resource disappearing or changing into a different state in the plant phylogeny and/or a change in the insects making them incapable of using the resource (Fig. 14). Notice that even if the late colonization model is correct, the reconstruction of the

coevolutionary history of the association might still indicate that an insect colonized a plant species that appears early in the plant phylogeny. However, this does not imply that the insect actually colonized that plant species; it simply means that the plant traits to which the insect is adapted originated in that plant species.

Because of the superficial resemblance between the patterns produced by the late colonization model and some of the other models, it is important to have some knowledge about the approximate age of the insect and plant groups in order to distinguish between the models. Notice that the late colonization model cannot be the only model explaining the evolution of an insect-host plant association unless practically all speciation events in the host plants have been completed before the plants are colonized by the ancestor of the insects.

Opportunist Model

According to the opportunist model, insects have switched to new, unrelated host plants numerous times throughout their

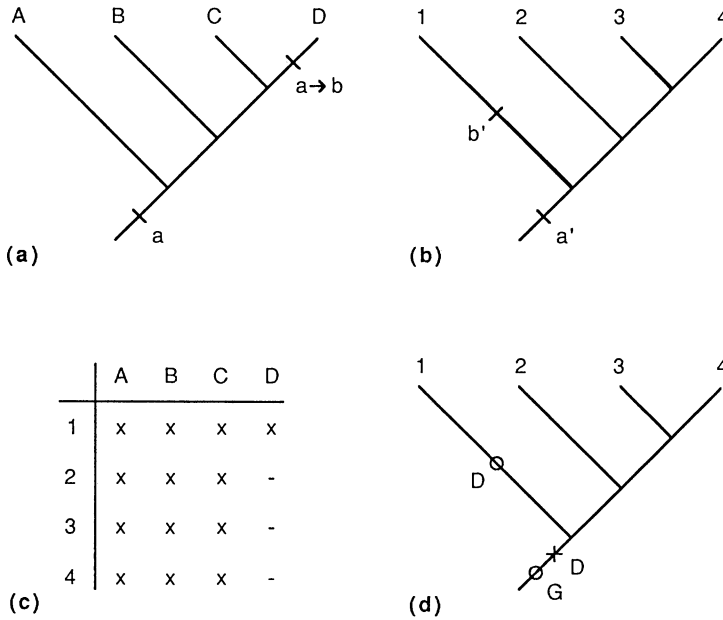


FIG. 14. Pattern predicted by the late colonization model. (a) Plant phylogeny. a and b are two different resources in the plants. (b) Insect phylogeny. a' and b' denote the origins of traits in the insects allowing them to use resources a and b, respectively. (c) Expected association matrix. (d) Correct reconstruction of the coevolutionary history of the association.

evolution (on the order of at least one colonization and exclusion event per speciation). If we try to reconstruct the coevolutionary history of such an association, we should see numerous equally or nearly equally parsimonious explanations, with a multitude of colonization and exclusion events. Thus, the pattern approach cannot be used to reconstruct the coevolutionary history of such associations.

BIRCHES AND GALL MIDGES—AN EXAMPLE OF THE PATTERN APPROACH TO THE STUDY OF THE EVOLUTION OF SPECIES ASSOCIATIONS

Gall midges of the genus *Semudobia* are specialized on birches (*Betula* spp.). Roskam (1984) has presented phylogenies for *Betula* and *Semudobia*, and has given data on the distribution of the species and the existing species associations. These data are reproduced in Figure 15a-c, with the association matrix completed with question marks for potential associations. Using the method described above, several alternative reconstructions of the coevolutionary history of the association are produced. The

reconstruction that best fits the distribution of defining traits is the one illustrated in Figure 15d. According to this, the ancestor of *Semudobia* lived on the ancestor of *Betula*, or, more correctly, the defining traits of the association arose in the ancestors of *Semudobia* and *Betula*, respectively. However, the *Betula* section *Acuminatae* hosts no gall midges and is postulated to have escaped from attack by the gall midges. Of the two descendant species after the first speciation event in the gall midges, one (*Semudobia skuhravae*) retains a broad host range and now induces galls in bracts of female catkins of birches belonging to all sections of *Betula* except *Acuminatae*. This is what we expect under the coevolutionary null model. The other species, the stem species of the remaining *Semudobia* species, specialized on birches belonging to the section *Excelsae*. The narrow host range of the latter species is explained by the exploitation of a new resource, deciduous fruits, a derived condition present only in birches belonging to the sections *Excelsae* and *Acuminatae*. For the remain-

