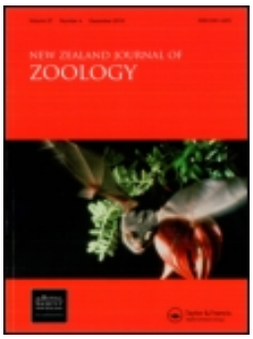

New Zealand Journal of Zoology

ISSN: 0301-4223 (Print) 1175-8821 (Online) Journal homepage: https://www.tandfonline.com/loi/tnzz20

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To cite this article: Robin Craw (1989) Quantitative panbiogeography: Introduction to methods, New Zealand Journal of Zoology, 16:4, 485-494, DOI: 10.1080/03014223.1989.10422917

To link to this article: https://doi.org/10.1080/03014223.1989.10422917

Published online: 06 Jan 2012.

New Zealand Journal of Zoology, 1989, Vol. 16: 485–494
0301–4223/89/1604–0485–$2.50/0

Quantitative panbiogeography: introduction to methods

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Abstract Quantitative track and area cladogram methods based on Croizat's panbiogeographic method are reviewed. A new quantitative track method based on clique and compatibility aspects of graph theory is outlined. These methods allow for statistical hypothesis testing in historical biogeography studies. A glossary is included.

Keywords biogeography; cladistics; graph theory; panbiogeography; vicariance

"The track is essentially a graph drawn to render visible and comparable the results of biogeographic investigation . . . ."
Croizat (1982: 300)

INTRODUCTION

Mapping biogeographic graphs or tracks (i.e., lines on distribution maps of taxa) is one way to reduce the complexity of these maps and to capture analytically any pattern/structure that there may be in the initial data. For spatial analysis of geographic distribution data graphical techniques, a vocabulary and a set of symbols are required.

Leon Croizat's panbiogeography (1958, 1964) was a pioneering attempt to explore the potential of graphical approaches to biogeographic analysis. Croizat's method was to plot distributions of organisms on maps and connect the disjunct distribution areas or collection localities together with lines he called tracks. Individual tracks for unrelated groups of organisms were then superimposed and if they coincided the resulting summary line was termed a generalised or standard track. A generalised track was interpreted by Croizat as indicating the preexistence of an ancestral biota that had subsequently become fragmented by tectonic and/or climatic change.

Although Croizat frequently alluded to a quantitative, statistical basis for his panbiogeographic method this was never demonstrated by him in any explicit, formal sense. Recent work in New Zealand has provided one approach to a repeatable, mathematical basis for track analysis (Page 1987) and a new attempt at quantification of panbiogeography is presented in this paper. Another approach to quantification of track analyses is known as cladistic biogeography (Humphries & Parenti 1986). This approach unites aspects of Croizat's track concept with Hennig's phylogenic systematics and allows for production of area cladograms (i.e., branching diagrams of area relationships). Panbiogeographic track methods use all four of Croizat's key concepts of track, baseline, node and main massing (see glossary for definitions); area cladogram methods have incorporated only the track concept.

Methods derived from Croizat's and Hennig's approaches find their mathematical basis in graph theory (Penny 1982; Page 1987). Interesting discussions on the use of graph theory in geographical spatial analysis, particularly with respect to the problem of reducing mapped data to lines, can be found in Unwin (1981) and Gatrell (1983).

STATISTICAL HYPOTHESIS TESTING

The development of methods for statistical testing of hypotheses in historical biogeography is needed for two reasons. Firstly, a statistical basis needs to be demonstrated in order to bring the discipline up to the scientific standards that apply in ecological

Received 15 October 1988; accepted 7 September 1989

biogeography (e.g., Birks 1987). Secondly, we need to know how much similarity between tracks or area cladograms is significant. Methods are thus required that demonstrate "how unlikely an observed degree of similarity would be if there were no common explanation . . . for a set of distributions" or "what degree of dissimilarity would cause [us] to reject a hypothesis" (Simberloff 1987a: 451). To do this there must be a stated null hypothesis with criteria for rejection incorporated into empirical biogeographic studies. One appropriate null hypothesis for biogeographic studies is a "random, individual dispersal hypothesis" for all taxa (Simberloff et al. 1981).

