

## **Unveiling vicariant methodologies in vicariance biogeography**

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## A survey of the scientific discipline of biogeography

Biogeography is the scientific discipline in which one tries to explain the distribution of groups of organisms, or taxa, over the surface of the earth. Depending on whether these distributions are explained on a short-term ecological or on a long-term evolutionary scale, the discipline of biogeography is subdivided into ecological and historical biogeography (Myers and Giller, 1988). The structure of the discipline of biogeography is summarized in Fig. 1.

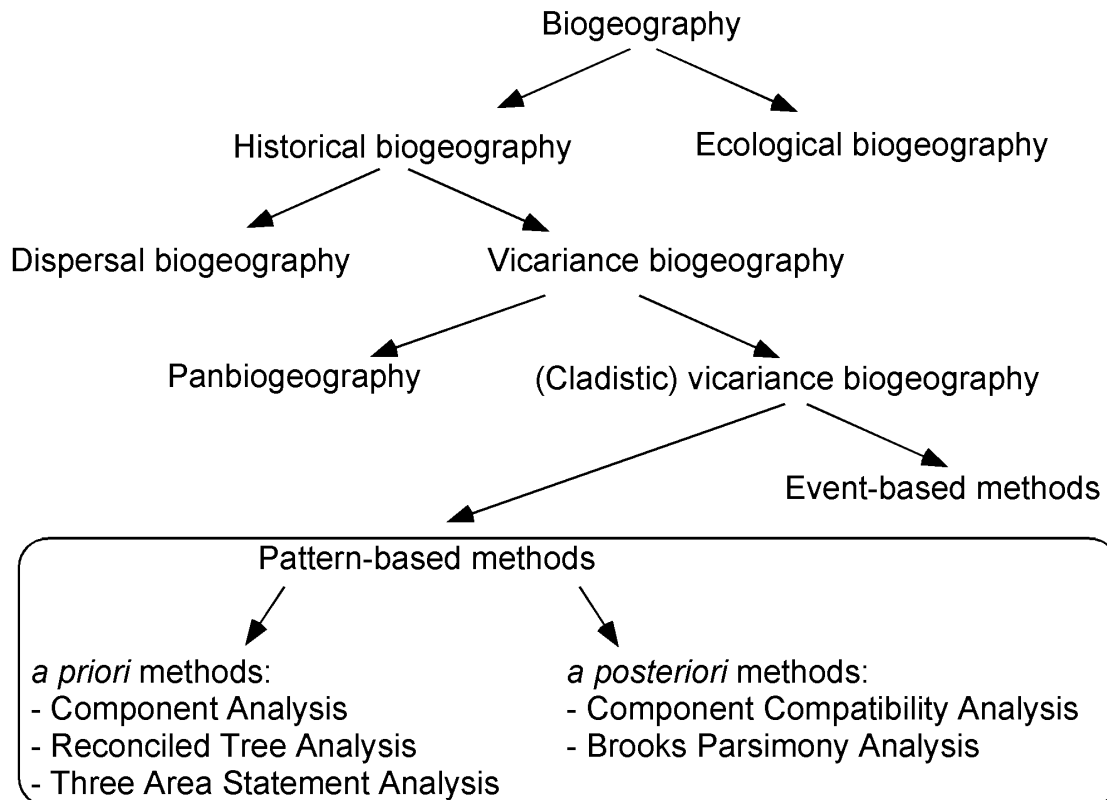


Fig.1. Hierarchical outline of the scientific discipline of biogeography.

Ecological biogeography examines the distribution of taxa to find out why they are at present restricted to that particular distribution (Nelson and Platnick, 1981). In historical biogeography, by contrast, the present-day distribution of taxa is combined with hypotheses on cladogenetic relationships between these taxa to infer historical connections among the areas or biota over which they are distributed (Rosen, 1978) and to explain how the taxa became distributed over these areas by processes including allopatric speciation, sympatric speciation, extinction, and dispersal. Within historical biogeography, dispersal biogeography explains disjunct distribution ranges of taxa by the dispersal of ancestor taxa over pre-existing barriers that originated as a result of (a)biotic events. If sympatric speciation takes place after

dispersal, descendant taxa are distributed over different areas separated by the (a)biotic barrier. Dispersal biogeographers start with a centre of origin for ancestor taxa and explain the distribution of descendant taxa by dispersal across pre-existing barriers (Myers and Giller, 1988; Bremer, 1992; Ronquist, 1994; Hausdorf, 1998). Vicariance biogeography, by contrast, explains disjunct distribution ranges of taxa by the process of vicariance, *i.e.* the process whereby allopatric speciation is triggered by an abiotic or a biotic event (Myers and Giller, 1988). As a result of such an event an ancestor taxon is divided into two (or more) disjunct populations that differentiate into two (or more) allopatric descendant taxa (Nelson and Platnick, 1981).

