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***A posteriori* and *a priori* methodologies for testing
hypotheses of causal processes in vicariance
biogeography**

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Abstract

Methods used in vicariance biogeography fall into the categories of *a posteriori* methods (e.g., Component Compatibility Analysis and Brooks Parsimony Analysis) and *a priori* methods (e.g., Component Analysis, Reconciled Tree Analysis, and Three Area Statement Analysis). Each category corresponds to a particular methodology that arrives at general area cladograms by testing null hypotheses in a particular way. *A posteriori* methods assume the process of vicariance only (A0) as common cause of the distribution of different monophyletic groups of taxa under the null hypothesis. Whenever a parsimony analysis of combined data from these monophyletic groups results in a general area cladogram with homoplasy, the null hypothesis is rejected and extinction and dispersal are invoked *a posteriori* as *ad hoc* process explanations. *A priori* methods assume not only vicariance (A0) but also combinations of vicariance with the processes of extinction (A1) and dispersal (A2) as possible causes of the distribution of the taxa of different monophyletic groups. Each assumed set of processes corresponds to a different null hypothesis. Under the assumption of independence and thus additivity of the processes involved, the sets of area cladograms obtained under A0, A1, and A2, from data of each monophyletic group must be inclusive (requirement I). Whenever no congruent area cladograms are found in the intersection of sets of area cladograms derived under the same assumption for different monophyletic groups (II), the corresponding null hypothesis is rejected.

Introduction

Whenever a geographical or ecological barrier arises, species lineages distributed on either side of the barrier may be split into allopatric units (micro-species; Kornet, 1993a). When those splits become irreversible (permanent splits; Kornet, 1993b), vicariant speciation, or vicariance, has occurred. The geographical or ecological event forming the barrier is called a vicariance event. All species produced by vicariance share a property: the history of the areas or biota in which they occur mirrors their history of speciation. All monophyletic groups of species produced by the same vicariance events, therefore, share a general evolutionary history that parallels the history of the areas and biotas in which they occur. Historical biogeographers have taken advantage of this connection between vicariant speciation and earth history to classify biogeographic patterns into two groups: general patterns and unique patterns.

General patterns are those exhibited by multiple monophyletic groups. The general assumption (A0) in vicariance biogeography is that these general patterns have vicariance events as their common cause (Van Veller *et al.*, 1999).

In vicariance biogeography a pattern of historical relationships between areas is represented in an area cladogram (Rosen, 1978; Nelson and Platnick, 1981). In this paper we apply vicariance biogeography in a taxon relationship approach (Hovenkamp, 1997; van Veller *et al.*, 1999). Thereby, we look for an explanation of the distribution of taxa of monophyletic groups over areas by the reconstruction of historical relationships between these areas.

On the basis of a first-order explanation of vicariance, several biogeographers have studied historical relationships between various areas for different monophyletic groups of taxa (*e.g.* Brooks and McLennan, 1991; Cracraft, 1986, 1988, 1994; Crisci

et al., 1991; Enghoff, 1995; Funk and Brooks, 1990; Green *et al.*, submitted; Humphries, 1982; Kluge, 1988; Ladiges, 1998; Linder and Crisp, 1995; Mayden, 1988; Morrone, 1993; Page and Lydeard, 1994; Rosen, 1978; Turner, 1996; Van Soest and Hajdu, 1997). From these empirical studies it appears that processes other than vicariance (extinction, dispersal) give rise to exceptions to the simple association between cladograms of monophyletic groups of taxa and the history of the areas in which they live.

The way to arrive at an area cladogram in vicariance biogeography is by replacing taxa in a taxon cladogram of a monophyletic group by their areas of endemism (Rosen, 1978; Nelson and Platnick, 1981). If each taxon is present in only a single area (*i.e.* no widespread taxa are present) and each area is inhabited by only a single taxon (*i.e.* no sympatric taxa are present), this replacement straightforwardly produces a taxon-area cladogram (*sensu* Morrone and Carpenter, 1994; Enghoff, 1996) that can be completely explained by vicariance (Rosen, 1978; Nelson and Platnick, 1981). However, when sympatric or widespread taxa are present, replacement of taxa by areas results in taxon-area cladograms with either the same area at different terminal nodes (due to sympatric taxa) or more than one area at the same terminal node (due to a widespread taxon), and subsequent analysis to resolve the taxon-area cladogram into resolved area cladograms (*sensu* Morrone and Carpenter, 1994; Enghoff, 1996) is needed (Nelson and Platnick, 1981).

General area cladograms are derived from taxon-area cladograms by the application of different methods of analysis. Van Veller *et al.* (2000) divided these methods into two categories, depending on how they infer area cladograms from the taxon-area cladograms under three sets of process assumptions, called assumption zero (A0: vicariance), assumption 1 (A1: vicariance + extinction), and assumption 2

(A2: vicariance + extinction + dispersal) (see also Zandee and Roos, 1987; Wiley, 1988a,b; and Nelson and Platnick, 1981).