The use of conventional statistical tests is inappropriate in historical biogeography because the available data do not meet the assumptions of those tests. Thus randomisation tests are used instead of conventional statistics (Pagel & Harvey 1988).

TRACK METHODS

Spanning graphs

Spanning tree track graphs are the simplest and most easily applied method for the analysis of distribution maps. A track is a line graph drawn on a map of the geographic distribution of a particular taxon (e.g., a species, species group, genus, or family) that connects the disjunct collection localities, or distributional areas of that taxon, or the subordinate taxa belonging to the taxon. The simplest way to construct such a graph is to form a minimal spanning tree, i.e., an acyclic graph that connects all localities/distributional areas occupied by a taxon, so that the sum of link lengths connecting each locality/distributional area is the smallest possible. For n localities the line graph connecting them will consist of $n-1$ links. Next a hypothesis of the baseline (diagnostic character) is proposed for each track depending on the particular ocean or sea basins, or major tectonic feature that the track crosses or circumscribes (Fig. 1) (Craw 1983, 1988; Page 1987; Craw & Page 1988).

Tracks for many groups can be constructed on the above basis, but more complex patterns of geographic distribution may require the use of additional biogeographic and/or phylogenetic criteria. Some of these aspects of track construction are shown in Fig. 2. Graphs represented in matrix form allow for the development of spanning tree track analysis into a quantitative biogeographic method. The simplest type of matrix applicable to track analysis is the connection (or adjacency) matrix. Connection matrices are $n \times n$ matrices where n is the number of points (i.e., localities or distribution areas) in the graphs. Two types of connection matrices for the tracks in Fig. 2 are shown in Fig. 3. Connection matrices allow for quantitative comparisons of tracks for a number of different taxonomic groups and also for the calculation of nodal values for each locality/distribution area.

Summary of spanning tree track method

Step 1. For the animal or plant taxon/taxa under biogeographic analysis construct the track/s by either:
(1) Connecting the collection localities/distribution areas using a minimal spanning graph. For taxa differentiated into distinct entities a minimal spanning tree is constructed for each entity; the separate subgraphs can then be linked together to form a single minimal spanning tree.
(2) Using the minimal distance criterion, along with additional biogeographic or phylogenetic criteria, to construct a spanning tree where localities/distributional areas are linked in terms of main massings and/or the geographically nearest sister group (Fig. 2a, c–f).

Step 2. Identify track baselines in terms of the sea or ocean basins, or major tectonic features that the track/s cross (Fig. 2b, g). Where tracks cross several of these the links between the main massings serve to identify baselines.

Step 3. Construct connection matrices for individual tracks and a summary connection matrix for all tracks. Sum the rows of the summary connection matrix so that nodal values for each locality/distribution area can be determined. Sum the individual nodal values and divide by the number of localities/distribution areas. Localities/distribution areas with a nodal value greater than the average nodal value are recognised as nodes.

Step 4. Use an appropriate statistical test to evaluate track congruence between individual connection matrices. Page (1987) suggests permutation tests of association but this approach has been criticised by Weston (1989, this issue). Search the summary connection matrix for circuits indicating incongruent tracks.

Step 5. Present analysis results on a map with tracks, baselines, nodes, and main massings identified for further research.

Compatibility track analysis

In this approach individual tracks are treated as biogeographic hypotheses of area relationship

