

A Comparative Review of Cladistic Approaches to Historical Biogeography of Southern South America

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Abstract

Cladistic historical biogeographic studies on the austral continents are briefly reviewed with special reference to southern South America. The biogeography of marsupials, southern beeches and the relationships of New Zealand and southern South America are compared. No general pattern of interrelationships is common to all the analyses. Differences in delimitation of areas, selection of taxa and techniques applied are discussed as possible causes of incongruities. The comparative review of these empirical studies reveals that, although it is valid to investigate the existence of a unique pattern of interrelationships among areas of endemism, this cannot be considered as an *a priori* assumption in the analyses.

Introduction

More than 10 years have passed since the first symposium on Vicariance Biogeography was held at the American Museum of Natural History, in New York. In the summary conclusions, Gareth Nelson (1981:525) stated:

‘Vicariance biogeography is not an attempt to explain everything, or even the greater part, of the geographical distribution of plants and animals, for its focus is allopatric differentiation as manifested by the phenomenon of endemism It begins by asking one question: Is there a cladogram of areas of endemism? Or, in other words: Are areas of endemism interrelated among themselves in a way analogous to the interrelationships of the species of a certain group of organisms?’.

Under this working model several historical biogeographic analyses on the austral continents have been carried out. We briefly review the current state of knowledge on patterns of relationships among austral regions, as revealed by four different cladistic approaches. In order to achieve this objective we compare Patterson’s (1981) study on historical biogeography of marsupials, Humphries’ (1981) analysis of the biogeography of southern beeches, Craw’s (1989) study of the biogeographic classification of New Zealand and Crisci *et al.*’s (1991) analysis of the relationships of southern South America.

Historical Biogeography of Marsupials

Patterson (1981) intended to explain the biogeographic history of marsupial mammals, which are mainly distributed in the southern hemisphere (South America, Australia and New Guinea) with one species in North America, and fossil records from Europe. Patterson (1981) applied the reduced area cladogram method (Rosen 1978).

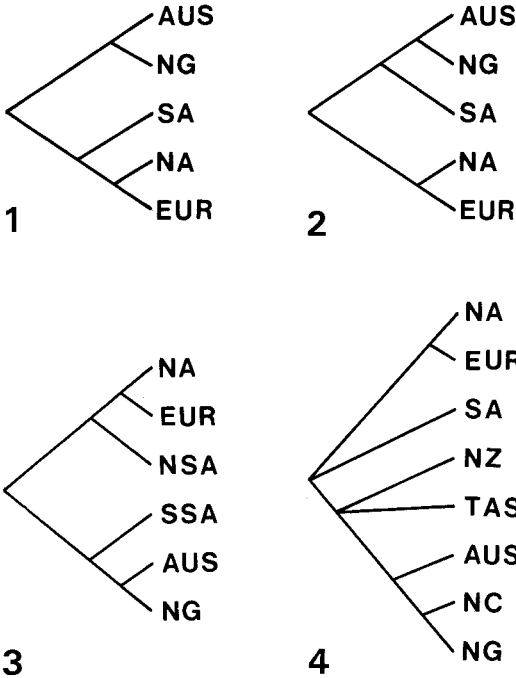
To compare the marsupial area cladogram, Patterson (1981) chose five vertebrate taxa (Table 1) of the same age as the marsupials. Based on these data, four reduced area cladograms were obtained. These were consistent with the marsupial area cladogram and were subsequently

