Journal of Biogeography, **28**, 157–168

The voice of historical biogeography

KEYNOTE PAPER

ABSTRACT

Historical biogeography is going through an extraordinary revolution concerning its foundations, basic concepts, methods, and relationships to other disciplines of comparative biology. There are external and internal forces that are shaping the present of historical biogeography. The external forces are: global tectonics as the dominant paradigm in geosciences, cladistics as the basic language of comparative biology and the biologist's perception of biogeography. The internal forces are: the proliferation of competing articulations, recourse to philosophy and the debate over fundamentals. The importance of the geographical dimension of life's diversity to any understanding of the history of life on earth is emphasized. Three different kinds of processes that modify the geographical spatial arrangement of the organisms are identified: extinction, dispersal and vicariance. Reconstructing past biogeographic events can be done from three different perspectives: (1) the distribution of individual groups (taxon biogeography) (2) areas of endemism (area biogeography), and (3) biotas (spatial homology). There are at least nine basic historical biogeographic approaches: centre of origin and dispersal, panbiogeography, phylogenetic biogeography, cladistic biogeography, phylogeography, parsimony analysis of endemicity, event-based methods, ancestral areas, and experimental biogeography. These nine approaches contain at least 30 techniques (23 of them have been proposed in the last 14 years). The whole practice and philosophy of biogeography depend upon the development of a coherent and comprehensive conceptual framework for handling the distribution of organisms and events in space.

Keywords
Historical biogeography, spatial analysis, vicariance, dispersal, phylogeny.

INTRODUCTION

In an essay entitled ‘The Voice of Poetry in the conversation of Mankind’, Michael Oakeshott develops the notion of knowledge as a community-owned social construct that is the result of our ability to participate in an unending conversation. Oakeshott says:

> As civilized human beings, we are the inheritors, neither of an inquiry about ourselves and the world, nor of an accumulating body of information, but of a conversation, begun in the primeval forests and made more articulate in the course of centuries. It is a conversation which goes on both in public and within each of ourselves’ (Oakeshott, 1959, p. 11).

According to Oakeshott, education, properly speaking, is an initiation into the skill and partnership of this conversation in which we learn to recognize the voices, to distinguish the proper occasions of utterance, and in which we acquire the intellectual and moral habits appropriate to conversation. And it is this conversation which, in the end, gives place and character to every human activity and utterance. Each voice is the reflection of a human activity, begun without premonition of where it would lead, but acquiring for itself in the course of the engagement a specific character and a manner of speaking of its own: and within each mode of utterance modulation is discernible.

Among the voices of biology, recently historical biogeography has acquired an authentic voice and language of its own. My proposal for this paper is to consider the voice of historical biogeography, its different tones of utterance, its manners of speaking, its modulation and its manner of thinking.

The definition of biogeography may be simple – the study of the geographical distributions of organisms – but this simplicity hides the great complexity of the subject. Biogeography transcends classical subject areas, it involves a range of scientific disciplines that includes geography, geology and biology. No one who studies biogeography can fail to be impressed, or perplexed, by the diversity of approaches to the subject. For convenience, some biogeographers have recognized two research traditions, to which may be attached labels such as ecological biogeography and historical biogeography (Myers & Giller, 1988).

The Swiss botanist de Candolle (1820), was the first author to distinguish between ecological and historical biogeography. According to him, explanation for the former depends upon ‘physical causes operating at the present time’, and for the latter, upon ‘causes that no longer exist today’.

Ecological biogeography is concerned with ecological processes occurring over short temporal and small spatial scales, whereas at the other end, historical biogeography is concerned with evolutionary processes over millions of years on a large, often global scale. Between the two extremes of ecological and historical biogeography is a compartment concerned with the effect of Pleistocene glaciations.

Historical biogeography is going through an extraordinary revolution concerning its foundations, basic concepts, methods, and relationships to other disciplines of comparative biology. In the last two decades considerable progress has been made especially because of the development of several quantitative methods (Morrone & Crisci, 1995).

The specific objectives of this essay are: to discuss the overall situation in which historical biogeography occurs, to outline the contemporary methodologies and to discuss several of the critical issues that need to be tackled.