Despite the fact that historical biogeography falls into two sub-disciplines, neither the process of dispersal nor the process of vicariance can be discounted *a priori* as irrelevant for the explanation of the distribution of any particular monophyletic group. Widespread and sympatric taxa indicate that not all biogeographical patterns result from vicariance alone, and suggest that dispersal takes place too. On the other hand, endemic taxa suggest vicariance as an explanation for biogeographical patterns. Though vicariance biogeography *a priori* assumes vicariance, the methodologies of its various approaches also include explanations in terms of dispersal.

The discipline of vicariance biogeography can be divided into two different approaches depending on how distribution histories are reconstructed.

Panbiogeography, founded by Croizat (1952, 1958), reconstructs distribution histories by drawing lines on a geographical map. These lines, called “tracks”, connect known distributions of related taxa in different areas. If two or more tracks of unrelated taxa coincide, they are called generalized tracks. These generalized tracks indicate the preexistence of widespread distributions of ancestral taxa that are subsequently fragmented by (a)biotic events (Morrone and Crisci, 1995). In panbiogeography, the cladogenetic relationships of the taxa from which distribution the tracks are drawn play a subordinate role.

The role of cladogenetic relationships between taxa is more important in the form of vicariance biogeography that dominates the discipline at present: cladistic vicariance biogeography. This approach combines cladograms of taxa and their distributions in areas to derive area cladograms. Such area cladograms are hypotheses of historical relationships between areas. Explanations of the distribution of taxa over areas by the processes of vicariance, extinction, and dispersal are obtained from these area

cladograms by the application of various methods. In this paper, this approach will be referred to as vicariance biogeography.

Two approaches can be distinguished within vicariance biogeography. The first set of approaches are methods that derive divergent patterns (*i.e.* area cladograms) on the basis of the assumption of vicariance. These methods are called biogeographic pattern analysis methods (Cracraft, 1988) or pattern-based methods (Ronquist and Nylin, 1990). The second set of approaches are event-based methods (Ronquist and Nylin, 1990) and are proposed by Ronquist (1997, 1998) and Charleston (1996) to accommodate reticulate biogeographical scenarios, representing the accretion of areas. In event-based methods, reticulate biogeographical scenarios are obtained by assigning differential costs to different processes (vicariance, dispersal, extinction, and sympatric speciation). An event-based protocol that reveals historical sequences of vicariance events (and not historical relationships among areas) has been developed by Hovenkamp (1997).

### **Evaluation of *a priori* and *a posteriori* methods in vicariance biogeography**

All pattern-based methods in vicariance biogeography derive divergent (general) area cladograms that hypothesize historical relationships between areas based on cladogenetic and distributional data of taxa that inhabit these areas. In order to explain the distribution of the taxa, explanations by the processes of vicariance, extinction or dispersal are inferred from the data and the (general) area cladogram(s) obtained. According to the way in which the pattern-based methods deal with the data in order to obtain explanations for distributions of taxa by the processes, two categories of methods are recognized: *a priori* and *a posteriori* methods. *A priori* methods include Component Analysis (CA: Nelson and Platnick, 1981; Page, 1988, 1990), Reconciled Tree Analysis (RTA: Page, 1993, 1994), and Three Area Statement Analysis (TAS: Nelson and Ladiges, 1991a,b,c). *A posteriori* methods include Component Compatibility Analysis (CCA: Zandee and Roos, 1987) and Brooks Parsimony Analysis (BPA: Brooks, 1990; Brooks *et al.*, 2001; Wiley, 1988a,b). Each of these methods has its proponents (*e.g.* Andersson, 1996; Page, 1989, 1990; Wiley, 1988a,b; Zandee and Roos, 1987; Ladiges, 1998; Van Veller and Brooks, 2001; Green *et al.*, 2002). Several studies (Cracraft, 1988; Crisci *et al.*, 1991; Enghoff, 1995; Morrone and Carpenter, 1994; Van Soest and Hajdu, 1997; Van Veller *et al.*, 2000, 2001) have

shown that the *a priori* and *a posteriori* methods in vicariance biogeography may infer different (general) area cladograms from identical empirical or theoretical data sets.