Table 1. List of taxa used in the reviewed studies

Taxa	Patterson Humphries (1981)	Craw (1989) analysis 1	Crisci et al. (1991)	Taxa	Patterson Humphries (1981)	Craw (1989) analysis 1	Crisci et al. (1991)
Fungi				Animals			
<i>Cytaria</i>			+	Molluscs			
Plants				Bullimulidae			
Cupressaceae		+		Vertebrates			+
<i>Cinodendron-Dobouzeia</i>			+	<i>Osteoglossum-Scleropages</i>	+		
<i>Peripentadenia</i>				Hyliidae	+		
Embothriinae			+	Chelidae	+		
Gevuinae	+			Ratites	+		+
Macadamiainae	+			Galliformes	+		
<i>Nothofagus-Fagus</i>	+		+	Marsupialia	+		
<i>Negria-Drepanthus</i>	+		+	Insects			
<i>Oreomyrhis</i>			+	Hydrobiosinae	+		
<i>Drapetes</i>			+	Siphonuridae			
<i>Drymis</i>			+	<i>Eriococcus-Madarococcus</i>			+
<i>Aristotelia-Vallea</i>	+		+	Podonominae	+		+
<i>Leptocarpus-Calopsis</i>			+	Diamessinae	+		+
<i>Lindenia</i>			+	Rhinotoridae	+		+
Phyllacae			+	<i>Chalcosyrphus</i>	+		
Donatiace			+	Sciadoceridae	+		
<i>Nicotiana</i>			+	<i>Pericompus</i>	+		
<i>Lagenifera-Solenogyne</i>			+	<i>Anisotarsus</i>	+		
<i>Oreobolus</i>			+	Metallicina			
				Pseudopsinae			+
				<i>Oxytrium-Ptomaphila</i>			+

combined by Seberg (1986) into a general area cladogram (Fig. 1), where South America is closely related to North America + Europe and New Guinea is related to Australia.

In a second step of the analysis, Patterson selected eight insect and four plant taxa (Table 1), which provided seven different reduced area cladograms. The patterns specified by these area cladograms could not be combined into any single general area cladogram; the Sciadoceridae cladogram was unique and the other 11 reduced area cladograms supported either the vertebrate general area cladogram or a new one (Fig. 2), where South America is related to Australia and New Guinea instead of being related to North America + Europe. Patterson then added the areas that he had previously omitted from the reduced area cladograms, such as south-eastern Asia and Africa.



Figs 1 and 2. General area cladograms in Seberg (1986) based on Patterson's (1981) analysis.

Fig. 3. General area cladogram of Parenti (1981) based on Patterson's (1981) analysis.

Fig. 4. General area cladogram after Humphries (1981).

AUS, Australia; EUR, Europe; NA, North America; NC, New Caledonia; NG, New Guinea; NSA, Northern South America; NZ, New Zealand; SA, South America; SSA, Southern South America; TAS, Tasmania.

Patterson (1981) concluded that the taxa showing congruent Australasian/South American patterns displayed two different patterns beyond these areas, one with younger relationships extending into northern areas and the other with older relationships extending into Africa.

As a summary of Patterson's analysis, Parenti (1981) presented a general area cladogram (Fig. 3) where South America is divided into two areas, northern South America and southern South America. Patterson's data set was also used by Wiley (1988) in a biogeographic parsimony analysis (Wiley 1988; Fig. 13). Based on a data matrix of 5 areas × 122 components, PAUP analysis (Swofford 1985) produced a single tree, identical with that shown in Fig. 1.

Historical Biogeography of Southern Beeches

In a study of the historical biogeography of the southern beeches *Nothofagus*, Humphries (1981) presented a general area cladogram as a summary of the historical relationships of land masses inhabited by austral and boreal groups, following Rosen's (1978) reduced area cladogram technique. Humphries based his study on the reduced area cladograms of 22 plant and animal taxa (Table 1), with endemic representatives in at least three of the areas occupied by *Nothofagus*.

