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HISTORICAL BIOGEOGRAPHY: Introduction to Methods

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ABSTRACT

The five basic historical biogeographic methods are: dispersalism, phylogenetic biogeography, panbiogeography, cladistic biogeography, and parsimony analysis of endemicity. Dispersalism derives from the traditional concepts of center of origin and dispersal. Bremer's recent cladistic implementation of dispersalism estimates the relative probability that different areas were part of the ancestral distribution of a group. Phylogenetic biogeography applies the rules of progression and deviation to elucidate the history of the geographical distribution of a group. Panbiogeography consists of plotting distributions of different taxa on maps, connecting their distribution areas together with lines called individual tracks, and looking for coincidence among individual tracks to determine generalized tracks. Generalized tracks indicate the preexistence of widespread ancestral biotas, subsequently fragmented by geological or climatic changes. Cladistic biogeography assumes a correspondence between taxonomic relationships and area relationships, where comparisons between area cladograms derived from different taxa allow one to obtain general area cladograms. The most important cladistic biogeographic procedures are: component analysis, Brooks parsimony analysis, three-area statements, and reconciled trees. Parsimony analysis of endemicity (PAE) classifies areas by their shared taxa, analogous to characters, according to the most parsimonious solution. We think the various methods are not mutually-exclusive alternatives, but some of them can be integrated in a single biogeographic approach, with the capability of resolving different problems, such as the recognition of spatial

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homology (panbiogeography), the identification of areas of endemism (PAE), and the formulation of hypotheses about area relationships (cladistic biogeography).

> O God, I could be bounded
> in a nutshell and count myself
> a King of infinite space
>
> *Hamlet,* II, 2

INTRODUCTION

Historical biogeography is going through an extraordinary revolution concerning its foundations, basic concepts, methods, and relationships to other disciplines of comparative biology (35, 36). In the last two decades considerable progress has been due especially to the development of cladistic biogeography (48, 71, 73, 120, 128, 133). Several quantitative methods have been proposed, and software is now available for applying most of them; however, confusion about methods has largely inhibited their application (100). On the other hand, most of the theoretical papers recently published on this subject are partisans of a particular method. For these reasons, we believe a critical review of the historical biogeographic methods available would be useful.

This paper is an introduction to historical biogeographic methods. We explain and illustrate the most frequently used procedures, briefly discuss the theoretical background of each, enumerate representative empirical studies, and provide information about relevant software. We also discuss an approach to integrate most of the methods as part of a single comprehensive analysis.

COMPARATIVE BIOLOGY AND BIOGEOGRAPHY

Metaphors are important components of any scientific paradigm, not only performing an explanatory function by bridging the gap between an abstract system and the real world, but also serving as the basic organizing relation of the paradigm (46). A metaphor created in 1964 by the Italian botanist Léon Croizat (39) suggests the central theme of comparative biology (120). This metaphor views the diversity of life as a historical phenomenon with three dimensions: form, space, and time. (Form in this context refers not only to the structure of organisms, but to all their attributes, be they structural, functional, molecular, or behavioral.)

If it is to allow us to understand the diversity of life, comparative biology must deal with three distinguishable elements: (*a*) similarities and differences in the attributes of organisms, (*b*) the history of organisms in space, and (*c*) the history of organisms in time (120). Biogeography is the discipline of

comparative biology primarily concerned with the history of organisms in space.

Ecological and Historical Biogeography

Candolle (46a) was the first author to distinguish between ecological and historical biogeography. According to him, explanations for the former depend upon "physical causes operating at the present time," and for the latter, upon "causes that no longer exist today." Ecological explanations were early recognized to be insufficient, because areas on different continents with the same ecological conditions can be inhabited by totally different taxa (120).

Myers & Giller (107) view biogeography as distributed along a spatiotemporal gradient. At one end, ecological biogeography is concerned with ecological processes occurring over short temporal and small spatial scales. At the other end, historical biogeography deals with evolutionary processes occurring over millions of years on a large scale. Between the two extremes of ecological and historical biogeography is a compartment concerned with the effects of Pleistocene glaciations. Within each approach, various theories, hypotheses, and models have been proposed, but due to the different interests of the various biogeographic traditions, they have been largely noninteractive.

The division between ecological and historical biogeography reflects the past predominance of narrative rather than analytical methods. Narratives allow authors to cast their explanations in terms of rival beliefs rather than rigorous inferences. When analytical methods are used in biogeography, patterns may prove to be neither wholly historical nor wholly ecological, and testing and reasoning are needed if the effects of the processes causing these patterns are to be distinguished (148). We believe that disciplinary boundaries between ecological and historical biogeography are circumstantial and that they can be fruitfully unified into a single research program (94). Reviewing historical biogeographic methods is a step toward that needed synthesis.

Historical Explanations in Biogeography

Disjunct distribution patterns are the most intriguing problem for biogeographers. Related taxa may show such a pattern: Either their common ancestor originally occurred in one of the areas and later dispersed into the other one, where descendants survive to present day, or their ancestor was originally widespread in greater areas, which became fragmented, and its descendants have survived in the fragments until now. These historical explanations are named, respectively, dispersal and vicariance (119, 120).

In the dispersal explanation, the range of the ancestral population was limited by a barrier, which was crossed by some of its members. If they colonize the new area and remain isolated from the original population, they may eventually differentiate into a new taxon. In the vicariance explanation, the ancestral

population was divided into subpopulations by the development of barriers they cannot cross. In time, the isolated subpopulations may differentiate into different taxa. In the vicariance explanation the appearance of the barrier causes the disjunction, so the barrier cannot be older than the disjunction. In the dispersal explanation the barrier is older than the disjunction.

Any particular distributional pattern, however, may be explained by either a dispersal or a vicariance explanation. Consider for example a taxon with three species (A, B, and C), one each in South America, New Zealand, and Australia (Figure 1a). According to their cladogram, the species from New Zealand is most closely related to the Australian species, and both constitute the sister taxon to the species from South America. Assuming a dispersal explanation (Figure 1b), the ancestor of B + C dispersed from South America to New Zealand, and the ancestor of C (or C itself) migrated from the latter
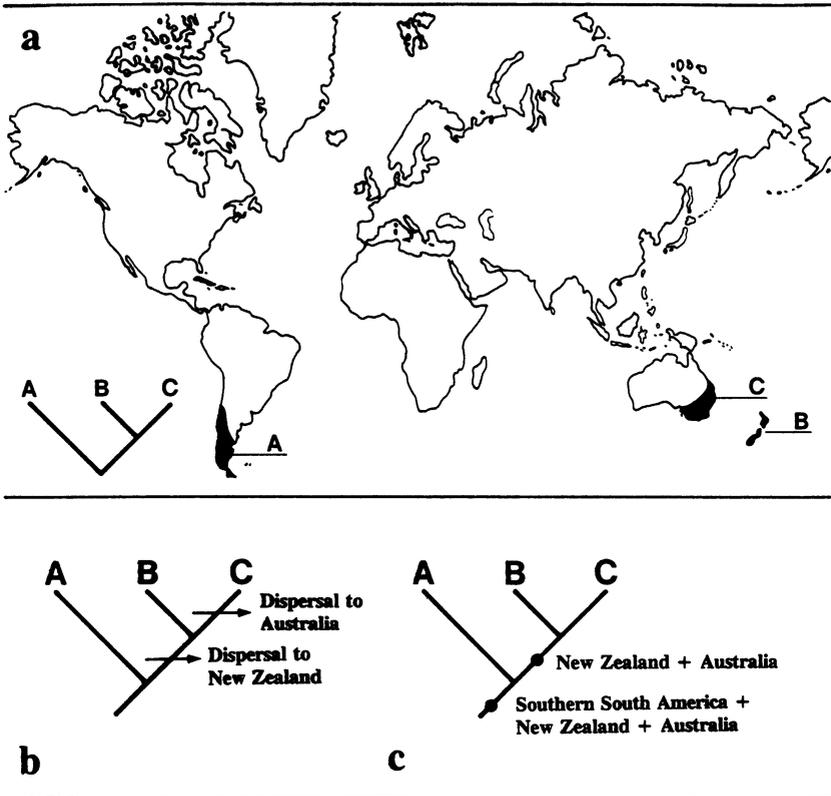
Figure 1   Historical explanations in biogeography. (*a*) geographical distribution and cladogram of three species (A, B, and C); (*b*) dispersal explanation; (*c*) vicariance explanation.