THE PERIOD

We admit that the present is an important time, as all present time necessarily is. We were wise indeed, could we discern truly the signs of our own time, and by knowledge of its wants and advantages, wisely adjust our own position in it. Let us look around us, for a little while, on the perplexed scene where we stand. Perhaps, on a more serious inspection, something of its perplexity will disappear, some of its distinctive characters and deeper tendencies more clearly reveal themselves; whereby our own relations to it, our own true aims and endeavours in it, may also become clearer.

Were we required to characterize the present of historical biogeography by any single phrase, we should be tempted to use Dickens' first paragraph of his book ‘A tale of two cities's (Dickens, 1859).

> It was the best of times, it was the worst of times, it was the age of wisdom, it was the age of foolishness, it was the epoch of belief, it was the epoch of incredulity, it was the season of Light, it was the season of Darkness, it was the spring of hope, it was the winter of despair, we had everything before us, we had nothing before us, we were all going direct to Heaven, we were all going direct the other way – in short, the period was so far like the present period, that some of its noisiest authorities insisted on its being received, for good or for evil, in the superlative degree of comparison only.

To us who live in the midst of all this, and see continually the faith, hope and practice of every biogeographer, it would be profitable to try to identify the external and internal forces that are shaping the present of historical biogeography.

External forces

Three external forces influence the discipline: global tectonics as the dominant paradigm in geosciences, cladistics as the basic language of comparative biology and the biologist's perception of biogeography.

Global tectonics as the dominant paradigm in geosciences

Geographic stasis was the big question during most of the 20th century. This was a question inherited from the 19th century and the activities of the early biogeographers (Nelson & Platnick, 1984). Alfred Wegener (Wegener, 1915) first proposed the idea of continental movement. Because the specific mechanism Wegener proposed to account for continental movement was not feasible, his theory fell into discredit with the great majority of geologists. In the early 1960s, new evidence developed that provided a mechanism for continental movement and crustal evolution, creating a scientific practice that originated a model from which sprang a particular coherent tradition of geosciences (Condie, 1997).

The biogeographical consequences of plate movements and interactions are enormous. The rearrangement of continental landmasses and island areas and the opening and closing of sea and ocean basins initiated by these movements and interactions have profoundly affected the distribution and history of organisms. Therefore, the whole idea of earth evolution has a strong influence on biogeography, which is reflected in the motto of Léon Croizat (1964, p. 858):

> Earth and life evolve together

Cladistics as the basic language of comparative biology

Cladograms resulting from the application of cladistics (Nelson & Platnick, 1981) have become a powerful language to communicate a system of relationships to other biologists (Crisci, 1998a). Biologically and historically the phylogenetic relationships between taxa and their geographical distribution are intimately linked. Nodes of a cladogram are potentially informative about the distributional history of the organisms and about relationships among geographical areas occupied by them (Crisci, 1998b). For this reason, cladistics is playing a crucial role in the current situation of historical biogeography. On the other hand, the increased use of quantifiable cladistic methods and statistical hypothesis-testing is forcing biogeographers towards a more precise formulation of methodological practices and theoretical ideas and the exact quantification of their implications.

The biologist's perception of biogeography

Biogeography (as a whole, not only historical biogeography) is perceived as a strange discipline by a vast majority of biologists (Crisci *et al*., 2000). Its extraordinary complexity and its diversity of approaches make biogeography a sort of uncomfortable side-effect of biology.

A quotation from Nelson (1978, p. 269) reflects this perception:

> Biogeography is a strange discipline. In general, there are no institutes of biogeography; there are no departments of it. There are no professional biogeographers – no professors of it, no curators of it. It seems to have few traditions. It seems to have few authoritative spokesmen.

Internal forces

Internally, the forces that are shaping the present of historical biogeography are: the proliferation of competing articulations (e.g. ecology vs. history, panbiogeography vs. cladistic biogeography, event-based methods vs. pattern-based methods); and recourse to philosophy and the debate over fundamentals (e.g. conceptions of space: absolute space vs. relative space).

A revolution in science can be recognized by old terms acquiring new meanings and by an increase in philosophizing by its practitioners (Heisenberg, 1958). Historical biogeography is clearly in the midst of a revolution and this is nowhere more evident than in the fact that, of the 30 techniques of historical biogeography currently in use, 23 (76%) have been proposed in the last 14 years.