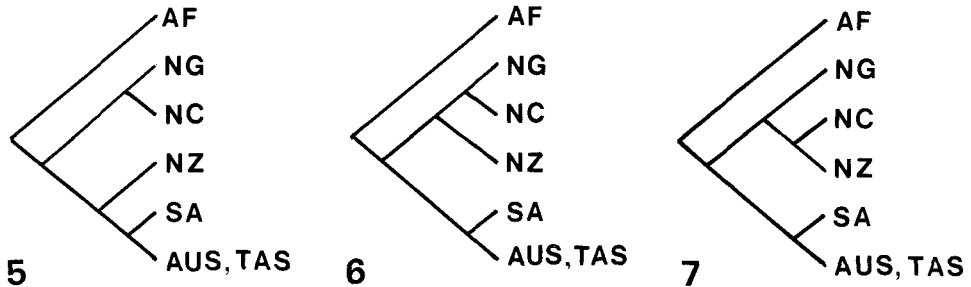
Different patterns of area relationships, particularly with regard to the position of South America, were obtained. The general area cladogram presented (Fig. 4) showed an unresolved position for South America, which could be either the sister group to North America + Europe or to the monophyletic group containing New Zealand, Australia, Tasmania, New Guinea and New Caledonia.

Humphries (1981) hypothesised that the two positions for South America supported the hypothesis that it is a composite area and should not be treated as a single area of endemism.

Biogeographic Classification of New Zealand

Craw (1989) conducted three cladistic biogeographic analyses based on Gondwanic and circum-Antarctic taxa to appraise varied views on the biogeographic classification and relationships of New Zealand. The analyses were performed using the Wagner parsimony algorithm of the computational program PAUP 2.4.1 (Swofford 1985).

Analysis 1. Craw applied a quantitative parsimony analysis (Wiley 1988; Fig. 13) to six original taxon cladograms (Table 1), considering South America, New Zealand, Australia + Tasmania, New Guinea, New Caledonia and Africa as the study areas.



Figs 5-7. General area cladograms based on a quantitative parsimony analysis (Craw 1989, analysis 1). AF, Africa; AUS, Australia; NC, New Caledonia; NG, New Guinea; NZ, New Zealand; SA, South America; TAS, Tasmania.

The Wagner parsimony analysis of the data matrix (6 areas \times 27 components) resulted in three general area cladograms (Figs 5-7), which agree in showing South America to be most closely related to Australia + Tasmania.

Analysis 2. Craw undertook a parsimony analysis of endemism (Rosen 1988; Fig. 8) based on the presence/absence of 73 plant and animal families and subfamilies. He analysed the relationships among Australia + Tasmania, New Zealand, South America, Africa and the Oriental region.



Fig. 8. Flow chart of the steps in the parsimony analysis of endemism.

The parsimony analysis of endemism led to three equally parsimonious general area cladograms that were combined by Craw (1989) into a strict consensus tree (Fig. 9). According to the information that can be extracted from the general area cladograms, Australia + Tasmania and New Zealand are most closely related to South America, and the relationships of Africa and the Oriental region are unresolved. By deleting the plant data, one fully resolved general area cladogram was obtained (Fig. 10), with Africa and the Oriental region constituting a monophyletic group.

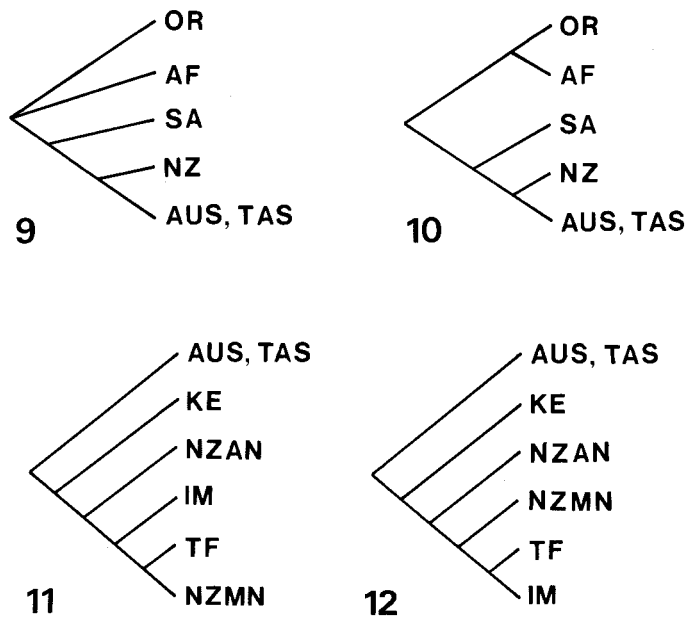
Analysis 3. Another parsimony analysis of endemism was applied, to 31 genera of the circum-Antarctic biota, considering New Zealand mainland, New Zealand subantarctic islands, Indian Ocean subantarctic islands, Tierra del Fuego, Islas Malvinas (Falkland Islands) and Australia + Tasmania.