A posteriori methods include Component Compatibility Analysis (CCA; Zandee and Roos, 1987) and Brooks Parsimony Analysis (BPA; Brooks, 1990; Wiley, 1988a,b; Brooks *et al.*, 2001; modified for analyses under A1 and A2 in Van Veller *et al.*, 2000). They originally deal with widespread taxa under A0, but can also deal with widespread taxa under A1 and A2 via increasing and inclusive degrees of freedom and without making any *a priori* process assumptions (other than vicariance) for explanation. They deal with sympatric taxa (under all assumptions) by combining all data and explaining incongruences *a posteriori* by invoking extinction or dispersal *ad hoc*.

A priori methods include Component Analysis (CA; Nelson and Platnick, 1981; Page, 1988, 1990a,b), Reconciled Tree Analysis (RTA; Page, 1993, 1994), and Three Area Statement Analysis (TAS; Nelson and Ladiges, 1991a,b). They deduce from the *a priori* process assumption(s) the modifications in the data to deal with widespread or sympatric taxa. These *a priori* modifications may overrule the historical relationships established in the taxon cladograms (Van Veller *et al.*, 2000; Van Veller and Brooks, 2001). The modifications are deduced from the assumption under consideration.

Nelson and Ladiges (1996) have developed a method for the derivation of area cladograms as paralogy-free subtrees. For this method redundancy in a taxon-area cladogram is described as geographic paralogy, which is defined as duplication or overlap in geographic distribution among related taxa.

Following this method, Nelson and Ladiges (1996) make a taxon-area cladogram by replacing taxa in a taxon cladogram by their areas of distribution. From this taxon-

area cladogram widespread taxa are reduced in favor of endemics under A2 (Nelson and Ladiges, 1996; Ladiges, 1998). With this *a priori* operation, the (removed) widespread taxa are dealt with before subtrees are derived and an explanation of the (removed) widespread taxa by either non-response to a vicariance event (A0) or widespread presence with extinction in part of its range (A1) is precluded. As a consequence of this *a priori* modification to the data in order to deal with widespread and sympatric taxa we also categorize “Paralogy-Free Subtree Analysis” as an *a priori* method.

The critical difference between *a posteriori* and *a priori* methods lies not in their implementations in software packages but in the different protocols that they use to derive area cladograms from cladogenetic and distributional data. For instance, Brooks Parsimony Analysis (*a posteriori* method by Brooks, 1990; Brooks *et al.*, 2001) allows no *a priori* modifications of the data to deal with widespread or sympatric taxa. Parsimony analysis with PAUP (Swofford, 1990) or Hennig86 (Farris, 1988) obtains area cladograms from a data matrix that directly represents the distributional and cladogenetic relationships of the data. Three Area Statement Analysis (*a priori* method by Nelson and Ladiges, 1991a,b) also uses parsimony analysis for obtaining area cladograms. However, when dealing with widespread or sympatric taxa, Three Area Statement Analysis allows *a priori* modifications of the data (depending on the assumption under which the analysis is performed) via the derivation of a matrix with three area statements. Due to this difference in methodological protocols that either forbid or allow *a priori* modifications of the data before using the *same* implementation (*i.e.* PAUP or Hennig86) for parsimony analysis, the methods TAS and BPA are categorized as *a priori* and *a posteriori* methods, respectively.

All methods mentioned so far have also been referred to as pattern-based methods (Ronquist and Nylin, 1990). Both *a posteriori* and *a priori* methods derive divergent patterns (area cladograms) based on a first-order explanation of vicariance and subordinate explanations by extinction or dispersal. In addition to these pattern-based methods, event-based methods have been proposed by Ronquist (1997, 1998) and Ronquist and Nylin (1990). In event-based methods, (reticulate) biogeographical scenarios are analyzed by assigning different costs to different processes (vicariance, dispersal, extinction, and duplication). In this paper we restrict ourselves to pattern-based methods.

Van Veller *et al.* (1999) developed two criteria for consistency of all (pattern-based) methods with respect to their implementation of the assumptions and their capacity for finding general area cladograms for different monophyletic groups. First, Van Veller *et al.* (1999) claimed that inclusive sets of area cladograms under A0, A1, and A2 should be obtained if one makes *a priori* assumption of inclusive sets of independent -and thus additive- processes under these assumptions (requirement I). Second, Van Veller *et al.* (1999) argued that these sets of area cladograms obtained for different monophyletic groups should be compared under the same assumption to obtain valid general area cladograms (requirement II).

After assessing the *a posteriori* and the *a priori* methods for the extent to which they satisfy these two requirements, Van Veller *et al.* (2000) found that none of the methods shows any problems with respect to requirement II, but that all the methods may violate requirement I under certain circumstances.

Van Veller *et al.* (accepted) suggested modifications to the various methods relating to area cladogram selection and succeeded in meeting both requirements I and II for both *a posteriori* and *a priori* methods. After these modifications are applied, all

methods show consistent behavior with respect to the (independent) processes assumed *a priori* and the derivation of general area cladograms. Even after correcting all methods so that they meet requirements I and II, *a posteriori* and *a priori* methods may still select different (general) area cladograms (Van Veller *et al.*, accepted). We think that these differences between the (general) area cladograms obtained with *a posteriori* and *a priori* methods indicate that the two categories represent different methodologies. These methodologies arrive at general area cladograms by different ways of testing hypotheses of causal processes for taxa of different monophyletic groups. The general area cladograms are explained by processes such as vicariance, extinction, and dispersal in different ways by the two categories.