to Australia. (An alternative hypothesis is that the ancestor of B + C dispersed to Australia and the ancestor of B dispersed into New Zealand.) In the vicariance explanation (Figure 1c), the ancestor of the group occurred in South America, Australia, and New Zealand. When South America separated from Australia + New Zealand, A was separated from the ancestor of B + C, and the separation of New Zealand from Australia later caused the disjunction between B and C. Both dispersal and vicariance are natural processes, so neither dispersal nor vicariant explanations can be discounted a priori.

Dispersal was the dominant explanation for centuries, based on strict adherence to the geological concept of earth stability. In the 1950s, Hennig & Brundin (66) proposed phylogenetic biogeography, mainly based on dispersal, but accepting vicariance in some cases. Croizat (38) was one of the first scientists to challenge vocally the dispersal explanation and to promote vicariance as the most important process, in an approach called panbiogeography. In the last two decades, Croizat's and Hennig's ideas were combined, creating cladistic biogeography, which emphasizes the search for congruent biogeographic patterns using cladograms, disregarding both dispersal and vicariance explanations a priori. More recently, BR Rosen (149) proposed another pattern-oriented method—parsimony analysis of endemicity—which uses a cladistic algorithm to analyze geographical patterns of distribution. The taxonomy and a list of representative empirical studies of the current methods available are detailed in Table 1.

DISPERSALISM

In accordance with the biblical account of the Garden of Eden, Linnaeus proposed that species originated through creation in one small area, then dispersed to other areas available for colonization. Since Linnaeus's time, both centers of origin and dispersal have been the prevailing explanations in historical biogeography (120). Darwin (45) and Wallace (163, 164) considered that species originate in one center of origin, from which some individuals subsequently disperse by chance, and then change through natural selection. The Darwin-Wallace tradition has continued until this century; among its most prominent exponents have been Cain (14), Darlington (43, 44), Matthew (85), Mayr (88), Raven & Axelrod (144), and Simpson (160).

Dispersalism is based on five basic principles (170):

1. Higher taxa arise in centers of origin, where subsequent speciation occurs.
2. The center of origin of a taxon may be estimated by specific criteria.
3. The distribution of fossils is essential, because the oldest fossils are probably located near the center of origin.
4. New species evolve and disperse, displacing more primitive species toward

Table 1   A taxonomy of historical biogeographic methods.

Methods	Representative empirical studies
1.0 Dispersalism	14, 43, 44, 88, 144, 160
1.1 Ancestral areas	1, 6
2.0 Phylogenetic biogeography	11, 12, 67, 154
3.0 Panbiogeography	5, 18, 19, 38, 39, 47, 52, 59, 161, 162
3.2 Spanning graphs	—
3.3 Track compatibility	27, 93, 96, 99, 104
4.0 Cladistic biogeography	155
4.1 Reduced area cladogram	68, 69, 136, 152, 153
4.2 Quantitative phylogenetic biogeography	81, 90
4.3 Ancestral species map	2, 84, 170, 174
4.4 Component analysis	3, 6, 7, 17, 20, 21, 34, 72, 78, 81, 82, 96, 103, 120, 126, 157, 165
4.4.1 Component compatibility	46b, 147, 167, 176
4.4.2 Quantification of component analysis	34
4.5 Brooks parsimony analysis (BPA)	9, 21, 29, 34, 62, 76, 83, 86, 103, 172, 173
4.6 Three-area statements (TAS)	79, 95, 103, 105
4.7 Reconciled trees	133
5.0 Parsimony analysis of endemicity (PAE)	22, 29, 99, 103, 106, 149

the peripheral areas, away from the center of origin, where most apomorphic species will be found.

5. Organisms disperse as widely as their abilities and physical conditions of the environment permit, so derived taxa "push" primitive taxa toward the edges of the group's range.

There have been many criticisms of the dispersalist approach (32, 38, 39, 42, 73, 111, 120). Cain (14) evaluated the criteria for determining centers of origin, concluding that none of the criteria could be trusted independently and that some were even contradictory, e.g. the location of the most primitive forms vs. the location of the most advanced ones. Dispersal explanations reside in narrative frameworks, constituting irrefutable hypotheses that do not provide a general theory to explain distributional patterns, but rather individual case stories for each taxon. Panbiogeographers and cladistic biogeographers consider that dispersalism is an ad hoc discipline that requires external causes to explain the patterns analyzed (42, 55, 73, 120, 141). As Nelson (111) stated, concentrating on improbable dispersals as explanations for distributions results in the "science of the rare, the mysterious and the miraculous." In addition, the acceptance of dispersal as the primary causal factor of geographical dis-

tribution creates a methodological problem: If every disjunction is explained in terms of dispersal, biogeographic patterns that result from vicariance will never be discovered. Craw & Weston (32) applied the methodology of scientific research programs, developed by Lakatos (80), to discuss biogeographic approaches, concluding that dispersal biogeography was not a scientific program in Lakatos's sense.

Ancestral Areas

Bremer (6) recently formalized a cladistic procedure based on the dispersalist approach. This author considered that understanding ancestral areas for an individual group is a valid part of the study of the natural history of that group, and that it was the previous approach to search for centers of origin, not the search per se, which was spurious. Bremer's (6) procedure allows one to identify the ancestral area of a group from the topological information of its cladogram. Each area can be considered a binary character with two states (present or absent) and optimized on the cladogram, using Camin-Sokal parsimony. By comparing the numbers of gains and losses, it is possible to estimate areas most likely to have been part of the ancestral areas.