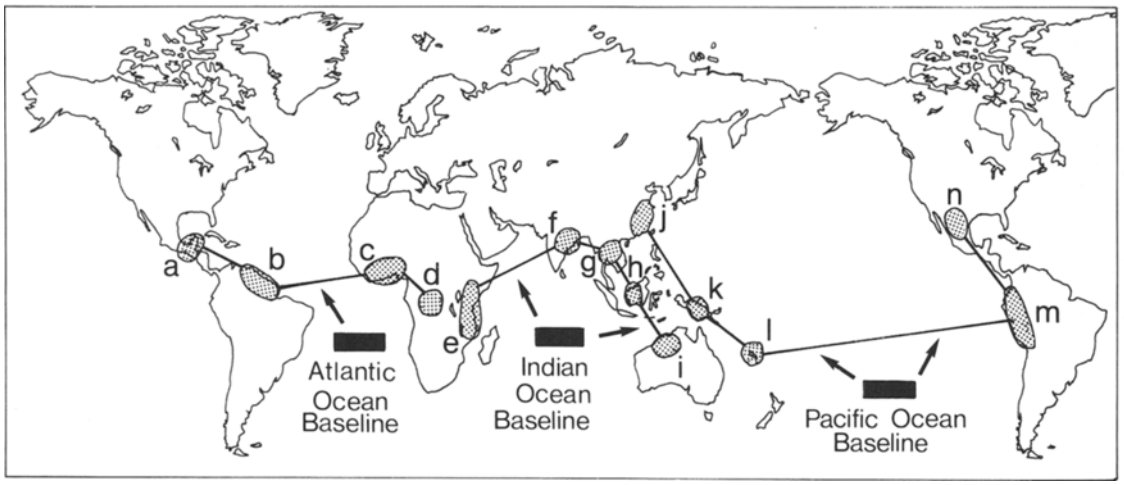


Fig. 1 The concepts of a track and its baseline. Tracks are minimal spanning graphs linking distributional areas/localities of a particular taxon or group of taxa. For instance, the hypothetical taxa distributed in the four areas a to d are linked by a three link minimal spanning graph. As the graph for these taxa crosses the Atlantic Ocean their track is interpreted as having an Atlantic Ocean baseline. (From Craw & Page 1988: fig. 1. Reproduced by permission of John Wiley & Sons Ltd., Chichester, England).

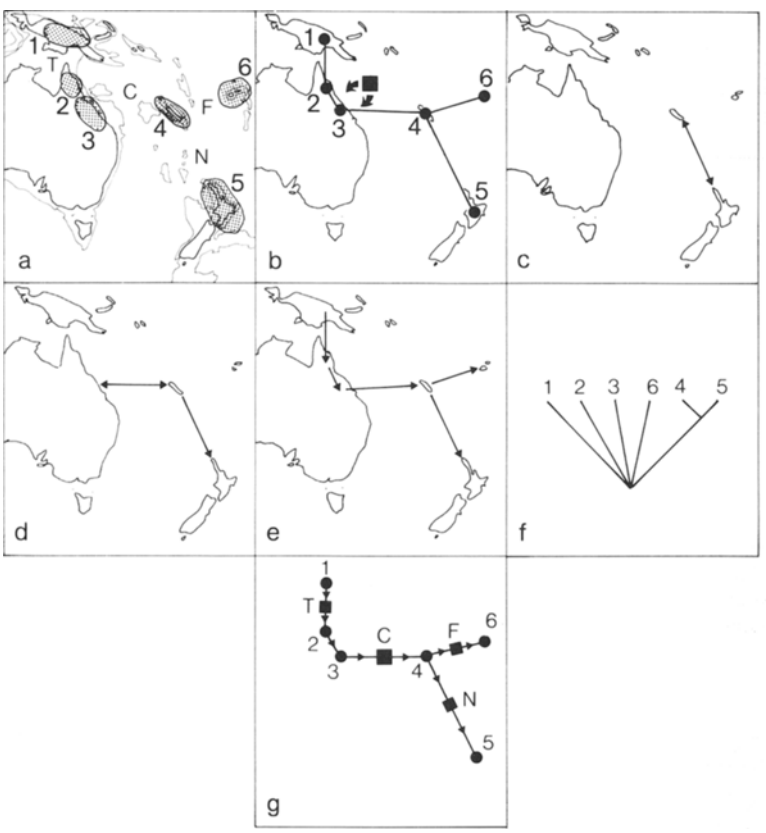


Fig. 2 Track construction, orientation, and baseline identification. (**a**) Hypothetical taxa 1 to 6 are geographically distributed in various parts of Australasia. Abbreviations: C-Coral Sea; F-Fiji Basin; N-Norfolk Ridge; T-Torres Strait. (**b**) The track for taxa 1 to 6 with the main baseline (Coral Sea) identified as the linkage joining the main massings. (Solid black square=main baseline). (**c**) The initial step in orienting the track by linking the sister taxa in areas 4 and 5. (**d**) The second link is formed between areas 3 and 4 which then serves to orient the link 4 to 5. (**e**) The links 1 to 2 to 3 are formed with area 6 being linked to the nearest neighbour in area 4. (**f**) The known unresolved phylogeny of taxa 1 to 6. (**g**) The fully oriented track for taxa 1 to 6 with baselines identified. (From Craw & Page 1988: fig. 2. Reproduced by permission of the publishers John Wiley & Sons Ltd., Chichester, England).