In this paper we discuss the differences between *a posteriori* and *a priori* methods in the testing of these hypotheses. We examine the need for A0, A1, and A2 in both *a posteriori* and *a priori* methods and see how these assumptions relate to the need for requirements I and II for both categories of methods.

The *a posteriori* methodology for vicariance biogeography

Process assumptions

In *a posteriori* methods the null assumption (A0) (comparable to the null model *sensu* Brooks and McLennan, 1991; Ronquist, 1997) is that the distribution of the taxa of a monophyletic group over areas is caused by the process of vicariance. In this respect, the *a posteriori* methodology does not differ from the *a priori* methodology. Contrary to the *a priori* methods, the *a posteriori* methods do not assume extra processes of extinction and dispersal (see below).

Formulating the null hypothesis

Under the null assumption (A0), the null hypothesis is that the cladogenetic relationships between taxa of several monophyletic groups (represented in their taxon cladograms) and their distributions over the same areas result in a single general area cladogram without homoplasy (Fig. 1). This single general area cladogram without any homoplasious components represents the pattern of the historical relationships between areas.

Testing the null hypothesis

Data on several monophyletic groups of taxa are provided by the taxon cladograms of all monophyletic groups and the distribution of the taxa of each monophyletic group over the areas (Fig. 2a). These data are used to derive an area-by-node data matrix (area-data matrix), either directly or indirectly. The direct derivation is by computing the Boolean inner product of the matrix representing the distribution of the taxa over the areas concerned and the matrix representing the cladogram of the taxa (Zandee and Roos, 1987). The indirect derivation of the area-data matrix uses an intermediate taxon-area cladogram (Fig. 2b). A taxon-area cladogram is derived from each taxon cladogram of a monophyletic group by replacing the taxa by the areas in which these taxa are distributed. Each taxon-area cladogram of a particular monophyletic group is translated into an area-data matrix via inclusive Oring (O'Grady and Deets, 1987) or additive binary coding with question marks standing in for missing data (Wiley, 1988a,b; Brooks, 1990; Brooks and McLennan, 1991) (Fig. 2c).

The *a posteriori* methods CCA (Zandee and Roos, 1987) and BPA (Brooks, 1990; Brooks *et al.*, 2001) combine the area-data matrices of several monophyletic groups in

one combined area-data matrix (Fig. 2d). This combination of area-data matrices is analogous to a total evidence approach in systematic phylogenetics (Kluge, 1989, 1998). From the combined area-data matrix, area cladograms are derived via parsimony analysis. The most parsimonious general area cladogram is selected.

If all components are congruent with this general area cladogram, the null hypothesis is not rejected and the distribution of taxa over areas is explained by vicariance. If at least one component is not congruent with the general area cladogram, *i.e.* the component is homoplasious, the null hypothesis is rejected.

Homoplasious components are explained *a posteriori* by *ad hoc* process explanations such as extinction or dispersal. In Fig. 2e we show some homoplasious components in the general area cladogram that is obtained with CCA or BPA from the data of three groups. The two parallelisms (open box and circle) can be interpreted as two dispersal events of taxon T1 from area A to area C and of taxon T13 from area A to area D. The two reversals and single reversal (grey ovals) obtained by BPA and CCA respectively can be interpreted as two (taxa T11 and T12) and one (taxon T11) extinctions in area C for BPA and CCA, respectively.

Why A0 is sufficient for *a posteriori* methods and requirements I and II therefore do not apply

As we described above and show in Fig. 2, in the *a posteriori* methods CCA and BPA the area-data matrices of all monophyletic groups distributed in the same areas are combined in one area-data matrix. Parsimony analysis on this combined area-data matrix, always results in one (or more) general area cladogram(s). In cases where the null hypothesis is not rejected, the common cause explanation is vicariance. A *posteriori ad hoc* explanation of the distribution of taxa of monophyletic groups by

processes of extinction or dispersal is needed whenever the null hypothesis is rejected. However, these extra processes (extinction or dispersal) are not assumed *a priori* in arriving at a general area cladogram. As a result, the data for all monophyletic groups can always be analyzed under the same assumption (*i.e.* A0) and requirement II is thus always met (see also Van Veller *et al.*, 2000). The *a posteriori* methods do not (necessarily) obtain sets of area cladograms under A1 or A2 (but only under A0 *sensu* Zandee and Roos, 1987; Wiley, 1988a,b) and, therefore, requirement I does not apply.

The *a priori* methodology for vicariance biogeography

Process assumptions

In *a priori* methods the null assumption (A0) is that the distribution of the taxa of a monophyletic group over areas is caused by the process of vicariance. In this respect the *a priori* methodology does not differ from the *a posteriori* methodology. Contrary to the *a posteriori* methods, the *a priori* methods assume combinations with the extra processes of extinction (A1) and dispersal (A2) (see below).