This analysis resulted in two equally parsimonious general area cladograms (Figs 11, 12), showing a close relationship between the New Zealand mainland and Tierra del Fuego and the Islas Malvinas.

Craw (1989) concluded that his three analyses supported three alternative views of the biogeographic relationship of New Zealand to Australia and South America.

Composite Origin of South American Biota

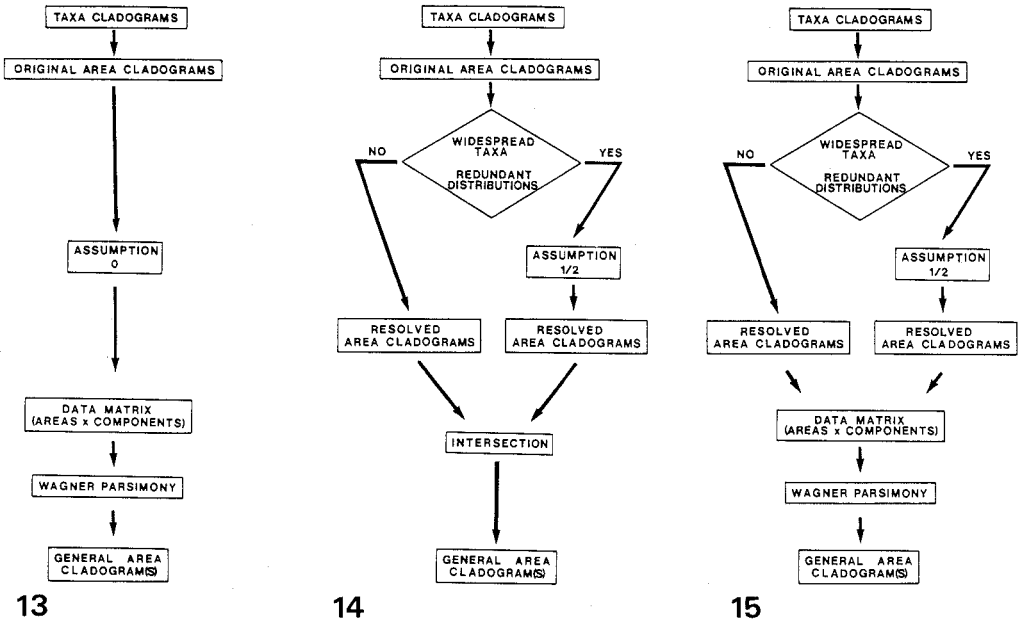
Crisci *et al.* (1991) tried to test the hypothesis of a hybrid origin for South America (Humphries 1981; Parenti 1981; Humphries and Parenti 1986). They conducted a study in which northern South America and southern South America were treated as independent units. To determine the areas which exhibit affinities with southern South America, a non-exhaustive search of distributional patterns of several plant and animal taxa was undertaken. Australia, New Guinea, New Caledonia, Tasmania, New Zealand, South Africa and North America were selected. Cladistic analyses were available for only 17 taxa of those showing austral patterns of relationships (Table 1). Three different techniques were applied: biogeographic parsimony analysis (Wiley 1988), component analysis (Nelson and Platnick 1981) and quantification of component analysis (Humphries *et al.* 1988). The main steps conducted under each technique are summarised in flow charts (Figs 13–15). Assumptions 1 and 2 (Nelson and Platnick 1981) and intersections (Nelson 1984; Page 1988) were performed using Component version 1.5 (Page 1989). Wagner parsimony analyses were performed using Hennig86 version 1.5 (Farris 1988), applying the implicit enumeration option for calculating trees (Farris 1989). When the parsimony analyses yielded more than two trees a Nelson consensus tree (Nelson 1979) of Hennig86 was calculated to be used as an illustration.