Furthermore, in the last 2 years four books articulating different points of view on the subjects were published: *Panbiogeography: tracking the history of life* (Craw *et al*., 1999), *Cladistic biogeography* (Humphries & Parenti, 1999), *Phylogeography: the history and formation of species* (Avise, 2000) and *Introducción a la teoría y práctica de la biogeografía histórica* (Crisci *et al*., 2000). This revolution may well testify to the healthiness of the subject, but more promisingly, it may presage major changes as predicted by the following quotation from Kuhn (1970, p. 91):

> The proliferation of competing articulations, the willingness to try anything, the expression of explicit discontent, the recourse to philosophy and to debate over fundamentals, all these are symptoms of a transition from normal to extraordinary research.

SPATIAL ANALYSIS

Spatial analysis is a modern approach to the study of phenomena that manifest themselves in space. It deals with formal models of spatial organization and assumes knowledge of spatial arrangements and space–time processes (Gatrell, 1983). The tradition of spatial analysis includes the study of three interrelated themes:

(1) spatial arrangement
(2) space–time processes
(3) spatial prediction (future arrangements) and postdiction (past arrangements)

By spatial arrangement I mean the pattern of location of the objects under study. The study of time-space processes concerns how spatial arrangements are modified by movement or spatial interaction.

Spatial prediction and postdiction seek, respectively, to forecast future spatial arrangements (prediction) or to establish on the basis of present evidence what the past spatial arrangements must have been like (postdiction = retrodiction).

This threefold scheme can be applied to historical biogeography: spatial arrangement is the distribution of the organisms throughout the geographical space, space–time processes are the events that can modify the geographical spatial arrangement of the organisms and postdiction (prediction has not much use in historical biogeography) is the possibility of determining past biogeographic events in terms of given observations. I will briefly discuss these three themes.

Spatial arrangement

No one will deny the value of the geographical distribution of organisms in biogeography, but unfortunately most books on biogeography approach the subject from an ecological perspective, hence the emphasis on ecosystem rather than areas (e.g. Cox & Moore, 2000). Recently, there has been an attempt (Craw *et al.*, 1999) to reintroduce and re-emphasize the importance of the spatial or geographical dimension of life's diversity for biogeography and for our understanding of evolutionary patterns and processes. Besides its partisan position of a particular method, this attempt, based on an approach called panbiogeography, has two important points for biogeography:

(1) to focus on the role of locality and place in the history of life; and
(2) to consider that an understanding of locality is a fundamental precondition to any adequate analysis of historical biogeography.

Space–time processes

Biogeographers have identified three different space-time processes that can modify the geographical spatial arrangement of the organisms:

(1) extinction
(2) dispersal
(3) vicariance

Extinction – the death of all individuals in a local population, a species, or a higher taxon – has been accepted by the biogeographers without controversy. This is not the case for the other two processes (dispersal and vicariance) that have been considered for many years competing explanations of the geographical distribution of organisms. This competition appears every time that a biogeographer tries to explain disjunct distribution patterns such as the one shown by the plant genus *Nothofagus* Blume ('southern beeches', Nothofagaceae). Either its common ancestor originally occurred in one of the areas and later dispersed into the other ones, where descendants survive to present day, or its ancestor was originally widespread in greater areas, which became fragmented, and its descendants have survived in the fragments until now (Hill & Jordan, 1993; Linder & Crisp, 1995). These historical explanations are named, respectively, dispersal and vicariance (Nelson & Platnick, 1984).

In the dispersal explanations, the range of the ancestral population was limited by a pre-existing 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 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 (Fig. 1).

For centuries dispersal was the dominant explanation for the distribution of organisms, based on strict adherence to the geological concept of earth stability. Two botanists, Stanley Cain (1944) and Léon Croizat (1958) in particular, were among the first scientists to challenge vocally the dispersal explanation as the main process in biogeography and promote vicariance as an equally important process.

According to Croizat (1964) and Craw *et al.* (1999) the vicariance-dispersal opposition can be resolved by applying a biogeographic model (the vicariance form-making or periodic mobilism) involving alternating cycles of dispersal and vicariance. This resolution recognizes both dispersal and vicariance as important processes by which organisms achieve their geographical distributions.