Formulating and testing hypotheses

With *a priori* methods, for each monophyletic group of taxa, the taxon cladogram (Fig. 3a) is converted into a taxon-area cladogram (Fig. 3b) by replacement of the taxa by the areas of distribution. From the taxon-area cladogram solution sets (S_i *sensu* Van Veller *et al.*, 1999), which contain area cladograms, are derived under assumptions zero, 1, and 2 (Fig. 3c).

In the application of the *a priori* methodology under each assumption zero, 1, and 2, a different null hypothesis is formulated. Thus, rather than using a single null hypothesis (as *a posteriori* methods do), *a priori* methods use different null hypotheses depending on the assumption applied.

Under A0 the null hypothesis states that the cladogenetic relationships between taxa of several monophyletic groups (represented in their taxon cladograms) and their distributions over the same areas result in a general area cladogram. Vicariance is assumed to be the cause of the distribution of the taxa of monophyletic groups over the areas. A general area cladogram is the result of comparing the solution sets of different monophyletic groups for congruent area cladograms (Fig. 3d). If the intersection of the solutions sets (Fig. 3d; S_i0) of the different groups is empty (no congruence), the null hypothesis is rejected.

If the null hypothesis under A0 is rejected, a new null hypothesis of congruence among solution sets is formulated under A1. Under this new null hypothesis extinction is added to vicariance in the set of assumed causes of the distribution of the taxa of monophyletic groups over areas. By dealing with widespread and sympatric taxa via modifications to the data deduced from A1, a larger set of area cladograms (S_i1) is obtained (Fig. 3c). The sets of area cladograms (Fig. 3d; S_i1) are again compared for congruent area cladograms and the null hypothesis (under the assumption that the distribution was caused by vicariance and extinction) is rejected if none is found.

Finally, if the null hypothesis under A1 is rejected, a new null hypothesis of congruence among solution sets is formulated under A2. Under this new null hypothesis dispersal is added to vicariance and extinction in the set of assumed causes of the distribution of the taxa of monophyletic groups over areas. Under A2,

widespread and sympatric taxa are dealt with in such a way that modifications to the data allowed by *a priori* assumption of vicariance, extinction or dispersal result in sets of area cladograms (S_i2) for each monophyletic group (Fig. 3c). These sets are again compared for congruent area cladograms (Fig. 3d; S_i2) that are considered to represent general patterns. However, if no congruent area cladograms are found, the null hypothesis of a general pattern of historical relationships between areas as explained by vicariance, extinction or dispersal in the taxa of all monophyletic groups is rejected. With this rejection of the null hypothesis that encompasses all these processes, the possibility of finding any general pattern for all monophyletic groups is ruled out.

Why and when requirements I and II apply in the *a priori* methodology

Van Veller *et al.* (accepted) suggested modifications to the *a priori* methods CA, RTA, and TAS that ensure that they obtain inclusive sets of area cladograms under A0, A1, and A2. By dealing with widespread taxa *a priori* under the different assumptions and dealing with sympatric taxa either via tree reconciliation (RTA) or “as is” (CA and TAS), the sets of area cladograms expand inclusively when analyses are performed under A0, A1, and A2.

Under the different assumptions, different null hypotheses are formulated, which are tested by looking for congruence in sets of area cladograms that result from the *a priori* assumption of the different sets of causal processes (vicariance; vicariance + extinction; vicariance + extinction + dispersal).

Van Veller *et al.* (1999) showed that under the assumption of the independence of these processes, and thus the additivity of the results obtained, requirements I and II must be met if any comparison of the solution sets obtained has to be valid.

Fig. 4 shows sets of area cladograms derived under A0 (S_{10} and S_{20}), A1 (S_{11} and S_{21}), and A2 (S_{12} and S_{22}) for two monophyletic groups of taxa. As we showed above, general area cladograms for these two monophyletic groups of taxa are found in the intersection of the solution sets obtained under the same assumption (requirement II).

Fig. 4a shows two intersections of solution sets (the solution sets derived under A1 and those derived under A2). Despite the fact that requirement II is met, it is not clear whether the general area cladogram(s) must be selected under A1 or A2. Neither the null hypothesis under A1 (vicariance + extinction assumed) nor the null hypothesis under A2 (vicariance + extinction + dispersal assumed) can be rejected. If, however, the processes are assumed to be dependent on each other and may interact, and therefore to be non-additive in their results, an external criterion for rejection is needed to choose between the general area cladograms. If, however, the processes are assumed to be independent, and therefore additive in their results, the solution sets represented in Fig. 4a do not show inclusion and violate requirement I.

In Fig. 4b we show again two intersections of solution sets (the solution sets derived under A1 and those derived under A2). Requirement II is met in this example too and general area cladograms can be selected under A1 or A2. The null hypotheses cannot be rejected either under A1 (vicariance + extinction assumed) or under A2 (vicariance + extinction + dispersal assumed). If one wishes to choose the general area cladogram(s) that is (are) explained by the smallest set of processes, one will select the general area cladogram(s) under A1 in Fig. 4b. However, because of inclusion of sets of area cladograms (requirement I), these general area cladogram(s) are selected under A2 also. By selecting these general area cladogram(s) (derived under both A1 and A2) and by giving explanations by vicariance and extinction (under A1) rather

than by vicariance, extinction and dispersal (under A2) one gains explanatory power (*i.e.* explanation by fewer processes for the same general area cladogram(s)).