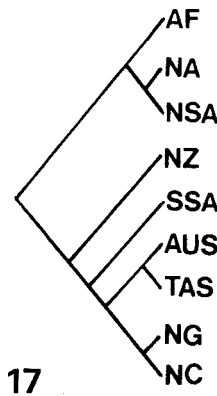
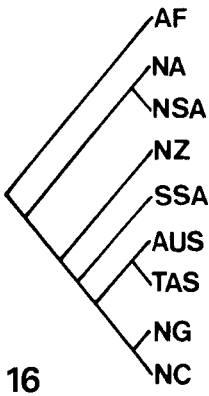
Figs 9 and 10. General area cladograms based on a parsimony analysis of endemicity for 73 plant and animal taxa (Craw 1989, analysis 2). *Fig. 9.* Consensus area cladogram based on plant and animal taxa. *Fig. 10.* General area cladogram for animal taxa only. Abbreviations as in Figs 5–7; AF, Africa; OR, Oriental Region.

Figs 11 and 12. General area cladograms based on a parsimony analysis of endemicity for circum-Antarctic land areas (Craw 1989, analysis 3). AUS, Australia; IM, Islas Malvinas; KE, Indian Ocean subantarctic islands, Kerguelen Province; NZAN, New Zealand subantarctic islands; NZMN, New Zealand mainland; TAS, Tasmania; TF, Tierra del Fuego.

Analysis 1. Biogeographic parsimony analysis (Fig. 13). The data matrix (10 areas × 93 components) yielded two general area cladograms (Figs 16, 17). These cladograms show North America and northern South America as sister areas, and southern South America included in a monophyletic group with Australia, Tasmania, New Guinea and New Caledonia, with New Zealand as the sister area. Both trees differ only in the position of the pair North America–northern South America. Either North America–northern South America is sister to South Africa or is the sister to the rest of the areas, exclusive of South Africa.



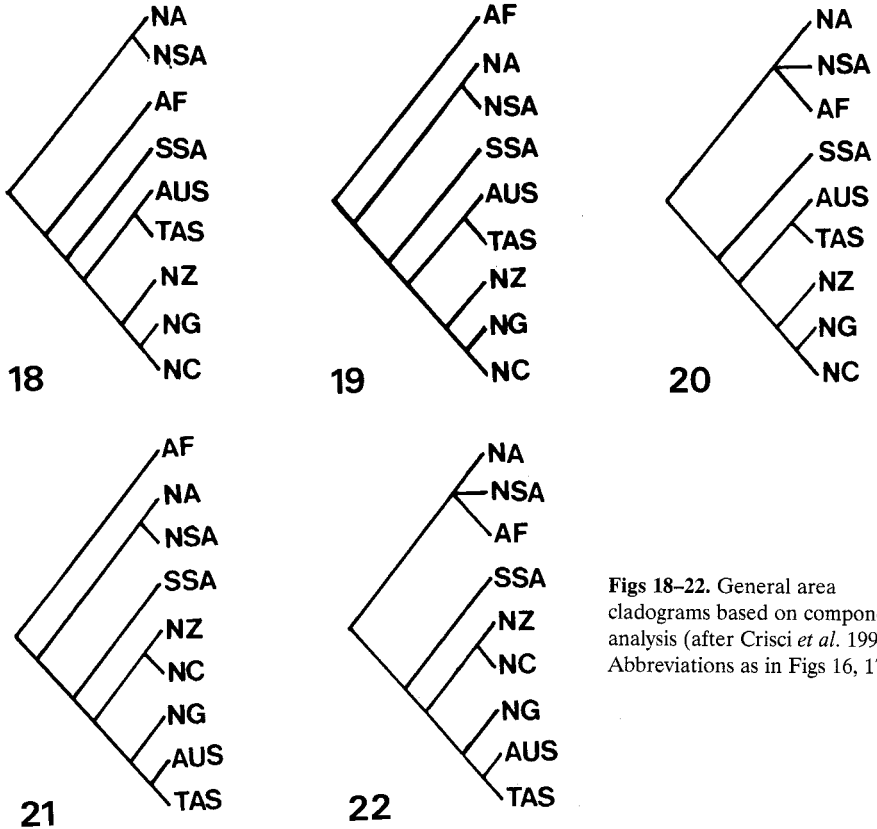
Figs 13–15. Flow charts for the steps in cladistic biogeographic techniques applied by Crisci *et al.* (1991). *Fig. 13.* Biogeographic parsimony analysis. *Fig. 14.* Component analysis. *Fig. 15.* Quantification of component analysis.