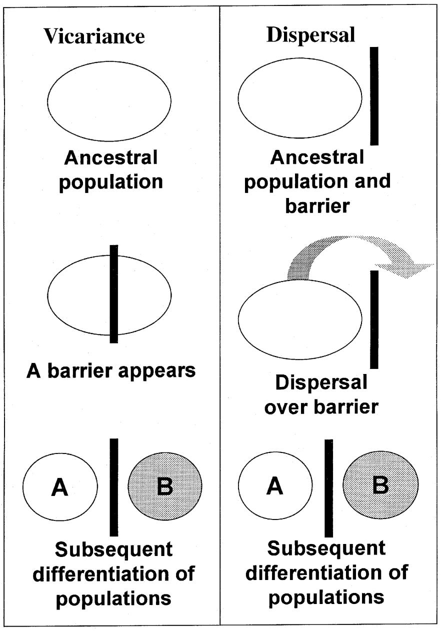

Figure 1 Historical explanations (vicariance, dispersal) of the disjunct distribution of two taxa (A, B). (Modified from Nelson & Platnick, 1984 and Cranston & Naumann, 1991).

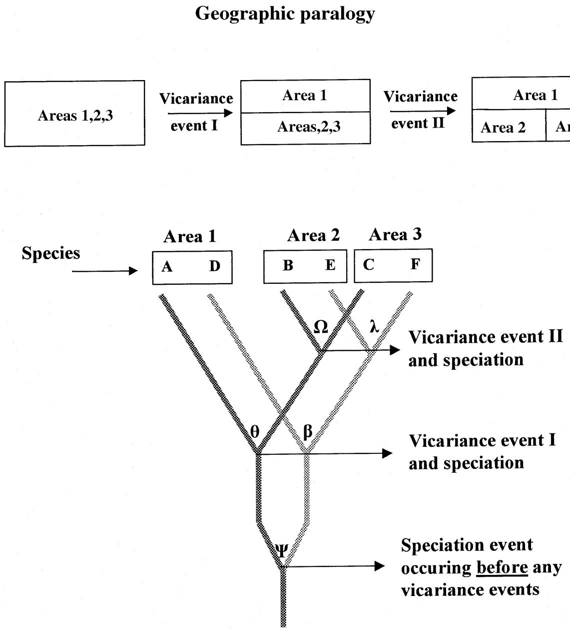

Figure 2 Geographic paralogy as a result of a speciation event (Ψ) independent of the vicariance of the area. Two subsequent events of speciation (*θ*, β) are related to vicariance event I and two further subsequent event of speciation (Ω, *λ*) are related to vicariance event II. Species A, B, C, D, E, F. Areas 1, 2, 3. (Modified from Crisci *et al.*, 2000).

Vicariance can be further subdivided into three kinds of events:

(1) vicariance followed by speciation (this process lead to sister species distributed in sister areas),
(2) vicariance events that lack allopatric speciation (this process retains widespread species), and
(3) vicariance events followed by speciation after a previous speciation event independent of the vicariance of the area (Nelson & Ladiges, 1996; this process lead to geographical paralogy, multiplication of lineages, sympatry, redundancy, Fig. 2).

Recently, Ronquist (1997b) has suggested the need to separate dispersal into two kinds of events. According to him dispersal in response to the disappearance of a previous dispersal barrier (predicted dispersal = range expansion) should be separate from random colonization of disjunct areas (random dispersal).

Postdiction

Reconstructing past biogeographic events in historical biogeography can be performed from three different perspectives that are related to three different goals:

(1) reconstructing the distributional history of individual groups ('taxon biogeography'),
(2) reconstructing the history of areas of endemism (search for general area relationships; 'area biogeography'), and
(3) reconstructing the distributional history of biotas (search for spatial homology).

TAXONOMY OF METHODS

The proliferation of competing articulations in historical biogeography has generated a great number of approaches to the subject. This diversity is difficult to present without some kind of taxonomy of methods. The taxonomy that I will present here, as all taxonomies, is debatable but it is used here as a way to organize the prevalent confused state of the discipline.

There are at least nine basic historical biogeographic approaches: (1) centre of origin and dispersal (2) panbiogeography (3) phylogenetic biogeography (4) cladistic biogeography (5) phylogeography (6) parsimony analysis of endemicity (7) event-based methods (8) ancestral areas, and (9) experimental biogeography.