Conclusions

Above we have discussed a general framework under which *a posteriori* and *a priori* (pattern-based) methods test null hypotheses of causes of the distribution of several monophyletic groups of taxa over areas. Both *a posteriori* and *a priori* methods derive area cladograms on the basic idea that cladogenetic and distributional data of monophyletic groups represent historical (divergent) relationships between areas. However, they formulate null hypotheses and test those null hypotheses in very different ways.

A posteriori methods such as CCA and BPA do not make *a priori* process assumptions besides vicariance. Under the null hypothesis (vicariance events as common cause for the distribution of taxa of different monophyletic groups) they assume that the cladogenetic relationships of the taxa of several monophyletic groups are associated with the historical relationships of the areas. For all monophyletic groups of taxa these methods derive area-data matrices which they combine in one matrix. Parsimony analysis of this combined area-data matrix results in a general area cladogram in which homoplasy forces a rejection of the null hypothesis. Whenever the null hypothesis is rejected, *a posteriori* methods use *ad hoc* explanations in terms of extinction or dispersal to explain the deviation from vicariance. As a result, we have shown that *a posteriori* methods test null hypotheses and derive general area cladograms without using A1 or A2. A0 suffices and both A1 and A2 are superfluous.

Neither requirement I nor requirement II (Van Veller *et al.*, 1999) can therefore be violated by *a posteriori* methods.

A priori methods such as CA, RTA and TAS use A0 and the extra assumptions 1 and 2 to deal with widespread and sympatric taxa *a priori*. In this paper we discuss a general framework for all *a priori* methods for testing null hypotheses derived under different assumptions in a consistent way. By comparing the sets of area cladograms derived for different monophyletic groups under the same assumption and searching for congruent patterns in the intersection of the different solutions sets, general area cladograms are found. If general area cladograms are found, the null hypothesis is not rejected and the set of processes assumed *a priori* appears to be sufficient for an explanation of the distribution of all taxa of the different monophyletic groups over areas. However, if no general area cladograms can be found, a different null hypothesis must be formulated under another assumption.

In this framework of testing null hypotheses by searching for congruence among area cladograms, requirement II (Van Veller *et al.*, 1999) should not be violated. Valid general area cladograms are only found for several monophyletic groups when the same null hypothesis under the same assumption (either A0, A1, or A2) for all groups is not rejected. Requirement I (Van Veller *et al.*, 1999), under the assumption of independence of processes, and thus additivity of results, is necessary to enable testing (and possible rejection) of the null hypothesis.

Requirement I is not an optimality criterion like minimal items of error (CA), minimal number of losses/duplications (RTA) or minimal number of steps (TAS). These optimality criteria describe difference in fit of cladogenetic and distributional data on area cladograms within a particular solution set, derived under A0, A1, or A2 for a single monophyletic group of taxa. Requirement I is a methodological necessity

over different solution sets (that are derived for a single monophyletic group of taxa under A0, A1 and A2) when independence of the causal processes (vicariance, extinction or dispersal) is assumed. Requirement I thereby does not compete with the description of fit of cladogenetic and distributional data on area cladograms within a particular solution set.

In this paper we show how *a posteriori* and *a priori* methodologies differ. Each is capable of deriving general area cladograms consistently. If the two methodologies agree in their results, no dilemma arises. In cases where their results differ, additional groups of taxa should give a decisive answer on the processes that have resulted in the distribution of taxa of several monophyletic groups over the same areas.