As an example, Bremer (6) considered a cladogram with four hypothetical species distributed in Malaya, Sumatra, Java, and Borneo (Figure 2a). Species *a*, *c*, and *d* are restricted to single areas, whereas *b* is widespread in both Malaya and Java. The simplest assumption implies that the ancestral area is identical to the area being considered, so all absences (equivalent to extinction or fragmentation due to vicariance) are plotted as losses (indicated by crosses in Figure 2b-e). Assuming that there were no losses and that all area presences are the result of gains, the ancestral area is empty, and the individual areas are
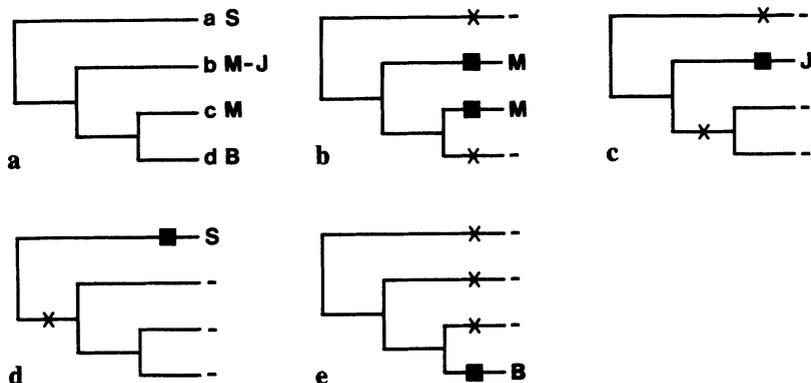
Figure 2 Bremer's ancestral areas approach. *a*, cladogram of four species (*a, b, c,* and *d*) inhabiting Sumatra (S), Malaya (M), Java (J), and Borneo (B); *b-e*, optimizations of the different areas.

plotted as gains (indicated by bars in Figure 2b-e). If there are more losses than gains for any individual area, it is excluded from the ancestral area. If there are more gains than losses, the individual area is identified as the ancestral area. The number of gains for Malaya (Figure 2b) and Sumatra (Figure 2d) equals the number of losses, and the number of losses for Java (Figure 2c) and Borneo (Figure 2e) exceeds the number of gains. Thus the ancestral area may have been limited to Malaya, Sumatra, or both, whereas Java and Borneo are less likely to have been part of the ancestral area for the group.

Ronquist (145) criticized Bremer's preference for Camin-Sokal parsimony instead of Wagner parsimony.

PHYLOGENETIC BIOGEOGRAPHY

Phylogenetic biogeography (11, 12, 66, 67) was the first approach to consider a phylogenetic hypothesis for a given group of organisms as the basis for inferring its biogeographic history. It was defined as the study of the history of monophyletic groups in time and space, taking into account cladogenesis, anagenesis, allopatry (evidence of vicariance), sympatry (evidence of dispersal), and paleogeographical events (12). Phylogenetic biogeography is based on two principles:

1. Closely related species tend to replace each other in space. Higher taxa also can be vicariant but usually show a certain degree of sympatry.
2. If different monophyletic groups show the same biogeographic pattern, they probably share the same biogeographic history. This principle had not been used, since phylogenetic biogeographers concentrated on the history of single groups rather than on congruent distributions shared by different groups inhabiting the same areas (170).

Phylogenetic biogeography applies two basic rules:

1. *Progression rule.* The primitive members of a taxon are found closer to its center of origin than more apomorphic ones, which are found on the periphery. Hennig (67) conceived that speciation was allopatric, involving peripheral isolates, and causally connected to dispersal. Within a continuous range of different species of a monophyletic group, the transformation series of characters run parallel with their progression in space.
2. *Deviation rule.* In any speciation event, an unequal cleavage of the original population is produced, where the species that originates near the margin is apomorphic in relation to its conservative sister species (12).

Although phylogenetic and dispersal biogeography may be lumped into the same approach, because both emphasize centers of origin and dispersal, some authors (73, 170) regard phylogenetic biogeography as an advance over dispersalism because of the explicit use of cladistic hypotheses instead of descrip-

tive enumerations and scenarios. The progression rule is based on the peripheral isolation allopatric mode of speciation, so it cannot be applied when other modes of speciation are considered, because it is rejectable a priori (110). In addition, interpreting cladograms as phylogenetic trees rather than synapomorphy schemes requires ad hoc assumptions not fully justified by the information on which they are based (73).

PANBIOGEOGRAPHY

In contrast to the two previous methods, which focus on dispersal, Léon Croizat postulated that "earth and life evolve together," meaning that geographic barriers evolve together with biotas—essentially vicariance. From this metaphor grew up the concept of panbiogeography (37–40, 55, 57, 60, 127). Croizat's method was basically to plot distributions of organisms on maps and connect the disjunct distribution areas or collection localities together with lines called tracks. Individual tracks for unrelated groups of organisms were then superimposed, and if they coincided, the resulting summary lines were considered generalized tracks. Generalized tracks indicate the preexistence of ancestral biotas, which subsequently become fragmented by tectonic and/or climatic change.

There are three basic panbiogeographic concepts:

INDIVIDUAL TRACK   A track represents the spatial coordinates of a species or group of related species, and operationally is a line graph drawn on a map of their localities or distribution areas, connected according to their geographical proximity (23, 25–27, 38, 42, 60). In graph theory, a track is equivalent to a minimal spanning tree, which connects all localities to obtain the smallest possible link length (123). After the track is constructed, its orientation (i.e. rooting) can be determined using one or more of the following three criteria:

1. *Baseline* Features such as the crossing of an ocean or sea basin, or a major tectonic structure (25, 27, 28, 31).
2. *Main massing* A concentration of numerical, genetical or morphological diversity within a taxon in a given area (25–28, 30, 123).
3. *Phylogeny* If cladistic information is available, it can be used to direct the track from the most primitive to the most derived taxa (123).

GENERALIZED TRACK   Coinciding individual tracks for unrelated taxa or groups constitute a generalized or standard track (23, 28, 123), which provides a spatial criterion for biogeographic homology (56).

NODE   The area where two or more generalized tracks intersect (24, 25, 27, 60, 112, 123). It means that different ancestral biotic and geological fragments interrelate in space/time, as a consequence of terrain collision, docking, or suturing, thus constituting a composite area.
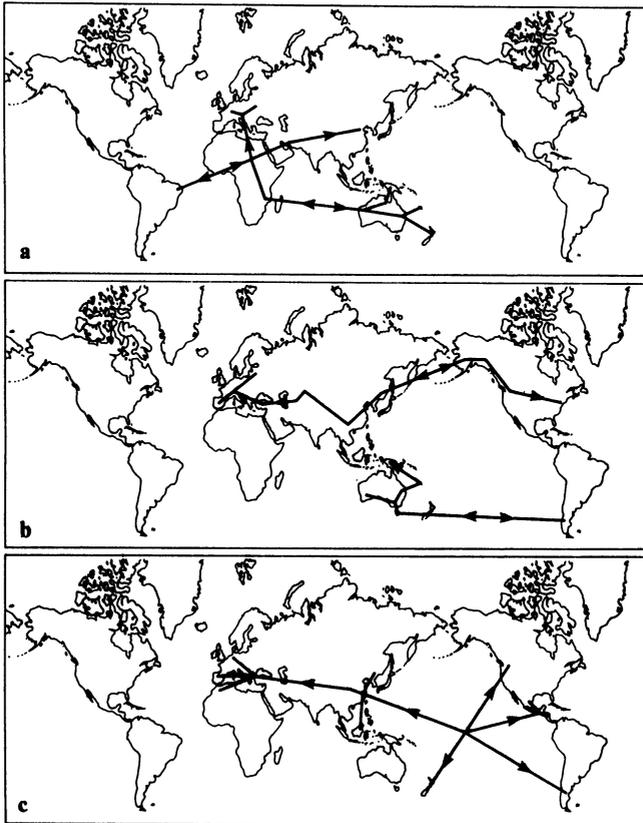
Figure 3 Individual tracks. (*a*) ratite birds; (*b*) *Nothofagus* (southern Hemisphere) and *Fagus* (northern Hemisphere); (*c*) *Leiopelma* and related taxa.