(1) Centre of origin and dispersal. This approach has been originated in the Darwin–Wallace tradition. They considered that species originate in one centre of origin, from which some individuals subsequently disperse by chance, and then change through natural selection. Among its most prominent exponents has been Matthew (1915). This approach assumes the possibility of dispersal and extinction, and its main concern is the distributional history of individual groups.
(2) Panbiogeography. This approach, originally proposed by Croizat (1958), basically plots distributions of organisms on maps and connects the disjunct distribution areas or collection localities together with lines called tracks. Individual tracks for unrelated groups of organisms are then superimposed, and if they coincide, the resulting summary lines are considered generalized tracks. Generalized tracks indicate the pre-existence of ancestral biotas, which subsequently become fragmented by tectonic and/or climate change. The area where two or more generalized tracks intersect is called node. 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. This approach assumes the possibility of dispersal, vicariance and extinction, and its main concern is the history of biotas.
(3) Phylogenetic biogeography. This was the first approach to consider a phylogenetic hypothesis for a given group of organisms as the basis for inferring its biogeographic history (Brundin, 1966). It was defined as the study of the history of monophyletic groups in time and space. Phylogenetic biogeography applies two basic rules: (a) Progression rule. The primitive members of a taxon are found closer to its centre of origin than more apomorphic ones, which are found on the periphery (b) 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. This approach assumes the possibility of dispersal and extinction, and its main concern is the distributional history of individual groups.
(4) Cladistic biogeography. This approach was originally developed by Rosen (1978), and Nelson & Platnick (1981). Cladistic biogeography assumes that the correspondence between phylogenetic 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. A cladistic biogeographic analysis comprises of two steps: the construction of area cladograms from different taxon cladograms and the derivation of general area cladogram(s). This approach assumes the possibility of dispersal, vicariance, and extinction, and its main concern is the history of individual groups, and subsequently the history of areas.

(5) Phylogeography. This approach was originally proposed by Avise *et al.* (1987) and is the study of the principles and processes governing the geographical distribution of genealogical lineages at intraspecific level using mitochondrial DNA (mtDNA) in animals and chloroplast DNA (cpDNA) in plants. In this approach the individuals are genotyped and assigned to maternal lineages and the resulting phylogeny is related to patterns of geographical distribution. This approach assumes the possibility of dispersal and vicariance, and implicitly extinction, and its main concern is the distributional history of populations, and subsequently the history of areas.

(6) Parsimony analysis of endemicity (PAE). This approach is a tool of historical biogeography that allows discovering the patterns of organism distribution using biota similarity (Rosen, 1988). The PAE classifies localities, quadrats or areas (analogous to taxa, if compared with the analysis of phylogenetic systematic) according to their shared taxa (analogous to characters) by means of the most parsimonious solution (parsimony principle). Occurrence of a particular taxon in an area can be interpreted as a character. Shared presence of taxa are treated as synapomorphies in cladistic analysis. This approach, as originally proposed by B. Rosen does not make assumptions about processes, however, according to Craw (1988) the 'character' reversions in the resulting cladogram(s) could be biogeographically interpreted as extinctions, while the parallelisms could be interpreted as dispersions. The main concern of this approach is the history of areas or localities.

(7) Event-based methods. This approach postulates explicit models of the processes that have an effect on the geographical distribution of living organisms (Ronquist, 1997a). The different types of processes (dispersal, extinction, and vicariance) are identified and assigned values of benefit-cost under an explicit model of functioning of nature. Consequently, the distributional history of a taxon is inferred on the basis of phylogenetic information and applying the criterion of maximum benefits and minimum costs respecting the biogeographical processes (e.g. maximizing vicariance and minimizing dispersal and extinction).

(8) Ancestral areas. Bremer (1992) formalized a cladistic procedure based on a dispersalist approach. The procedure allows one to identify the ancestral area of a group from the topological information of its cladogram given the information of their presence on deep and numerous branches in that cladogram. Each area can be considered a binary character with two states (present or absent) and optimized on the cladogram. By comparing the numbers of gains and losses, it is possible to estimate areas most likely to have been part of the ancestral areas.