Figs 16 and 17. General area cladograms based on biogeographic parsimony analysis (after Crisci *et al.* 1991). AF, South Africa; AUS, Australia; NA, North America; NC, New Caledonia; NG, New Guinea; NSA, northern South America; NZ, New Zealand; SSA, southern South America; TAS, Tasmania.

Analysis 2. Component analysis (Fig. 14). Eleven out of the 17 original area cladograms showed widespread taxa and/or redundant distributions; assumptions 1 and 2 were applied, producing a variable number of resolved area cladograms. No general area cladogram common to the 17 sets of area cladograms derived under assumption 1 could be found. The same was true for the analysis under assumption 2. Even though not supported by the 17 sets of trees,

searches for a tree shared by a smaller number of sets of area cladograms were performed. As a result of this procedure the largest number of sets able to share one or more cladograms was 10. Under assumption 1, two general area cladograms were obtained (Figs 18, 19) which differed in the basal branch, which may be either South Africa or the pair North America–northern South America. The southern temperate areas (southern South America, Australia, Tasmania, New Zealand, New Guinea and New Caledonia) constitute a monophyletic group, where southern South America is the sister area of the other five.



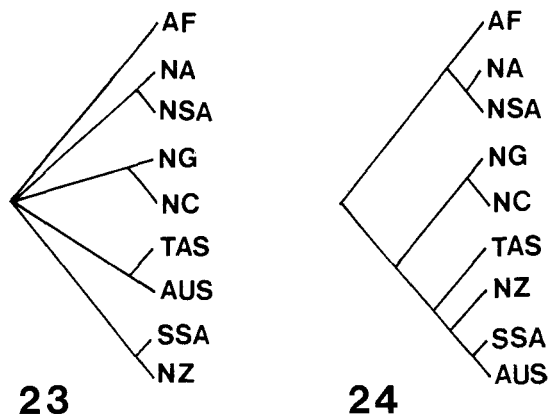
Figs 18–22. General area cladograms based on component analysis (after Crisci *et al.* 1991). Abbreviations as in Figs 16, 17.

Under assumption 2, four general area cladograms were found through the intersection of two groups of trees derived from 10 taxa each. One of these replicates the second general area cladogram obtained under assumption 1 (Fig. 19); another is consistent with both general area cladograms obtained under assumption 1 (Fig. 20); the remaining two are consistent with the others obtained under assumption 2, with the exception of the placement of New Guinea (Figs 21, 22).

Analysis 3. Quantification of component analysis (Fig. 15). Two data matrices (areas × components) were extracted from the sets of resolved area cladograms obtained under assumptions 1 or 2, and from the original area cladograms that showed neither widespread taxa nor redundant distributions. Under assumption 1, the parsimony analysis of the data matrix (10 areas × 102 components) produced nine general area cladograms. The Nelson consensus tree (Fig. 23) for these general area cladograms shows the pairs of sister areas: Australia–Tasmania, New Guinea–New Caledonia, southern South America–New Zealand, and northern South America–North America.