The panbiogeographic approach may be exemplified by analyzing three Austral taxa (26, 38, 56): the ratite birds (Figure 3a), the southern beeches (*Nothofagus*; Figure 3b), and the frog *Leiopelma* (Figure 3c). Their individual tracks show that these taxa do not share spatial homology. Only the Ratites are clearly Gondwanic, having their distribution oriented by the Atlantic and Indian Ocean basins. In spite of partial sympatry in Australia and southern South America, only *Leiopelma* and *Nothofagus* are geographically homologous, belonging to the same ancestral biota, which is different from that of the Ratites. This result contrasts with biogeographic studies in which Ratites and *Nothofagus* have been assumed a priori to belong to the same ancestral biota (68, 69, 136).

The last two decades have shown an intensification of the debate between proponents of panbiogeography and those of cladistic biogeography (24, 25,

27, 32, 35, 41, 74, 87, 101, 123, 130, 143, 156). The panbiogeographic approach has been subject to several criticisms. In many instances, panbiogeographers use systematic treatments in an uncritical way (136, 156). Main massings have been considered similar to centers of origin (74, 143). Platnick & Nelson (143) rejected the use of geographical proximity for drawing tracks, because they considered cladistic information a prerequisite to any historical biogeographic analysis.

Track Compatibility

Craw (27, 28, 29) developed a quantitative panbiogeographic procedure, which treats tracks as characters of the areas analyzed. Matrices of areas × tracks are then analyzed for track compatibility in a way analogous to character compatibility (89). Two or more individual tracks are regarded as compatible with each other if they are either included within, or replicated by, one another. (Panbiogeography uses the concept of compatibility in a restricted way, because nonoverlapping tracks are incompatible, although they would be compatible under the original concept.)

In the example of Figure 4, there are four individual tracks (A, B, C, and D; Figure 4a–d). The matrix of areas × tracks (Figure 4e), analyzed with a compatibility algorithm, produces a generalized track (Figure 4f) based on tracks A, B, and D, with C incompatible with them. For a track compatibility analysis, the *CLIQUE* computer program of *PHYLIP* package (all types of PCs; 51) can be used.

An alternative quantitative panbiogeographic procedure was proposed by Page (123), based on graph theory; however, it has not been yet applied to real data.

CLADISTIC BIOGEOGRAPHY

Cladistic biogeography was originally developed by DE Rosen, G Nelson, and N Platnick, (108–112, 119–121, 143, 151). Cladistic biogeography assumes that the correspondence between taxonomic relationships and area relationships is biogeographically informative. Comparisons between area cladograms derived from different plant and animal taxa that occur in a certain region allow general patterns to be elucidated (73, 124). A cladistic biogeographic analysis comprises two steps (Figure 5): the construction of area cladograms from different taxon cladograms, and the derivation of general area cladogram(s).

Construction of Area Cladograms

Area cladograms are constructed by replacing the names of terminal taxa with the names of the areas in which they occur. The construction of area
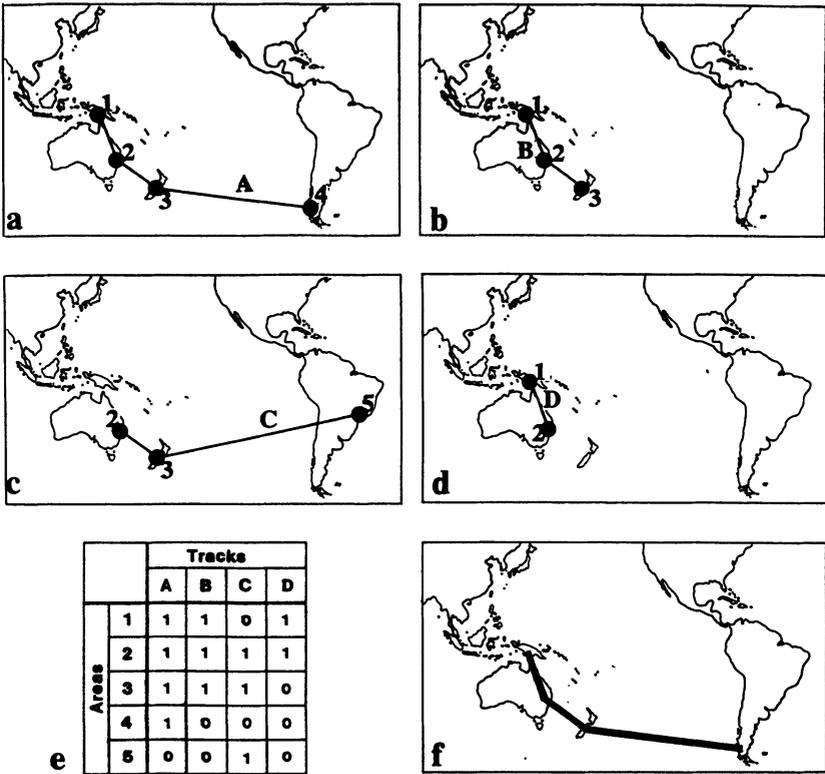
Figure 4   Track compatibility analysis. (a–d), individual tracks; (e), areas × species matrix; (f), generalized track.

cladograms is trivial if every taxon is endemic to a unique area and every area harbors one taxon, but it is complicated for taxon cladograms including widespread taxa (taxa present in more than one area), missing areas (areas absent in a cladogram), and redundant distributions (areas with more than one taxon). In these cases, area cladograms must be converted into resolved area cladograms, by applying assumptions 1 and 2 (120) and assumption 0 (176).