(9) Experimental biogeography. This approach, proposed by Haydon *et al.* (1994), exploits computers to model faunal build-up repeatedly against a fixed vicariant background over ecological and evolutionary time scales. This approach enables a biogeographer to know both vicariant history and actual phylogeny. Moreover, history can be replayed repeatedly to accumulate a sample of multiple phylogenies and to estimate probability density functions for biogeographic variables. Roles of stochastic, historical and ecological processes in adaptive radiations can also be assessed. This approach assumes the possibility of dispersal, vicariance and extinction.

The main characteristics of the nine approaches are summarized in Table 1. The astonishing complexity of the subject can be illustrated by the diversity of techniques proposed under the nine approaches: Table 2 shows 30 techniques, 12 of them under the cladistic biogeographic approach.

CRITICAL ISSUES

The preceding sections have carried a schematic description of the current state of historical biogeography as far as it can go in this paper. If this description has at all caught the essential structure of a discipline's revolution, it will simultaneously have posed a special problem. If a scientific revolution is a sign of a transition to a new paradigm (Kuhn, 1970), what needs to be done to generate the new foundation? A foundation that will define implicitly the problems and methods of historical biogeography for succeeding generations of practitioners.

It is absolutely clear that the whole practice and philosophy of biogeography depend upon the development of a coherent and comprehensive conceptual framework for handling the distribution of organisms and events in space. It is impossible to present here an exhaustive list of critical issues that need to be tackled to produce this conceptual framework, but a short discussion on several of them will illustrate the task ahead.

Table 1 Main characteristics of the nine historical biogeographic approaches (N/A = not applicable)

	Processes			History					Rank		
	Dispersal	Dispersal and vicariance	Extinction	Area	Taxon	Biota	Phylogeny	Explicit model	Below species level	Species level, above species level	Biota similarity
Centre of origin and dispersal	✔		✔		✔					✔	
Panbiogeography		✔	✔			✔			✔	✔	
Phylogenetic biogeography	✔		✔		✔		✔			✔	
Ancestral areas	✔		✔		✔		✔		✔	✔	
Cladistic biogeography		✔	✔	✔	✔		✔			✔	
Event-based methods		✔	✔		✔		✔	✔		✔	
Phylogeography		✔	✔	✔	✔		✔		✔		
Parsimony analysis of endemicity	N/A	N/A	N/A	✔						✔	✔
Experimental biogeography		✔	✔	✔			✔	✔	✔	✔	

A solution for the ecology–history opposition is certainly needed. Ecology and history have played roles together at all times, they are indissolubly tied together. Therefore, the long established division between ecology and history is an obstacle to the progress of biogeography (Morrone, 1993).

One important area of the required conceptual framework is the issue of methods, including the question: which is the best approach? Currently, the answer to this question is not clear. In fact, despite their various shortcomings, each approach makes a contribution in addressing a different type of biogeographical question (e.g. history of areas, distributional history of taxa or history of biotas). According to Morrone & Crisci (1995) the future biogeographic methodologies will probably use an integrated approach that will take advantage of the merits of each method.

Among other questions of methods are:

(1) hierarchical vs. nonhierarchical techniques (Ronquist, 1997a,b);
(2) optimality criteria (Page, 1994a; Ronquist, 1997a);
(3) tests for assessing significance of biogeographic hypotheses (Morrone & Crisci, 1995);
(4) interaction between molecular studies and biogeography (e.g. testing the timing of biogeographic events using molecular divergence based on molecular clocks, Caccone *et al.*, 1994);
(5) interaction between palaeontology and biogeography (e.g. fossils as timing and palaeoecological indicators in biogeography, Pascual & Ortiz Jaureguizar, 1990); and
(6) the developing of a single method that will encompass historical associations in: molecular systematics (organisms–genes), parasitology (hosts–parasites) and biogeography (areas–taxa) (Page, 1994a).

Controversies are common in historical biogeography today and they need to be faced to find a way out of them. Two of these controversies are:

(1) the proposition that organisms that are less capable of altering their geographical distribution are better historical subjects than the ones that possess powers of dispersal that allow them to alter their distribution more readily (see, Haydon *et al.*, 1994); and
(2) the question of whether there exist areas of endemism (Hovenkamp, 1997) and in the case that they do, how to recognize them (Morrone, 1994).