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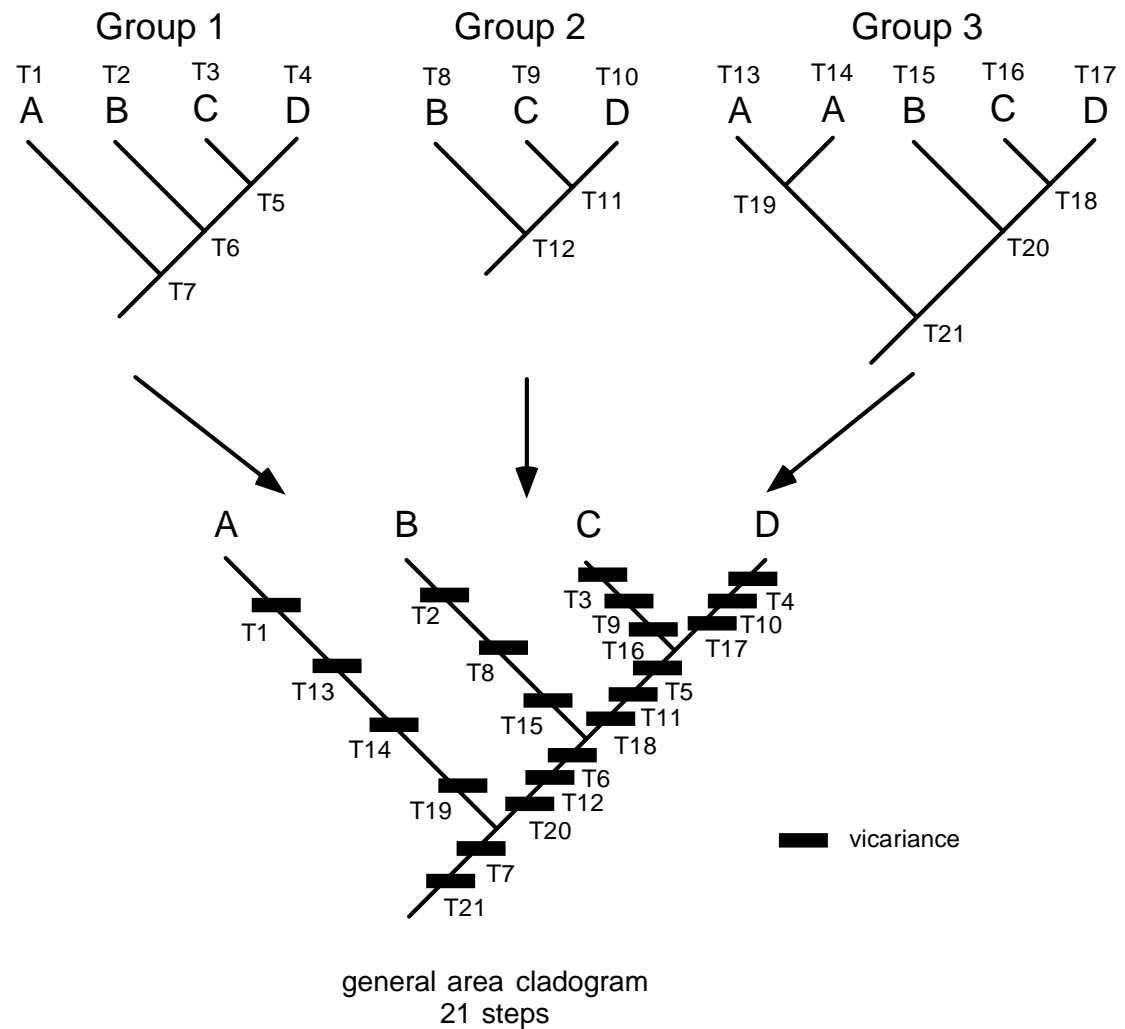


FIG. 1. No rejection of the null hypothesis when parsimony analysis with *a posteriori* methods results in a general area cladogram without any homoplasy (T1-T21=taxa; A-D=areas).