Figure 6 shows the treatment of a widespread taxon under the three assumptions. Under *Assumption 0*, widespread taxa become synapomorphies of the areas inhabited by them, so that the area relationships are considered to be monophyletic (sister areas). *Assumption 1* allows the area relationships to be mono- or paraphyletic in terms of the widespread taxon inhabiting them. Under *assumption 2* each occurrence is treated separately and can "float" on the
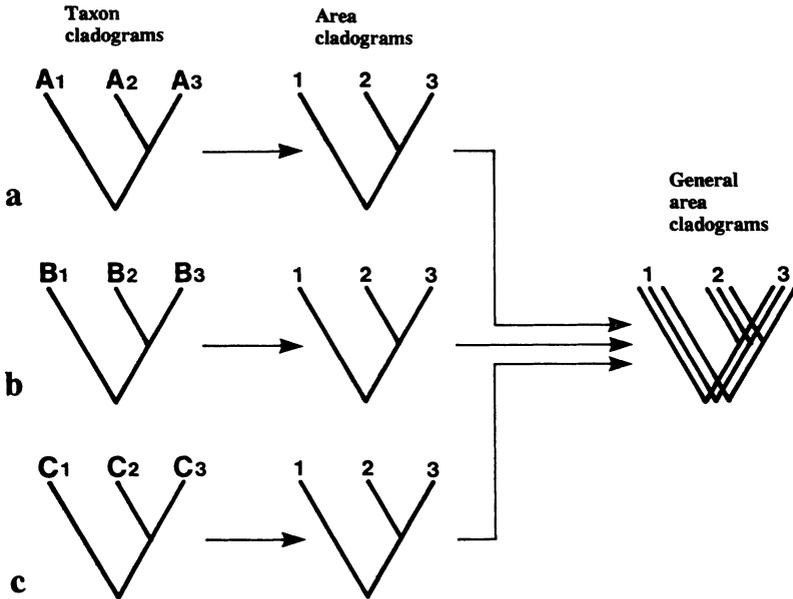
Figure 5 Steps of a cladistic biogeographic analysis: construction of area cladograms and derivation of a general area cladogram.

resolved area cladograms, so the area relationships can be mono-, para-, or polyphyletic. Missing areas are treated as uninformative under assumptions 1 and 2, and as primitively absent under assumption 0. Regarding redundant distributions, assumptions 0 and 1 consider that if two taxa are present in the same area, their occurrences are both valid, whereas under assumption 2, each occurrence of a redundant distribution is considered separately (e.g. in different resolved area cladograms). Assumptions are not mutually exclusive, so different assumptions can be combined to treat the different problems, such as treating widespread taxa under assumption 2 but redundant distributions under assumption 0 (128).

Authors generally prefer assumption 2 (70, 73, 100, 120, 128). Its implementation, however, can produce many resolved area cladograms in complex data sets (17, 36). Nelson & Ladiges (116) considered current implementations of assumption 2 to be deficient because it can obscure possibly real complexity. They suggested that the set of assumption 2 area cladograms could be further resolved by evaluating nodes in terms of three-area statements analysis, reducing widespread ranges in favor of endemics. A possible approach to minimize the impact of both widespread and redundant ranges might be to remove redundant, widespread distributions before analysis (98, 100).
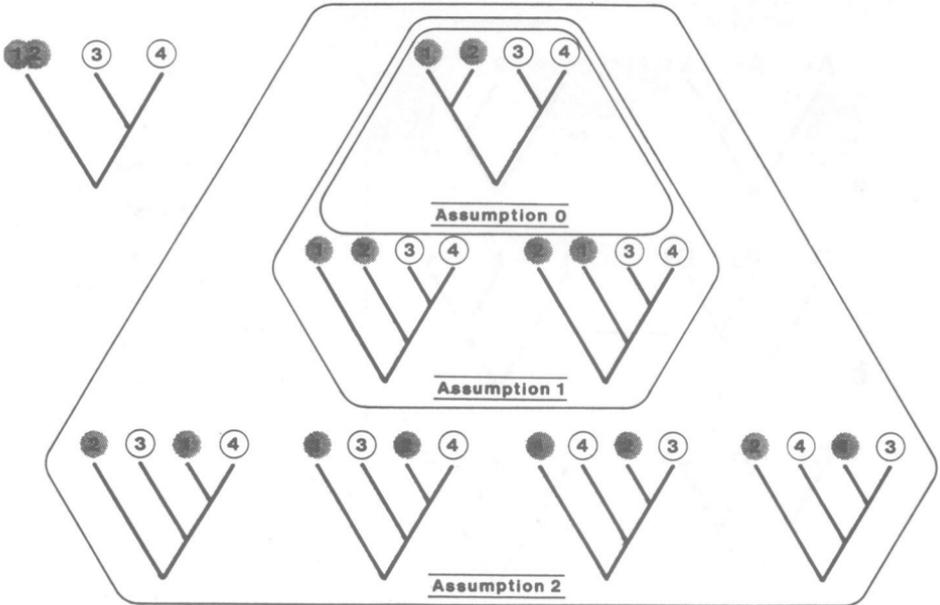
Figure 6 Cladogram with a widespread taxon in areas 1 and 2, and application of assumptions 0, 1, and 2 to produce resolved area cladograms.

Derivation of General Area Cladogram(s)

Based on the information in either the area cladograms or the resolved area cladograms, general area cladograms are derived. The main procedures for deriving general area cladograms are: component analysis (113, 120, 124), Brooks parsimony analysis (9, 171–173), three-area statements (114–116), and reconciled trees (133). Three other procedures are currently not applied: the reduced area cladogram (152, 153), quantitative phylogenetic biogeography (90), and the ancestral species map (169, 170).

Component Analysis

Component analysis (71–73, 113, 120, 124, 126, 128, 137, 176) derives sets of fully resolved area cladograms from the taxon cladograms under analysis, applying assumptions 0, 1, and 2. The general area cladogram is derived by the intersection of the sets of area cladograms for the taxa analyzed (113, 126). If no general area cladogram is found through intersection, or the intersect contains multiple cladograms, a consensus tree can be constructed (124). In Figure 7, application of assumption 2 produces 11 area cladograms for a taxon cladogram with a widespread taxon (Figure 7a), two area cladograms for a
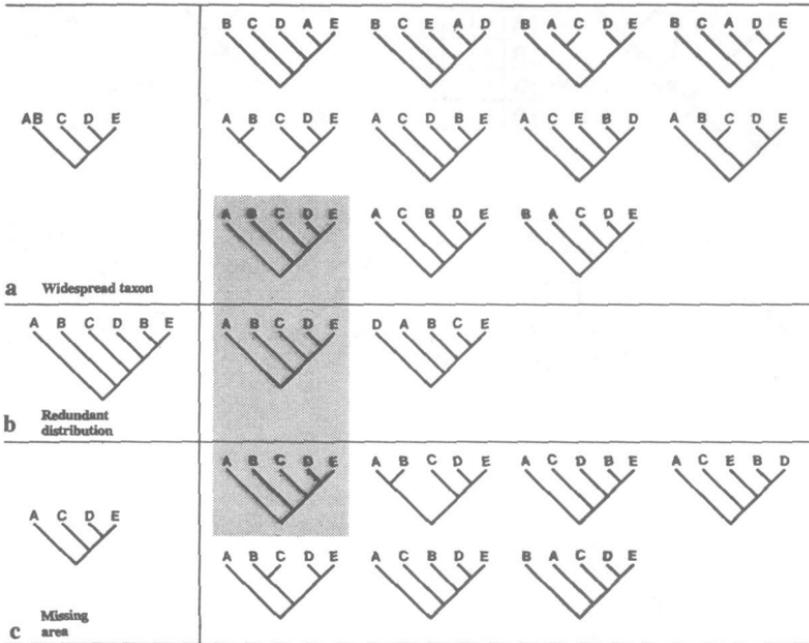
Figure 7 Application of component analysis under assumption 2: (*a*) area cladogram with a widespread taxon; (*b*) area cladogram with a redundant distribution; (*c*) area cladogram with a missing area. Intersection of the three sets of resolved area cladograms (indicated by shading) includes the general area cladogram.

taxon cladogram with a redundant distribution (Figure 7b), and seven area cladograms for a taxon cladogram with a missing area (Figure 7c). Their intersection leads to a single general area cladogram (indicated by shading). There is one software package available for applying component analysis: *COMPONENT,* version 1.5 (MS-DOS, IBM compatible; 125).