In an earlier evaluation of different methods used in vicariance biogeography, Morrone and Carpenter (1994) compared area cladograms obtained by CA, RTA, TAS, and BPA for different data sets. They found that the methods often do not agree in their results and concluded that agreement among the obtained area cladograms cannot serve as a criterion for preferring one of the methods over another.

Furthermore, they found that even their criterion of counting the number of so-called “items of error” (Nelson and Platnick, 1981) for the area cladograms obtained with the various methods failed to identify any of the methods as preferable. Their use of items of error as an evaluation criterion, however, is questionable, because items of error may serve in CA and RTA as an optimality criterion for the selection of area cladograms. As a result, the criterion for the evaluation of methods used by Morrone and Carpenter (1994) was not independent of the optimality criterion within methods. The methods use different inputs from the same data set for the derivation of area cladograms. An optimality criterion such as items of error (used with CA and RTA) or number of steps (used with TAS and BPA) cannot be used for comparison between all methods because it is restricted to a particular method.

For a comparison between all methods in vicariance biogeography, two methodological requirements (requirements I and II) are derived (Van Veller *et al.*, 1999). These requirements concern the use of processes assumed a priori under assumptions zero (A0: vicariance), 1 (A1: vicariance + extinction), and 2 (A2: vicariance +extinction +dispersal).

Requirement I is illustrated in Fig. 2a. Under this requirement inclusive sets of area cladograms should be derived under A0, A1 and A2. The different processes underlying the assumptions are *a priori* considered to be independent in their effect. That is, requirement I *a priori* precludes that, for instance, the susceptibility of a particular monophyletic group to extinction is related to its dispersal capabilities. Of course, a poor disperser may have a higher chance of extinction. However, such a dependence should not be assumed *a priori* but should be revealed from the data *a posteriori*.

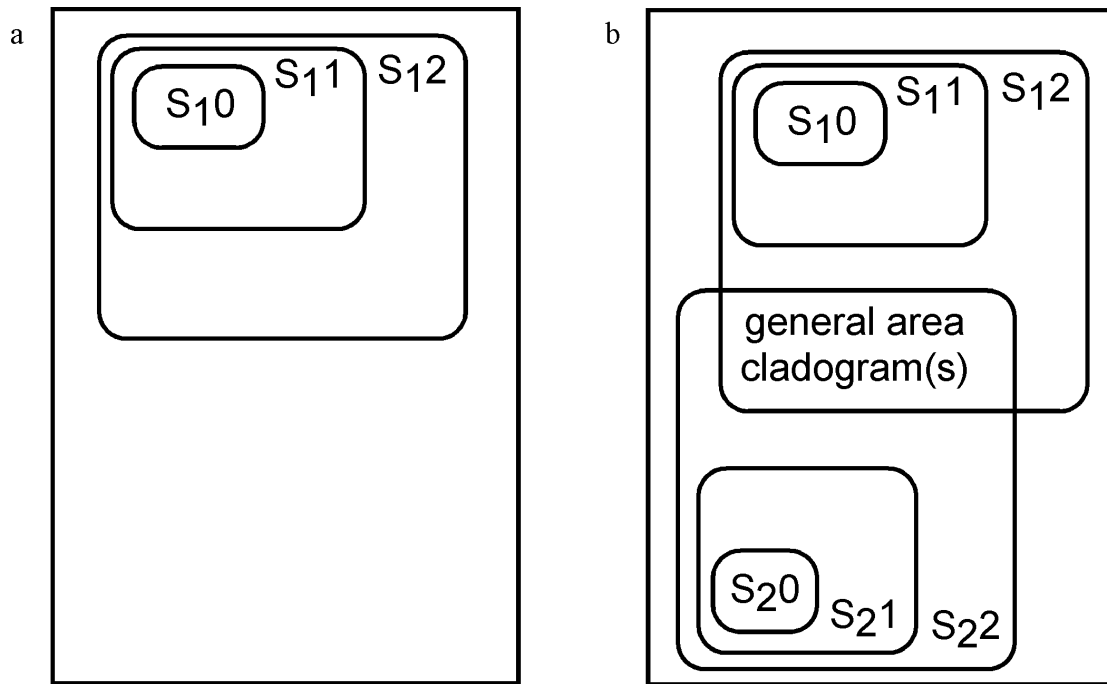


Fig. 2. Methodological requirements for obtaining (general) area cladograms under assumptions zero, 1 and 2 (a: Requirement I, b: Requirements II) ( $S_{i0}$ ,  $S_{i1}$  and  $S_{i2}$ =sets of area cladograms derived under  $A_0$ ,  $A_1$  and  $A_2$  for monophyletic group  $i$ ).