	1	2	3	4	5	6
1	–	1	0	0	0	0
2	1	–	1	0	0	0
3	0	1	–	1	0	0
4	0	0	1	–	1	1
5	0	0	0	1	–	0
6	0	0	0	1	0	–

A

FROM / TO

	1	2	3	4	5	6
1	–	1	0	0	0	0
2	0	–	1	0	0	0
3	0	0	–	1	0	0
4	0	0	0	–	1	1
5	0	0	0	0	–	0
6	0	0	0	0	0	–

B

Fig. 3 Connection matrices derived from the tracks in Fig. 2. (A) Connection matrix for the track in Fig. 2(b). (B) Connection matrix for the track in Fig. 2(g). Note: The symbol "0" indicates no link; "1" indicates a link.
(From Craw & Page 1988 fig. 3. Reproduced by permission of the publishers John Wiley & Sons Ltd.,

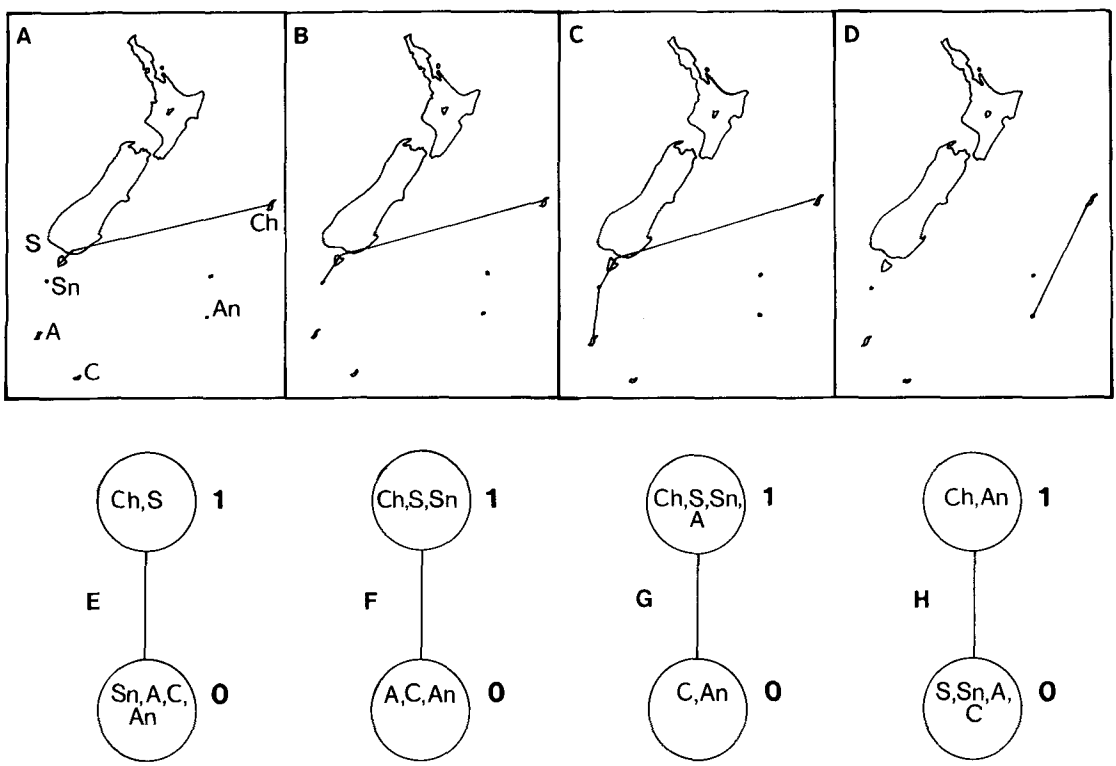


Fig. 4 A–D Individual tracks for taxa distributed in the Chatham Islands, Southern New Zealand, and the subantarctic islands. Abbreviations: A-Auckland Islands, An-Antipodes Islands, C-Campbell Islands, Ch-Chatham Islands, S-Southern New Zealand (includes Stewart Island), Sn-Snares Islands. **E–H** Individual tracks A–D interpreted as hypotheses of area relationship.