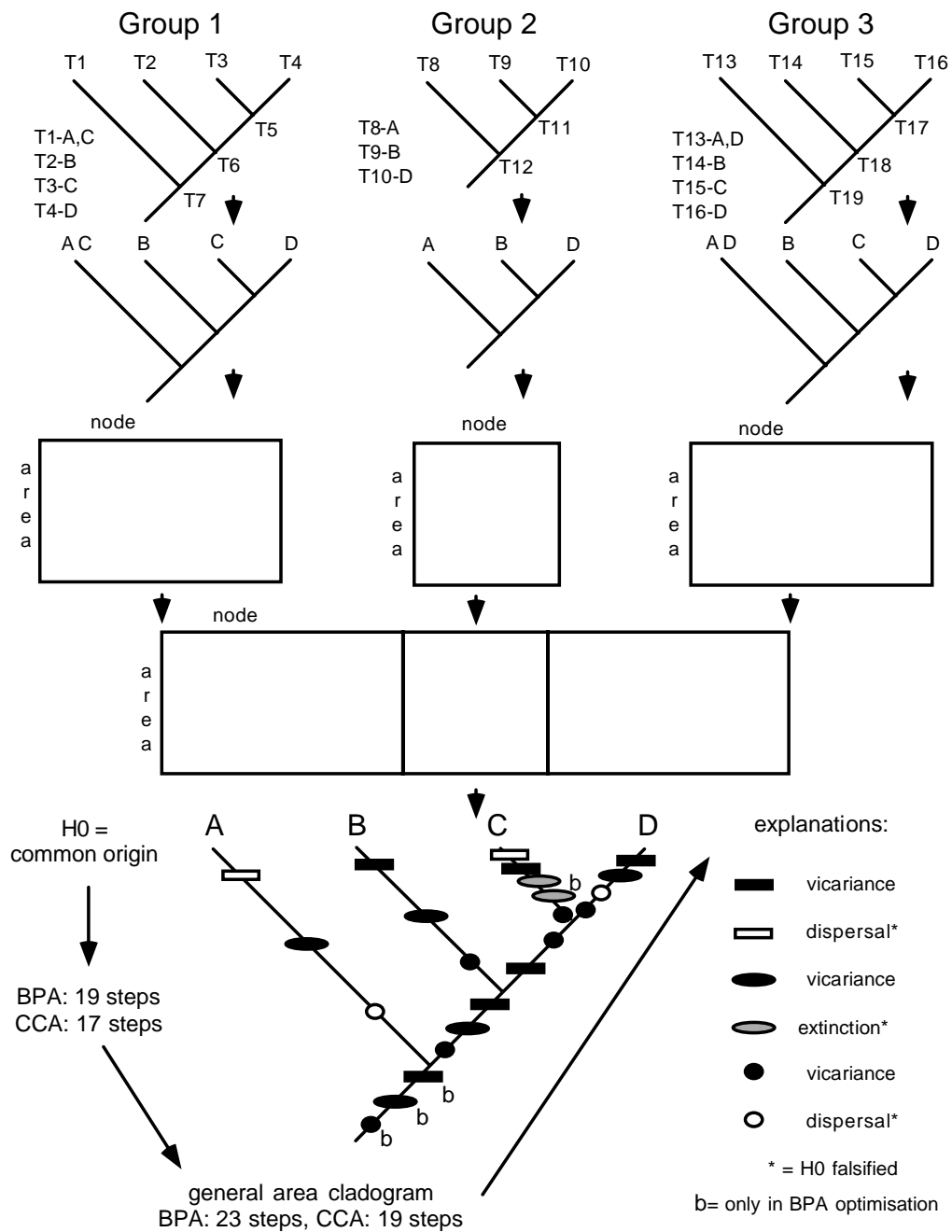


FIG. 2. A framework for testing the null hypothesis (that the distribution of taxa of several monophyletic groups over the same areas is caused by vicariance) with *a posteriori* methods and *ad hoc* explanations when this null hypothesis is rejected (by extinction or dispersal) (a: taxon cladograms for separate groups, b: taxon-area cladograms for separate groups, c: area-data matrices for separate groups, d: combined area-data matrix, e: general area cladogram) (T1-T19=taxa; A-D=areas).