Requirement II is illustrated in Fig. 2b. Under requirement II, valid general area cladograms are obtained by comparison of sets of area cladograms obtained for different monophyletic groups under the same assumption. For such obtained general area cladograms only a single set of processes is *a priori* assumed to have affected both monophyletic groups. Of course, different sets of processes may have governed the pattern of distribution of both monophyletic groups. However, since (mostly) there is no *a priori* knowledge of the relative importance of these processes, all taxa are *a priori* considered to have responded equally to the possible processes. The degree to which this actually makes sense to a particular monophyletic group is indicated by the degree of fit of its particular cladogenetic and distribution history to the general area cladogram.

The applicability of the assumptions to all examined methods allows the generalization of the requirements over all these methods. The *a priori* and *a posteriori* methods CCA, BPA, CA, RTA, and TAS (and their implementations in software) obtain area cladograms from cladogenetic and distribution data of the taxa of monophyletic groups under the different assumptions. For an evaluation of these methods, their corresponding implementations are used to derive sets of area cladograms (*i.e.* solution sets) for both theoretical and empirical data sets

(*Heterandria*, *Xiphophorus*, *Cyttaria*, *Eriococcus/Madarococcus*) under A0, A1, and A2. The results are examined to assess whether requirements I and II are met by *a priori* and *a posteriori* methods (Van Veller *et al.*, 2000).

This evaluation of the methods shows that requirement II is never violated and that no modifications to the methods are necessary to meet this requirement. From the same evaluation, however, it follows that all the methods may under certain circumstances violate requirement I.

Modifications (presented in Van Veller *et al.*, 2001) to the computer programs that implement CCA, BPA, CA, RTA, and TAS enable them to meet both requirements I and II. However, after application of these measures, it appears that *a priori* and *a posteriori* methods do not always deliver the same general area cladograms. The reason is that the two categories of methods represent different research methodologies in the testing of hypothesis concerning the causal processes that yield the distribution of taxa over areas (Van Veller *et al.*, 2002).

The category of *a posteriori* methods assumes under the null hypothesis the process of vicariance only (A0) as common cause of the distribution of different monophyletic groups. This null hypothesis is rejected and extinction and dispersal are invoked *a posteriori* in case parsimony analysis of combined data (from the different monophyletic groups) results in a general area cladograms with homoplasy.

The category of *a priori* methods assumes besides only vicariance (A0) also combinations of vicariance with the processes of extinction (A1) and dispersal (A2) as possible causal processes for the distribution of different monophyletic groups. Each of the assumed set of processes corresponds to a different null hypothesis. A particular null hypothesis is rejected when no congruent area cladograms are found in the intersection of sets of area cladograms derived under A0, A1, and A2. In case a general area cladogram is selected under a particular assumption, the corresponding null hypothesis cannot be rejected and information on the importance of vicariance, extinction and dispersal follows from the processes *a priori* assumed.

Both categories of *a posteriori* and *a priori* methods are capable of deriving general area cladograms consistently (Van Veller *et al.*, 2002). If the methodologies agree in their results, no dilemma arises. However, in case their results differ we prefer the results that are obtained with *a posteriori* methods because this category does not

need *a priori* assumption of the independence of the causal processes (vicariance, extinction and dispersal) for meeting requirement I.

### **The future of *a posteriori* methods**

The research described above leads us to attach a methodological preference to *a posteriori* methods. The two methods in this category, BPA and CCA, code cladogenetic and distributional data of taxa of monophyletic groups in one area-data matrix that they use as input in a parsimony analysis.

Whereas the parsimony analysis in CCA is profitably constrained by the components and cliques that are extracted from the data matrix (Zandee, 1999; Van Veller *et al.*, 2000), BPA uses only a standard (unconstrained) parsimony algorithm as implemented in PAUP (Swofford, 1990) or Hennig86 (Farris, 1988). As a result, BPA sometimes finds more parsimonious (general) area cladograms than CCA, which, however, may contain nodes that are supported only by homoplasious components (*i.e.* reversals or parallelisms). This has already been reported by Van Welzen (1990). If one requires that all nodes in (general) area cladograms are supported by at least one non-homoplasious component, this may count as a reason for choosing the less parsimonious cladograms obtained by constrained parsimony analysis (as in CCA) rather than the more parsimonious cladograms obtained via standard parsimony analysis (as in BPA).