(Fig. 4). This method treats a track graph of a taxon's distribution as a vertex in a bipartite graph representing the relationship between areas which are or are not connected by that particular track (Fig. 5).

Coding individual tracks in this fashion makes it possible to construct an area *x* track matrix that can be analysed for track congruence or compatability, by exploiting the analogy with the compatability

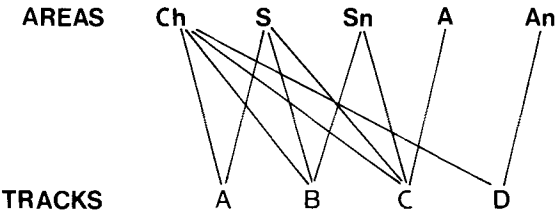


Fig. 5 Areas and tracks from Fig. 4A–D represented as a bipartite graph. Abbreviations as in Fig. 4.

approach to phylogenetic systematics (see Meacham 1984 for a summary of this approach). Individual tracks are regarded as being congruent or compatible with each other if, and only if, one track is a subset of the other or they are the same in a pairwise comparison (i.e., tracks are either included within, or replicated by, one another).

In the example given (Fig. 4) tracks A, B, and C are all compatible with each other (Fig. 6) whereas track D is incompatible with all three tracks (Fig. 7). The set of compatible tracks, termed a clique, is then used to construct a tree connecting the areas (Fig. 6B).

This method involves finding the simplest form of area tree. This tree is then mapped onto a geographic map as a line graph in order to determine standard track geometry and to identify the standard track's baseline (Fig. 8). The tree is constructed from the largest clique of compatible distributions in a distributional compatibility matrix, identified as a standard track, and interpreted as a trace of an ancestral biota (after Craw 1989). Connor (1988) has suggested independently a similar approach to track analysis but provides no details or empirical applications.

Summary of compatability track analysis

Step 1. Construct an $r \times c$ matrix, where r, the rows, represent localities/distribution areas and c, the columns, represent tracks. Each matrix entry m_{ij} is 1 or 0 depending on whether track i is present or absent in location j (Table 1).

Step 2. Use a compatability analysis program (e.g., clique compatability, Felsenstein 1986) to find the largest clique of compatible tracks (Table 2).

Step 3. Map out the largest clique as a tree connecting the areas/ locations (Fig. 7). Treat the largest clique of compatible tracks as a generalised or standard track.

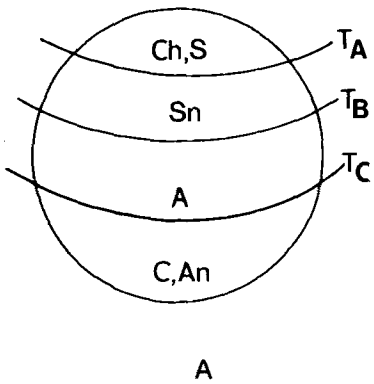
Step 4. Use the BIPART algorithm (Wormald 1984) to generate 1000 or more equiprobable random matrices with given row and column sums. This algorithm allows random (null) incidence matrices to be generated within the constraints of given row and column sums. The biotic richness of areas and the frequencies of different taxa are retained by these constraints. The percentage of randomly generated matrices in which the largest clique size is as large or larger than the largest clique in the actual data matrix, provides a statistical test of the level at which the largest clique attains significance. If more than one largest clique, or several cliques of considerable size, are found and these cliques are outside the constraints of what might be expected randomly, then a hypothesis of the existence of several standard tracks linking the areas in different ways can be considered. Alternatively the intersection (i.e., those tracks common to all the largest cliques) of the largest cliques could be treated as a standard track.