Further variations of component analysis consist of constructing a data matrix of components by areas, based on the area cladograms, and analyzing it with a compatibility algorithm (176) or with a Wagner parsimony algorithm (72). The former procedure is implemented in software CAFCA (all types of PCs; 175).

Wiley (171–173) criticized component analysis because of the preference for assumptions 1 and 2 instead of assumption 0, which he considered most parsimonious. Some authors (162b, 171, 173, 176) criticized the use of consensus techniques to obtain a general area cladogram. Page (126) argued that linking component analysis and consensus techniques is misleading, because it confounds the construction of area cladograms with the comparison of area
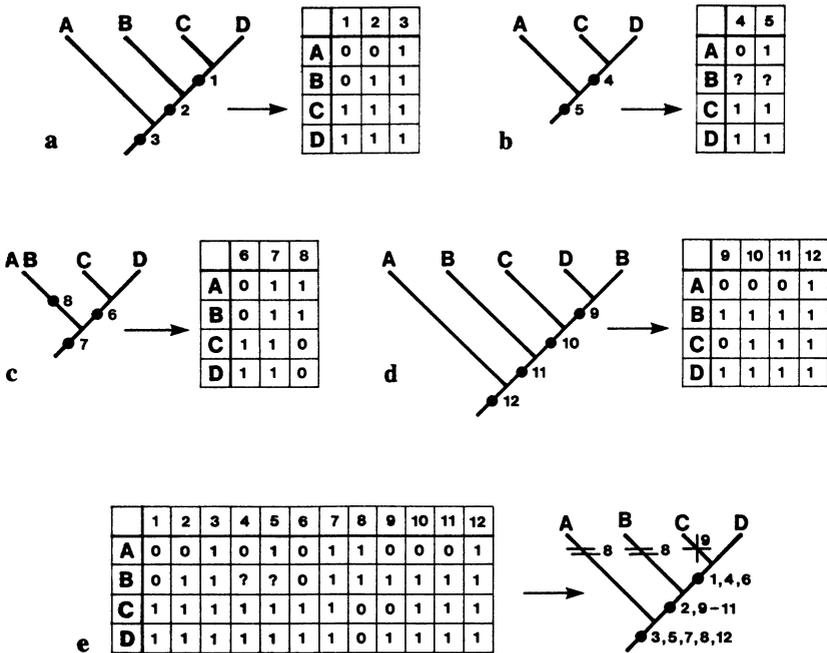
Figure 8   Brooks parsimony analysis. (*a*) area cladogram with complete data; (*b*) area cladogram with a missing area; (*c*) area cladogram with a widespread taxon; (*d*) area cladogram with a redundant distribution; (*e*) resulting data matrix (areas × components) and general area cladogram obtained after Wagner parsimony analysis.

cladograms. Clear justification of component analysis is provided by Page (124, 126, 128), Platnick (138), and Platnick & Nelson (142).

Brooks Parsimony Analysis

Brooks parsimony analysis (BPA) was proposed by Wiley (171, 172, 173), based on the ideas originally developed by Brooks (8, 9) for historical ecology. It is a Wagner parsimony analysis of area cladograms, which are coded and analyzed as characters. BPA is based on assumption 0, differing only in treating missing areas as uninformative rather than as primitively absent.

BPA uses an area × taxon matrix, produced by binary coding of the terminal taxa and their hypothetical ancestors. Four examples of data coding are shown in Figure 8: 1) a group with complete data (Figure 8a); 2) an example in which a member of the group is missing in one area (B in Figure 8b); 3) an example with a widespread taxon (present in areas A and B; Figure 8c); and 4) a

redundant distribution (two taxa in area B; Figure 8d). In each case, the corresponding data matrix is also figured. All the information is combined in a single data matrix (Figure 8e), which, after applying Wagner parsimony analysis, results in a general area cladogram.

For applying BPA, an appropriate Wagner parsimony program like Hennig86 (MS-DOS, IBM compatible; 50) may be used. Kluge (76) presented a modification of Brooks parsimony analysis, which differs in the treatment of widespread taxa, which are considered irrelevant and so are coded as missing data, and in a weighting procedure for redundant distributions.

There has been extensive criticism of BPA (16, 115, 128, 133, 138, 146, 162b). According to Carpenter (16), the codings used in BPA to represent the taxon cladograms are not independent, and this can lead to bizarre results. The application of parsimony in biogeography has yet to be precisely defined and convincingly justified (77).

Three-Area Statements

Three-area statements (TAS) (114–116) code distributional data for area cladograms as a suite of three-item statements (117, 122), and the output is a data matrix for Wagner parsimony analysis. The data matrix can be obtained with the TAS program (MS-DOS, IBM compatible; 116), implemented for assumptions 0 and 1. Assumption 2 can be applied by prior manipulation of the data set (79, 116) or with the TASS program (MS-DOS, IBM compatible; 118). The matrix produced with TAS may then be analyzed with Hennig86 (50). Figure 9 shows the application of TAS to the same example used for BPA, with the corresponding three-area statements matrices, and the resulting general area cladogram.

The three-item statements approach has been criticized (77) mainly for its taxonomic applications. Some of these criticisms, e.g. the addition of missing data where none existed, which added ambiguity, may be also applied to TAS.