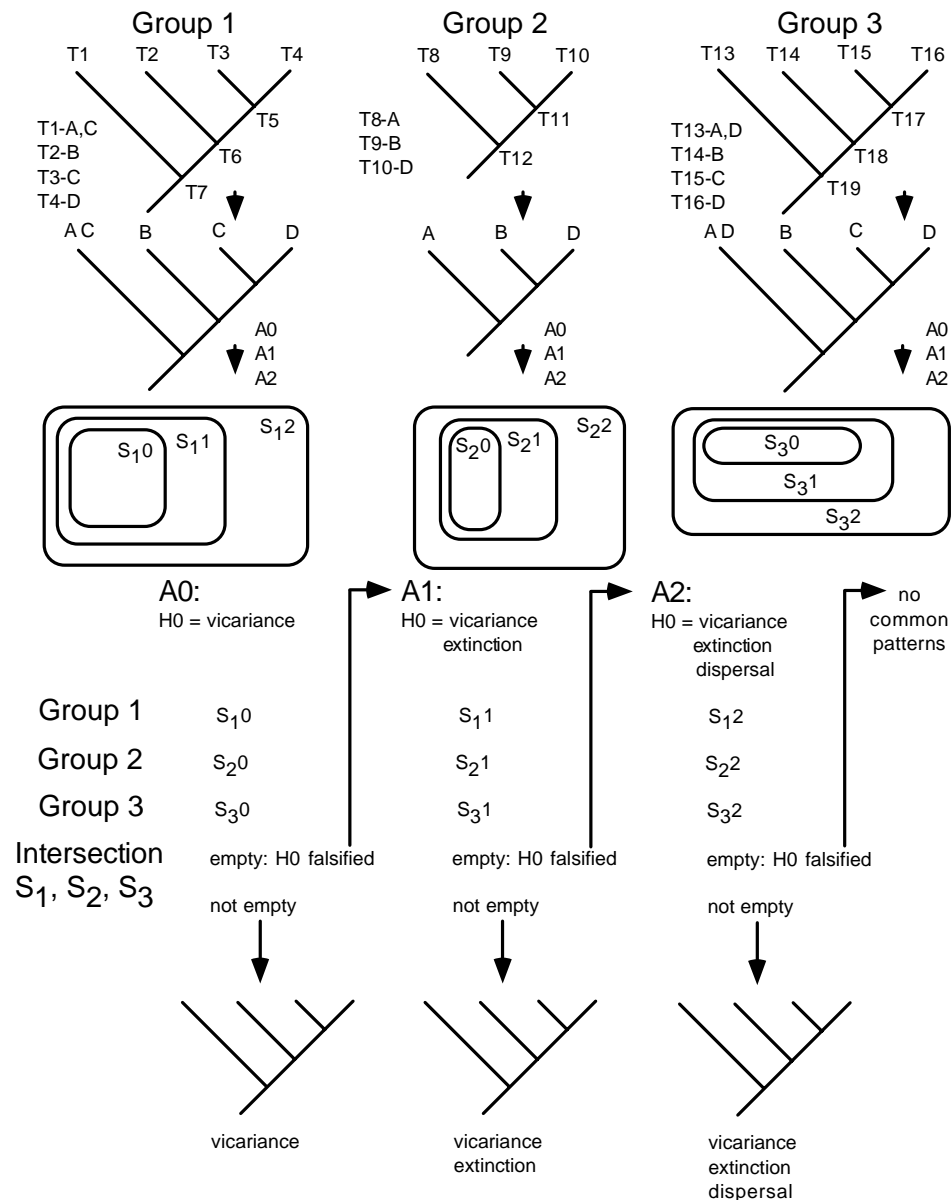
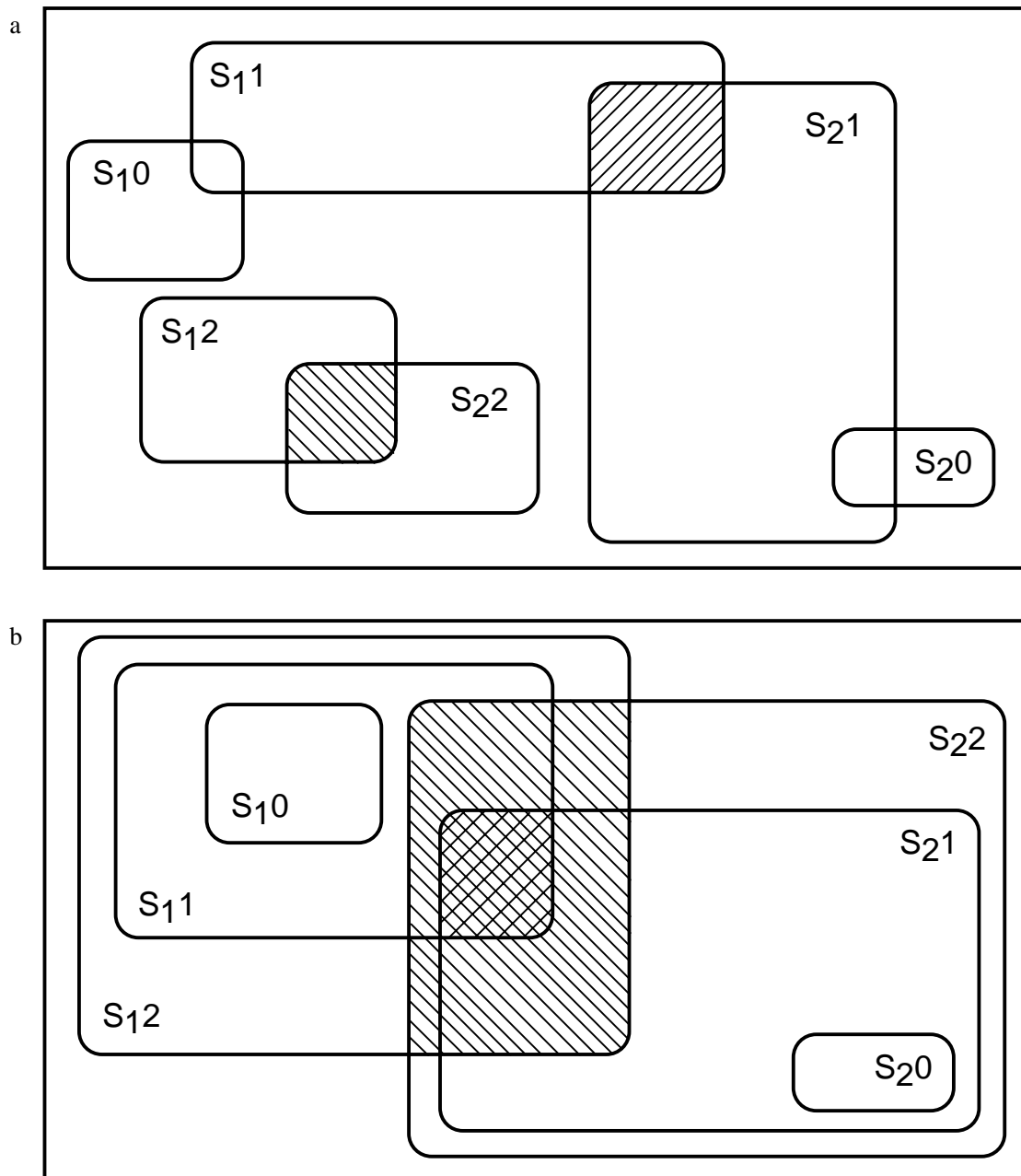


FIG. 3. A framework for testing hypotheses (that the distribution of taxa of several monophyletic groups over the same areas is caused by vicariance, vicariance or extinction, vicariance or extinction or dispersal) with *a priori* methods (a: taxon cladograms for separate groups, b: taxon-area cladograms for separate groups, c: sets of area cladograms, derived for separate groups under assumptions zero, 1, and 2, d: comparison of sets of area cladograms for several groups of taxa under the same assumption for finding general patterns) (T1-T19=taxa; A-D=areas; S_i0, S_i1 and S_i2=sets of area cladograms derived under A0, A1 and A2 for monophyletic group i).





general area cladograms under A1  and A2 

FIG. 4. The case for requirement I with *a priori* methods (a: sets of area cladograms and general area cladograms (in intersections) when requirement I is violated, b: sets of area cladograms and general area cladograms (in intersections) when requirement I is met) (S_{i0} , S_{i1} and S_{i2} =sets of area cladograms derived under A_0 , A_1 and A_2 for monophyletic group i).