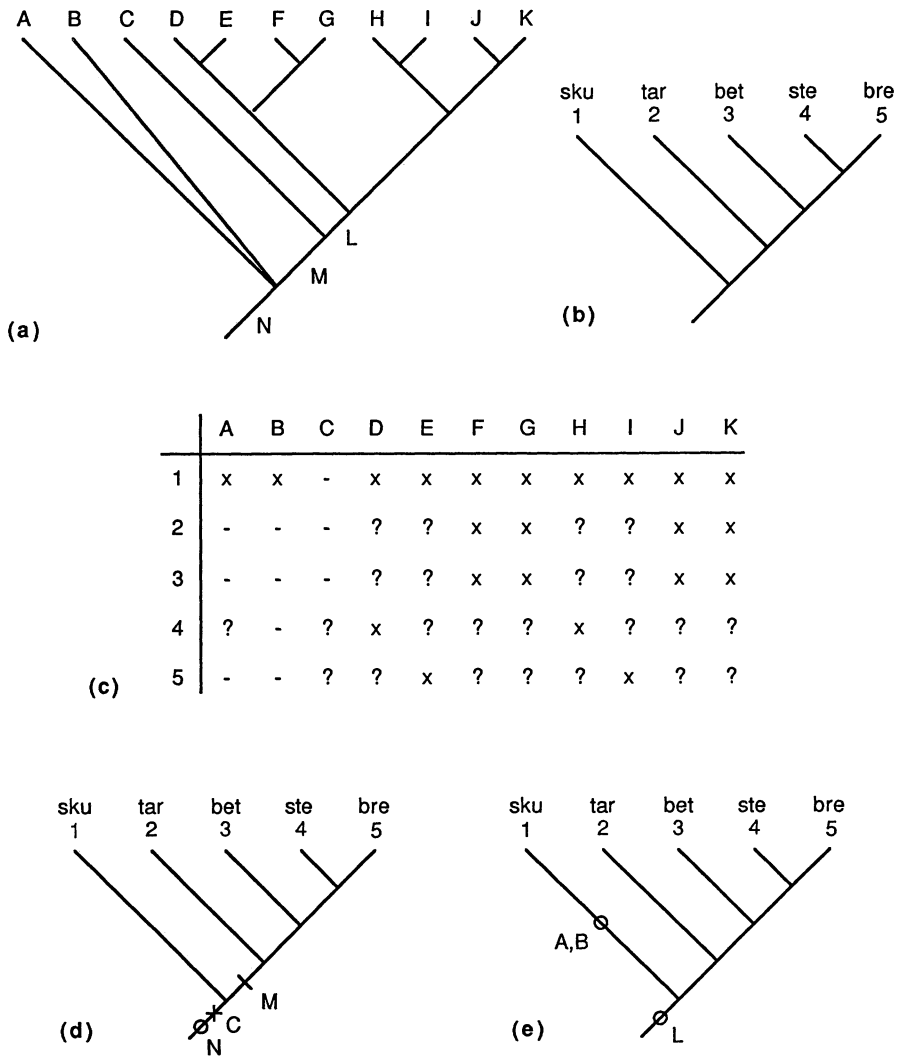


FIG. 15. Evolution of the association between *Semudobia* gall midges and birches (*Betula* spp.). (a) Phylogeny of *Betula*. A, section Costatae; B, section Humiles; C, section Acuminatae; D, *B. coerulea* group; E, *B. populifolia*; F, *B. platyphylla*; G, *B. pendula*; H, *B. fontinalis*; I, *B. papyrifera*; J, *B. davurica*; K, *B. pubescens*; L, section Excelsae; M, stem species of sections Excelsae and Acuminatae; N, stem species of *Betula*. (b) Phylogeny of *Semudobia*. 1 (sku), *S. skuhravae*; 2 (tar), *S. tarda*; 3 (bet), *S. betulae*; 4 (ste), *S. steenisi*; 5 (bre), *S. brevipalpis*. (c) Association matrix completed with question marks (?) for potential associations. (d, e) Two alternative reconstructions of the coevolutionary history of the association. Data from Roskam (1984).

ing species, the host plant range is restricted mainly by distribution patterns, and there is no evidence for violation of the coevolutionary null model. However, some specialization is seen in that, in the Palearctic region, *Semudobia tarda* predominates on *Betula pubescens*, whereas *Semudobia betulae* predominates on *Betula pendula* (Roskam and van Uffelen, 1981).

An alternative scenario is illustrated in Figure 15e. According to this, the ancestor of *Semudobia* was specialized on birches belonging to the section Excelsae, and *S. skuhravae* later colonized birches belonging to the sections Costatae and Humiles. The scenario requires that the colonization event(s) in *S. skuhravae* can be explained by apomorphic traits present in that spe-

cies. At present there is no evidence to support this reconstruction of the history of the association.

In terms of coevolutionary process models, the birch gall midges show few deviations from the null model. In the favored reconstruction, there is one postulated exclusion event and one specialization event (Fig. 15d). In the host plants, the exclusion event occurs in the *Betula* section *Acuminatae*. If it could be demonstrated that evolution of a novel defense mechanism in these birches makes them unavailable as host plants for the gall midges, this would lend support for the arms race model type II. The single specialization event that is postulated is explained by the gall midges exploiting a new, previously nonexistent resource, namely deciduous fruits. The primitive condition is that the fruits remain in the catkins over the winter, which presumably makes them unavailable as resources for the gall midges (Roskam, 1984, 1985). Deciduous fruits can hardly be seen as a defense mechanism against gall midges, and, thus, this specialization event in the midges does not support the arms race models but rather the specialization model.

In conclusion, the analysis demonstrates the strength of the pattern approach and the proposed method for reconstructing the coevolutionary history of an association. The method identifies deviations from the coevolutionary null model and thus locates instances where it is fruitful to seek evidence for the different coevolutionary scenarios. Using an explicit method also ensures that important aspects of the data are not missed. For instance, in the scenario in Figure 15d, the method points out that the absence of gall midges from birches belonging to the section *Acuminatae* needs a special explanation, something that was overlooked in the original analysis (Roskam, 1984, 1985). Furthermore, the method produces alternative scenarios (e.g., Fig. 15e) that were not considered in the original analysis.

Phylogenetic patterns are often underestimated as tests of the predictions of process models. We hope that the present

paper will contribute to a better understanding of coevolutionary processes through the patterns they create, and that it will stimulate further work on the process-pattern interface.

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