Reconciled Trees

The concept of reconciled trees arose independently in molecular systematics, parasitology, and biogeography as a means of describing historical associations between genes and organisms (53), hosts and parasites (91), and organisms and areas (128, 129, 132, 133). Page (133) proposed a cladistic biogeographic procedure that maximizes the amount of codivergence (shared history) among different area cladograms, which implies minimizing losses (i.e. extinctions or unsampled taxa) and duplications (i.e. speciation events independent of the vicariance of the areas) when combining different area cladograms into a single general area cladogram. Horizontal transfer (i.e. dispersal) should be also minimized, but that is not considered in the procedure. Page (134) describes a procedure to incorporate dispersal.
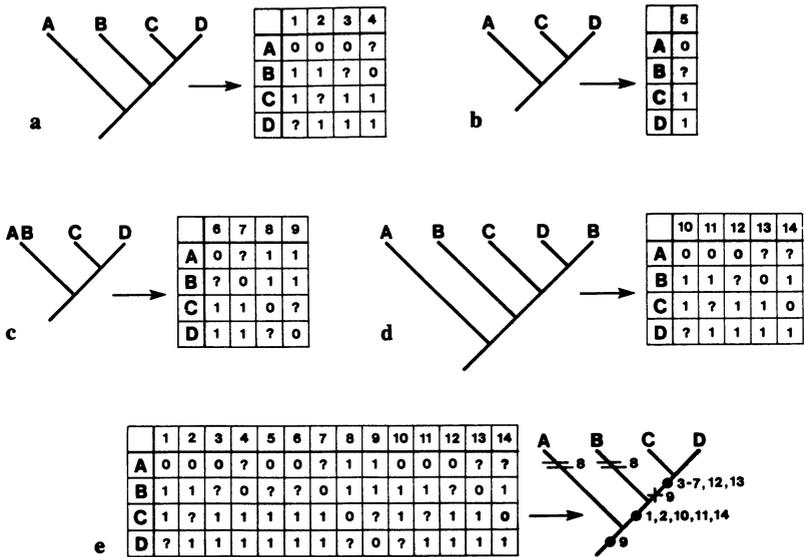
Figure 9 Three-area statements. (a) area cladogram with complete data; (b) area cladogram with a missing area; (c) area cladogram with a widespread taxon; (d) area cladogram with a redundant distribution; (e) resulting data matrix (area × three-area statements) and general area cladogram obtained after Wagner parsimony analysis.

Figure 10a shows a simple example of a reconciled tree between an area cladogram and its general area cladogram, where there is a maximum of codivergence. Figure 10b shows a more complex example of a similar situation, where a duplication (node f in the area cladogram) is needed to reconcile both trees. In biogeography there is often no host tree (general area cladogram) to reconcile with the associate (area cladogram). In that case we must search for the general area cladogram with maximal codivergence to the area cladograms.

Algorithms for obtaining reconciled trees are implemented in *COMPO-NENT* version 2.0 (Microsoft-Windows, IBM-compatible; 131). In order to identify the taxa that may have dispersed, each taxon can be deleted in turn and a reconciled tree computed for the remaining taxa. Those taxa whose deletion greatly increases congruence between area cladograms and taxon cladograms are likely to have dispersed (133).

Page (133) considered assumptions 0, 1, and 2 to suffer from the limitation that they simply follow an algorithm rather than optimizing an optimality criterion, which makes it impossible to find the general area cladogram that is optimal for two or more area cladograms. According to him the reconciled
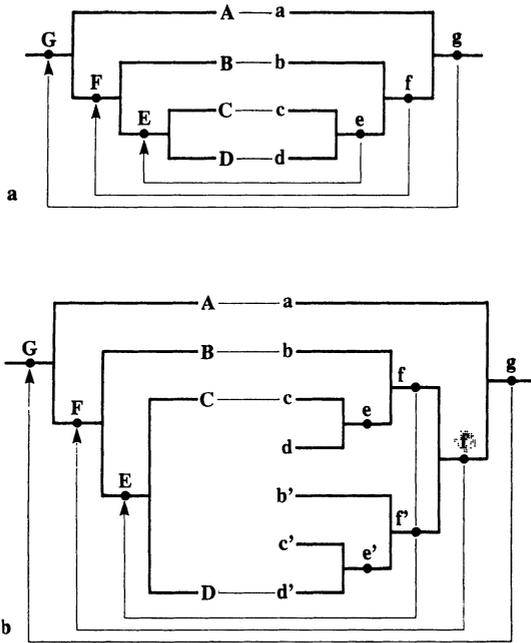
Figure 10 Reconciled trees. (*a*) between an area cladogram and its general area cladogram; (*b*) more complex example where a duplication is needed to reconcile both trees. Left, general area cladograms; right, area cladograms.

trees approach has an optimality criterion (i.e. maximize codivergence for all the area cladograms).

PARSIMONY ANALYSIS OF ENDEMICITY

Parsimony analysis of endemicity (PAE; 149, 150) classifies areas or localities (analogous to taxa) by their shared taxa (analogous to characters) according to the most parsimonious solution. PAE data consist of area × taxa matrices, and PAE cladograms represent nested sets of areas, in which terminal dichotomies represent two areas between which the most recent biotic interchange has occurred.

This method was originally proposed in a paleontological context, with cladograms based upon data collected from successively older geological horizons, and older interchange events in one horizon were assumed to be corroborated by the younger events in the next. With a poor fossil record or when treating only extant distributions, PAE is carried out on the data from a

single time plane, using different taxonomic levels. This allows an interpretation of the history of space occupancy by taxa through time, assuming that subsequent dispersal has not obliterated the vicariant pattern, and that extinctions are random.

The main criticism of PAE is that it ignores cladistic relationships among taxa, considering only their distributions (70). Some authors (22, 99, 106) incorporate cladistic information to PAE, by adding supraspecific natural groups (containing two or more species) to the matrix.

DIFFERENT METHODS OR DIFFERENT PROBLEMS?

All the historical biogeographic methods discussed were originally proposed as alternatives. We believe, however, that most can be integrated into a single approach. Dispersalism and phylogenetic biogeography are excluded from this discussion because they mainly explain histories of single taxa instead of seeking replicated patterns. This integrative approach consists of using each method in a different step of one analysis, restricting its use to a specific problem. A historical biogeographic analysis should include at least three steps: recognition of spatial homology, identification of areas of endemism, and formulation of hypotheses about area relationships.

1. Recognition of spatial homology   The first step should consist of determining if the plant and animal taxa analyzed belong to the same biota. A panbiogeographic procedure could be employed (36, 61, 96, 98, 101) to find generalized tracks, which represent ancestral biotas and spatial homologies (56). Each generalized track then should be analyzed separately, thus avoiding the extreme incongruent patterns that result from mixing different ancestral biotas in the same analysis.

2. Identification of areas of endemism   Once biogeographic homologies have been recognized, we must identify the units of study. An area of endemism is defined by the congruent distributional boundaries of two or more species, where "congruent" does not demand complete agreement on those limits at all possible scales of mapping but does require relatively extensive sympatry (139).

Several authors have recently discussed the determination of areas of endemism (4, 33, 63, 65, 139). Morrone (97) proposed the use of PAE to identify areas of endemism, by using quadrats as operational units, and employing the sets of quadrats as a basis for choosing the species to be mapped. After drawing quadrats on a map of the region to be analyzed (Figure 11a), a data matrix $r \times c$ is constructed, where r (rows) represent the quadrats and c (columns) the species. An entry is 1 if a species is present and 0 if it is absent (Figure 11b).