Step 5. Identify baseline for standard track as according to criteria used in spanning tree analysis.

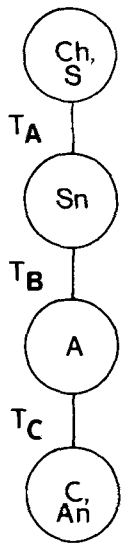
Step 6. Map distribution tracks for taxa that are not part of the largest clique (Fig. 9). Compare these tracks with the geometry of the standard track in order to identify incompatibilities/incrongruencies caused by mobilism (e.g., tracks 3, 17), extinction, and/or non-collection (e.g., tracks 5, 11).

AREA CLADOGRAM METHODS

These methods exploit an analogy between biogeography and systematics by treating a taxon's presence in an area as a derived character of that area, its absence as a primitive character, and phylogenetic lineages of taxa as transformation series linking different areas into an area history (Wiley 1987; Brundin 1988; Rosen 1988). In these approaches character reversals are interpreted as equivalent to extinction events and character convergence or parallelism as equivalent to dispersal events (Zandee & Roos 1987). Two of the simplest methods for area cladogram construction will be outlined. More complex and sophisticated methods exist but are much more challenging to apply to available data. For these see Nelson & Platnick (1981), Page (1988), and Zandee & Roos (1987). Page (1988) and Simberloff (1987b, 1988) have considered protocols for statistical tests of the significance of observed degrees of congruence between area cladograms. Recently, the construction of geological area cladograms, using numerical cladistic analysis of data matrices of geological characters for geographic areas, has been demon-strated for the first time (Craw 1989).

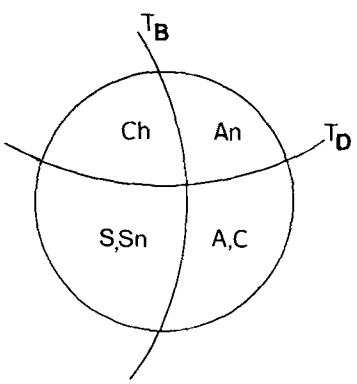


A

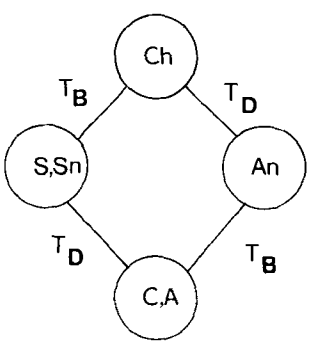


B

Fig. 6 (A) Set diagram of three compatible tracks (from Fig. 4A–C) (B) The corresponding tree linking the six areas based on A. T_A = Track A from Fig. 4, etc.



A



B

Fig. 7 (A) Set diagram of two incompatible tracks (from Fig. 4B, D). (B) The corresponding cycle graph linking the six areas based on A.

Parsimony analysis of endemicity

This type of analysis produces one of the simplest forms of area cladogram from which initial hypotheses concerning area history, relationship, and classification can be derived (details can be found in Rosen 1988).

Step 1. Construct an $r \times c$ matrix where r, the rows, represent localities/distribution areas and c, the columns, represent taxa. Each matrix entry m_{ij} is 1 or 0 depending on whether taxon i is present or absent in location j. An alternative is to treat putatively monophyletic clades (i.e., species groups, genera, families) as characters (i.e., columns) and their constituent taxa or combinations of taxa (if taxa are sympatric) as character states (see Craw 1989 for an example).

Step 2. Include in the data matrix a hypothetical area coded 0 for all columns in order to provide a root for the resulting Wagner network.

Step 3. Perform a Wagner parsimony analysis on this data matrix using an available program (e.g., PAUP, Swofford 1985).