Under assumption 2, the analysis of the data matrix (10 areas × 172 components) led to only one general area cladogram (Fig. 24). This cladogram shows northern South America, North America and South Africa as a monophyletic group in which the first two are sister areas. The southern temperate areas constitute a monophyletic group in which southern South America is the sister area to Australia.

Crisci *et al.*'s (1991) three analyses support the hybrid origin of the South American biota, with northern South America most closely related to North America and southern South America always constituting a monophyletic group together with Australia, Tasmania, New Guinea, New Caledonia and New Zealand, reflecting the existence of an ancient austral biota. Four conflicting hypotheses of area relationships concerning southern South America and the other austral areas suggest that southern South America may be a composite area in itself.



Figs 23 and 24. General area cladograms based on quantification of component analysis (after Crisci *et al.* 1991). *Fig. 23.* Nelson consensus tree of the nine general area cladograms obtained under assumption 1. *Fig. 24.* General area cladogram obtained under assumption 2. Abbreviations as in Figs 16, 17.

Discussion

Comparison of the results obtained under the different studies reviewed seems to show no single pattern of interrelationships of southern South America with the other austral areas. The incongruities among the different general area cladograms may be due to at least three methodological causes.

Areas. The lack of a universal methodology to define areas of endemism is one possible cause that leads to incongruities in empirical studies. Although we reviewed only those papers dealing with austral regions, we found that the areas of study are not equivalent. Basically two approaches for the delimitation of South America were followed in the papers reviewed. South America was considered as a single area by Patterson (1981), Humphries (1981) and Craw (1989, analyses 1 and 2) or treated as a composite (Craw 1989, analysis 3; Crisci *et al.* 1991). Craw (1989) considered the subantarctic portion of South America, including only Islas Malvinas and Tierra del Fuego in his analysis 3, whereas Crisci *et al.* (1991) divided South America into northern and southern South America.

The comparison of descriptive biogeographic schemes also presents problems. When searching for a unique descriptive biogeographic scheme for austral biota, we could not find one. Depending on the criteria for delimiting different areas, whether based on flora, fauna or ecology, the areas are defined in different ways. Recent examples of different points of view can be found in Fleming (1987) and Udvardy (1987) on the Antarctica biogeographical realm.

Taxa. Another cause of incongruity may be due to different sets of taxa used in different studies. From the 39 taxa listed in Table 1, only two (*Nothofagus* and Diamesinae) are common to all the data sets compared, thus making comparison more difficult.

The consequences of choosing different sets of taxa are clearly seen in most of the studies reviewed. Patterson (1981) found that through selection of taxa two different patterns of area relationships could be obtained. A secondary selection from the original taxa in Craw's (1989) second analysis and that of Crisci *et al.*'s (1991) application of component analysis allowed one to obtain resolved results from unresolved cladograms.

Differences in selection of taxa in the studies reviewed suggest that, if we accept the analogy between systematic and biogeographic analyses, a comparable criterion to homology is still lacking in biogeography. At present, the solely dubious criterion to choose taxa is related to the availability of cladistic analyses. Furthermore, the unreliability of taxon cladograms may bring noise to the system (Seberg 1986).

Techniques. A third cause of incongruity is due to different techniques. This is clearly shown in Crisci *et al.* (1991), where different results were obtained through the application of three techniques on the same data.

Finally, even though there were accepted universal methodologies for delimitation of natural areas, for selection of taxa and agreement on the most appropriate technique, the real world could also generate apparent incongruities. Cracraft (1988) has already stated that area-hybridisation, disappearance of barriers, origination of new barriers within areas, randomisation effects of population dispersion, and extinction, are some of the processes which threaten the integrity of areas and cause complex historical patterns.

Ten years after Nelson's (1981:525) question, the empirical studies seems to reveal that, although it is valid to investigate the existence of a unique pattern of interrelationships among areas of endemism, it cannot be accepted as an *a priori* assumption of the analysis.

Acknowledgments

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