Differences in (general) area cladograms obtained via CCA or BPA are possibly caused by their different coding of the cladogenetic relationships of the taxa distributed over the areas. BPA uses additive binary coding of the inner nodes of the taxon cladogram to obtain an area-data matrix with a separate column for each inner node. By contrast, CCA represents these columns as a single multistate character. The states of this character represent the additive binary codes of the inner nodes of the taxon cladogram, and are treated accordingly during the cladogram optimization. Further research and agreement on the coding and optimization of the inner nodes of taxon cladograms that are used as input in biogeographical analyses with CCA and BPA are expected to make these methods more similar in their results.

Pattern-based methods (the *a posteriori* as well as the *a priori* methods) can be used only to reconstruct divergent patterns. However, areas should be expected not only to break up but also to collide, yielding reticulate patterns (Cracraft, 1988; Craw, 1982,

1983; Hovenkamp, 1997). At present, pattern-based methods are unable to represent such reticulate patterns in (area) cladograms. Future research might result in modifications to *a posteriori* methods (CCA or BPA) to enable them to infer reticulation events and to explain these events in biogeographic scenarios. A way to infer and explain reticulation events has recently been described in Brooks *et al.* (2001) by applying a two-step procedure to an updated BPA.

Comments on pattern-based methods have been provided by Hovenkamp (1997) and Ronquist and Nylin (1990). Hovenkamp criticizes pattern-based methods (such as BPA, TAS, and CA) for their assumption of an analogy between areas (and taxa) in a historical biogeographic analysis and taxa (and characters) in a phylogenetic systematic analysis. He argues not only that the history of areas is rarely exclusively divergent but also that taxa are less reliable indicators for the history of areas because of (putative) dispersal. Though the assumed analogy of these methods in vicariance biogeography might not always hold, this is not a reason to eliminate this analogy *a priori*. In the pattern-based methods, the analogy is a starting point that is tested in the analysis. Whenever the analogy does not hold, alternative explanations are provided. Ronquist and Nylin (1990) discuss four problems with the use of pattern-based (parsimony mapping) methods. First, they state that it is not sufficient to investigate the congruence between the phylogenies of a single host and a single parasite group to test for coevolutionary process models. This practise can be considered analogous to the derivation of an area cladogram from data provided by a single monophyletic group in vicariance biogeography. But, just as in coevolutionary studies, several monophyletic groups are necessary to obtain a general area cladogram. In this general area cladogram, common speciation events for the several monophyletic groups that are triggered by a single (a)biotic event are explained as vicariance events. The absence of taxa of a monophyletic group in any of the areas studied (the problem of missing taxa) is explained *a posteriori* by optimization of its distributional and cladogenetic data on the general area cladogram.

Second, Ronquist and Nylin (1990) discuss the assumption of allopatric cospeciation as the null model in coevolutionary studies. This assumption is analogous to the assumption of vicariance as the null model in vicariance biogeography. It may happen that taxa of a particular monophyletic group failed to speciate when vicariance took place. However, this is not a problem for the methodology of pattern-based methods,

as such methods use data from several monophyletic groups to derive one or more general area cladogram(s). The vicariance event (that did not result in speciation for a particular monophyletic group) is inferred from the general area cladogram when other monophyletic groups speciated as a result of the vicariance event.

The third problem for pattern-based methods that Ronquist and Nylin discuss corresponds to the problem of the interpretation of (general) area cladograms in vicariance biogeography. The *a posteriori* methods CCA and BPA sometimes differ in their results because of their different coding of the cladogenetic relationships of the taxa distributed over the areas. As mentioned above, however, future research is expected to result in greater agreement on coding and optimization of the data and to result in less ambiguous interpretations of the results of CCA or BPA.

Ronquist and Nylin's fourth problem with pattern-based methods corresponds to the treatment of widespread taxa that occur in more than one area. To explain these distributions they need a general method that *a priori* assumes not only vicariance but also dispersal. This idea inspired Ronquist (1996) and Charleston (1996) to develop new methods such as Dispersal-Vicariance Analysis (DIVA: Ronquist, 1996) and Jungles (Charleston, 1996). However, all these methods use *a priori* assigned costs to processes such as vicariance, extinction, dispersal or sympatric speciation in order to arrive at hypotheses that represent histories of areas and process explanations for the distribution of taxa in these areas. Such *a priori* assigned costs make these methods immune to test the relative importance of the different explanatory processes.

Future research might result in a further development of *a posteriori* methods (such as CCA or BPA) that can deal with divergent and reticulate patterns without assigning any costs to particular processes (vicariance, extinction, dispersal or sympatric speciation) *a priori*.

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