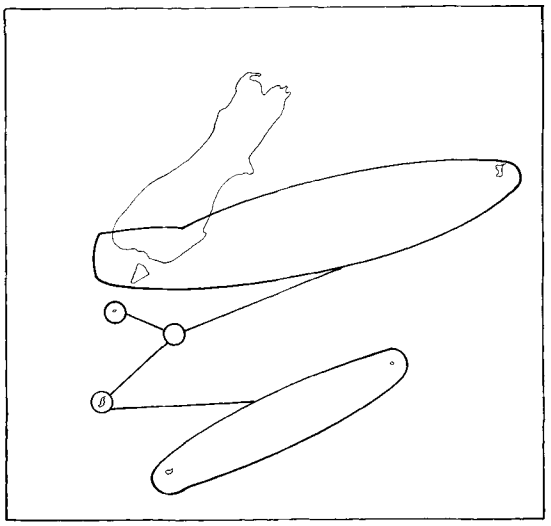


Fig. 8 Tree based on largest clique of compatible tracks from Tables 1 and 2 drawn on a map (from Craw 1989).

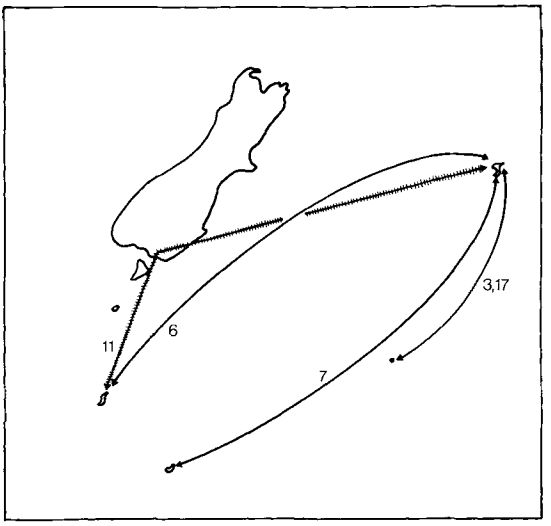


Fig. 9 Track graphs not belonging to the largest clique in Tables 1 and 2 (from Craw 1989).

Table 1 Area x track distribution matrix (for details of data set see Craw 1989).

	Tracks																	
Areas	5					10					15					18		
Campbell	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1
Auckland	1	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1
Snares	1	1	0	1	1	0	0	1	1	1	0	1	0	0	1	1	0	0
Southern NZ	1	1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	1
Antipodes	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
Chatham	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 2 Matrix of track compatibilities. The largest clique of compatible tracks in this matrix consists of tracks 1, 2, 4, 8, 9, 10, 12–16, 18). 1=compatible; 0=incompatible.

Tracks	**5**					**10**					**15**					**18**		
	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1
	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
	1	1	0	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1
5	1	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1
	1	1	0	0	1	1	0	1	0	0	1	1	0	0	1	0	0	1
	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	1
	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1
	1	1	0	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1
10	1	1	0	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1
	1	1	0	0	0	1	0	1	0	0	1	1	1	1	1	0	0	1
	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	1	1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	1
	1	1	0	1	0	0	0	1	1	1	1	1	1	1	1	1	0	1
15	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1
	1	1	0	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1
	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
18	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

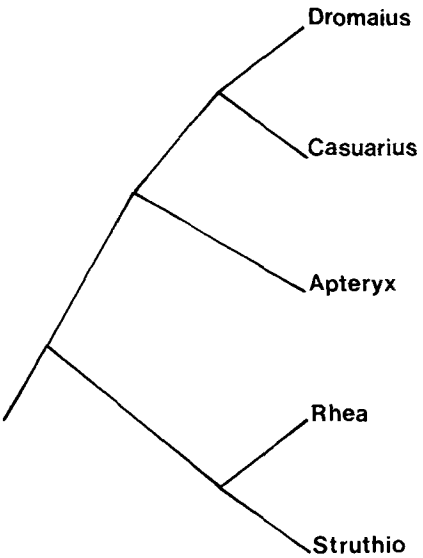


Fig. 10 Phylogeny of the ratite birds (after Sibley & Ahlquist 1987).

Step 4. If more than 1 most parsimonious cladogram found (almost invariably there will be more than 1) construct a consensus tree.

Step 5. Compare area cladogram or consensus tree with area cladograms/consensus trees derived from independent data sets (e.g., based on geological information).