The data matrix table (b) showing:

		Species				
		1	2	3	.	n
Quadrats	1	1	0	0	.	1
	2	1	0	0	.	1
	3	1	1	0	.	1
	.	.	.	.	.	.
	15	0	0	1	.	0
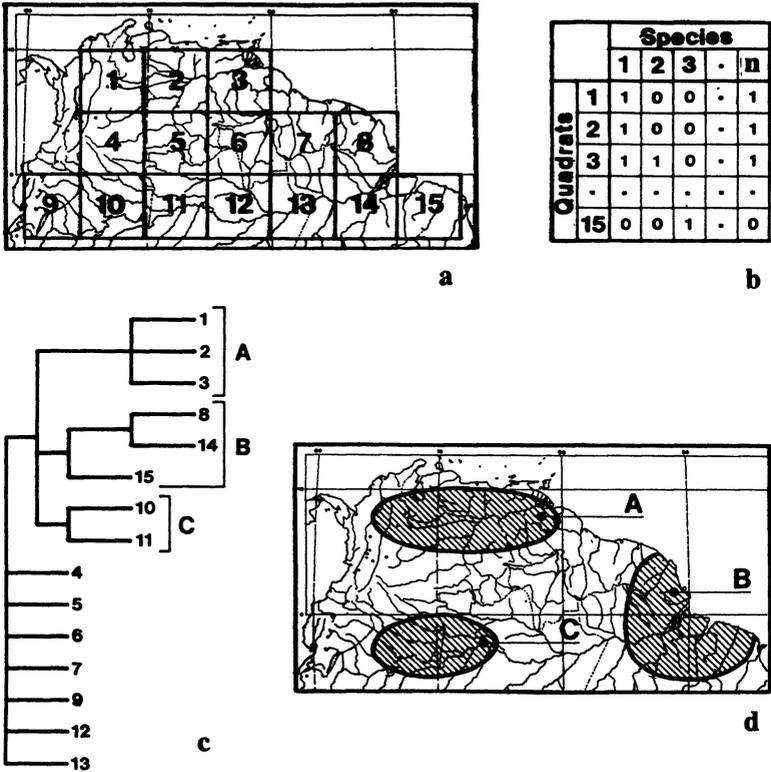
Figure 11   Use of parsimony analysis of endemicity to identify areas of endemism. (*a*) map of northern South America showing 15 quadrats; (*b*) *data matrix of species by quadrats;* (*c*) cladogram of the quadrats obtained applying Wagner parsimony; (*d*), areas of endemism based on the groups of the cladogram.

Application of Wagner parsimony analysis to the data matrix produces a cladogram (Figure 11c). Species endemic to each group of quadrats (defined by at least two species) are mapped, to delineate the boundaries of each area (Figure 11d).

3. Formulation of hypotheses about area relationships   Page & Lydeard (135) have suggested three criteria to choose taxa for this step: maximizing endemicity, sampling exhaustively within each clade, and including as many relevant areas as possible. The cladistic analysis of these taxa should then be carried out. Once we have the taxon cladograms, the four reviewed procedures (component analysis, Brooks parsimony analysis, three-area statements, and

reconciled trees) can be applied to obtain the area cladograms and general area cladograms.

A GLIMPSE INTO THE FUTURE

We have reviewed the current analytical methods in historical biogeography. But the most important question has as yet gone unanswered: Which is the best method? The answer is not clear. In fact, despite their various shortcomings, each method makes a contribution in addressing a different type of biogeographical question. An integrative approach, like that proposed here, can take advantage of the merits of each method. One clear conclusion, however, is that the basic language of historical biogeography will be area cladograms, which allow the testing of hypotheses of general patterns (90, 119, 135).

To search for an optimal cladistic biogeographic procedure, Morrone & Carpenter (100) compared the application of component analysis, Brooks parsimony analysis, three-area statements, and reconciled trees to different data sets, mapping the area cladograms onto the general area cladograms (produced by the four procedures) and calculating the items of error (i.e. number of nodes added to the general area cladograms in order to explain the area cladograms). They also applied two accessory criteria: the number of cladograms produced and their degree of resolution. They found that none of the procedures was consistently superior. The lack of a consistent superiority of one of the procedures is caused by the influence of different sources of ambiguity (differentially present in the data sets), which seem to affect distinctively the alternative procedures. Primary sources of ambiguity are dispersal (100) and speciation events independent of the vicariance of the areas (that lead to multiple lineages), combined with extinction and unsampled taxa (129). For example, BPA is more affected by dispersal than is component analysis, whereas the latter is more affected by multiple lineages. Nelson & Ladiges (116) recommend treating clades having the same areas separately to avoid the ambiguity due to multiple lineages, but this might not generally resolve all area relationships, particularly when multiple lineages are combined with many widespread taxa.

Some statistical tests of biogeographical hypotheses have been proposed. Craw (27) formalized a test for assessing the significance of generalized tracks obtained by a track compatibility analysis. In cladistic biogeography, several tests have been proposed to determine if the agreement between area cladograms is greater than expected due to chance alone (10, 128, 129, 158, 159). The use of these tests has been criticized, based on problems with the definition of "chance" (see Farris [49]). Testing of the timing of biogeographic events using molecular divergence, based on molecular clocks, has been proposed by

RDM Page (129). Although most biologists now accept a broad correlation between the amount of molecular divergence (at least for proteins and DNA) and time, it is far from established that rates are constant (92). Therefore, the utility of molecular clocks in biogeography is, at this point, debatable.

The following represents a nonexhaustive list of critical issues in biogeography that need to be tackled:

1. Areas can have more than one history, in contrast with systematics where organisms have a single history (21, 34). This situation leads to complex and conflicting patterns of area relationships that represent obstacles to their discovery.
2. The origin of biogeographic patterns is never wholly historical nor wholly ecological (54, 94), but a combination of both, which is an obstacle for the progress of biogeography. Because biogeographic patterns reflect this complex origin, analysis of those patterns requires a combination of approaches.
3. The scarcity of high quality data hampers the development of historical biogeography (138; RDM Page, personal communication).
4. The progress of cladistic biogeography will depend heavily on the development of a procedure (or the improvement of one already proposed) that takes fully into account all the complexities of real data, like dispersal, multiple lineages, and extinction (100).
5. The molecular revolution is starting to influence biogeography (13, 64). More empirical studies are strongly needed to establish the promising connection between molecular systematics and biogeography (e.g. molecular clocks).
6. A critical evaluation is needed of the tests for assessing the significance of biogeographic hypotheses or the development of new ones, like those proposed in systematics (75).
7. Geological area cladograms derived from specific analyses of geological characters, in the same way that characters are analyzed in systematics (27), would be useful to allow comparisons with general area cladograms (100).
8. It has been recently suggested that the biodiversity question is really a biogeographic one, since it is a question of where the limited financial and human resources should be applied (140). Historical biogeographic analyses, however, are not playing the significant role in biodiversity conservation that they should (58, 61, 102, 105).

Prospects for research in biogeography are by no means hopeless, and the field for developing a new biogeographic synthesis is wide open. Anyone entering this field should be able to combine a feeling of intellectual adventure with imagination and a knowledge of tradition. New challenges will have to be faced, some biogeographic problems will have to be rethought, and new

methods will have to be developed. In the next few years, biogeographers will witness, not without *horror vacui,* this fascinating perspective.

ACKNOWLEDGMENTS

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