Quantitative parsimony method for deriving a general biological area cladogram

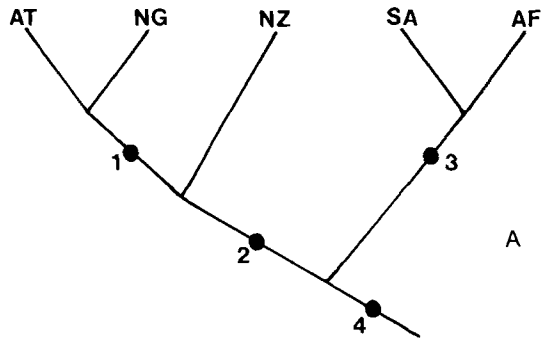
This method produces a summary area cladogram from analysis of two or more individual area cladograms based on the phylogenies of unrelated taxa. The rationale for, and details of, the method can be found in Wiley (1987).

Step 1. Compile the widest possible variety (taxonomically and ecologically) of phylogenies (cladograms) for taxa occupying the areas of interest (e.g., the main Southern Hemisphere landmasses).

Step 2. Replace taxon names in phylogenies (Fig. 10) with localities/distribution areas those taxa occupy (Fig. 11A).

Step 3. Construct an area *x* clade matrix for each area cladogram (Fig. 11B). If an area under study is not occupied by a taxon in a particular cladogram then that area is coded "missing" (=9) in the matrix.

Step 4. Construct a general area *x* clade matrix for all area cladograms. Include in this general matrix a row for a hypothetical area coded "0" for all columns in order to root resulting networks.



CLADES

AREAS	1	2	3	4	
AF	0	0	1	1	
AT	1	1	0	1	
NC	9	9	9	9	B
NG	1	1	0	1	
NZ	0	1	0	1	
SA	0	0	1	1	

Fig. 11 (A) Conversion of ratite birds phylogeny into an area cladogram. (B) Area x clade matrix derived from the area cladogram in B. Abbreviations: AF- Africa, AT- Australia (includes Tasmania), NC- New Caledonia, NG- New Guinea, NZ- New Zealand, SA- South America.

Step 5. Perform a Wagner parsimony analysis on this data matrix in order to derive the simplest area cladogram summarising all the available data.

Step 6. Compare summary area cladogram with area cladograms derived from independent data sets (e.g., geological information).

GLOSSARY

baseline a feature such as crossing an ocean or sea basin, or a major tectonic structure that is interpreted as a diagnostic character uniting individual tracks that may otherwise have little in common.

clade a monophyletic lineage or group.

cladogram a branching diagram relating terminal taxa based on the distribution of derived character states among the taxa.

clique (1) a set of vertices in a graph each of which is adjacent (i.e., connected) to the rest; (2) a set of objects in which each individual object is related in some way to every other object.

compatible (1) adjacent in a graph; (2) specifying the same set of relationships.

consensus tree a branching diagram summarising a set of equally parsimonious cladograms with differing topologies.

generalised track see standard track.

incompatible (1) not adjacent in a graph; (2) specifying different sets of relationships.

main massing concentration of diversity within a taxon in biogeographic space.

minimal spanning tree an acyclic graph that connects all the localities/distribution areas occupied by a taxon such that the sum of the lengths of the links connecting each locality is the smallest possible.

nodal value the sum of the number of links a particular distribution area/collection locality has with other distribution areas/collection localities in a track graph.

node (1) an area/locality where two or more standard tracks overlap; (2) an area/locality with a higher than average connectivity value.

orientation assignment of direction to a track.

parsimony a methodological principle of which the basis is that observed data are to be explained in the simplest way possible (otherwise known as Ockham's razor).

standard track the set comprising two or more individual tracks that are compatible/congruent according to some previously specified criteria (e.g., shared baseline, compatible distributions, or congruent area cladograms).

track a biogeographic graph, e.g., a line graph drawn on a map of the localities/distribution areas for a particular taxon or group of taxa.

ACKNOWLEDGMENTS

I am grateful to Rod Page and Russell Gray for many fruitful discussions on quantitative methods in biogeography. Chris Triggs and Nick Wormald kindly analysed several data sets.

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