Another critical issue is the scarcity of high quality data that hampers the development of historical biogeography (Morrone & Crisci, 1995). Donn Rosen's Caribbean data from the 1970s have become legendary because almost everyone proposing a new technique still uses them.

Finally, a critical issue is the relationship between biogeography and conservation (Craw *et al.*, 1999). The biodiversity question is really a biogeographic one, as it is a question of where the limited

Table 2 Historical biogeographic techniques listed under the corresponding approaches and with their original authors. 'Reconciled trees' may also be listed under cladistic biogeography

Techniques	Author(s)
Centre of origin and dispersal	Matthew (1915)
Panbiogeography	
Track analysis	Croizat (1958)
Spanning graphs	Page (1987)
Track compatibility	Craw (1988)
Phylogenetic biogeography	Brundin (1966)
Ancestral areas	
Camin & Sokal optimization	Bremer (1992)
Fitch optimization	Ronquist (1994)
Weighted Fitch optimization	Hausdorf (1998)
Cladistic biogeography	
Reduced area cladogram	Rosen (1978)
Ancestral species map	Wiley (1980)
Quantitative phylogenetic biogeography	Mickevich (1981)
Component analysis	Nelson & Platnick (1981)
Brooks parsimony analysis	Wiley (1987)
Component compatibility	Zandee & Roos (1987)
Quantification of component analysis	Humphries *et al.* (1988)
Three-area statements	Nelson & Ladiges (1991)
Integrative method	Morrone & Crisci (1995)
WISARD	Enghoff (1996)
Paralogy free subtrees	Nelson & Ladiges (1996)
Vicariance events	Hovenkamp (1997)
Event-based methods	
Coevolutionary 2-dimensional cost matrix	Ronquist & Nylin (1990)
Dispersal-vicariance analysis	Ronquist (1997a)
Reconciled trees (Maximum cospeciation)	Page (1994a, b)
Jungles	Charleston (1998)
Combined method	Posadas & Morrone (in press)
Phylogeography	Avise *et al.* (1987)
Parsimony analysis of endemicity	
Localities	Rosen (1988)
Areas of endemisms	Craw (1988)
Quadrats	Morrone (1994)
Experimental biogeography	Haydon *et al.* (1994)

financial and human resources should be applied (Crisci *et al.*, 1999). Historical biogeographic analyses, however, are not playing the significant role in biodiversity conservation that they should.

CONCLUSION

My conclusion will be simple. We have made enormous strides in the past few years; in other words, we have started to babble in the language with which the traces of the past are telling us the history of life on earth. But we are also in the precise moment that we discover the provisionality of our knowledge and that this history is so complex that probably we will never see it totally revealed.

Does this mean that our attempt to understand the distribution of organisms is a hopeless enterprise? Two voices can answer this question. The first one is the voice of science, when Karl Popper (1959, p. 281) says:

> Science never pursues the illusory aim of making its answers final, or even probable. Its advance is, rather, towards the infinite yet attainable aim of ever discovering new, deeper, and more general problems, and of subjecting its ever tentative answers to ever renewed and ever more rigorous tests.

> The wrong view of science betrays itself in the craving to be right; for it is not his *possession* of knowledge, of irrefutable truth, that makes the man of science, but his persistent and recklessly critical *quest* for truth.

The second voice is the voice of art. It is a painting – 'Sinbad the Sailor – of the Swiss artist Paul Klee. It shows an oarsman in a small boat in a zone of light amidst a 'sea' of darkness. There is little light, but enough to permit in rather slow motion the progress of the oarsman.

That is the way it is in any scientific enterprise, including biogeography. A journey like this is a difficult task that requires an attitude of modesty but not submission and, no doubt, it is a fascinating adventure.

I certainly believe that in the perseverance of the oarsman is based his own glory.

ACKNOWLEDGMENTS

First of all I would like to express my gratitude for the honor that the Program Committee of the XVI International Botanical Congress (St Louis, Missouri, USA, August 1999) has bestowed on me by inviting me to present the plenary lecture that originated this paper. I would like to thank P. Berry, M. Bonifacino, C. Cingolani, M. Donato, H. Enghoff, P. Hoch, K. Hurlbert, P. Ladiges, R. Miranda Esquivel, J.J. Morrone, G. Nelson, F. Ocampo, E. Ortiz Jaureguizar, P. Posadas, J. Price, S. Roig-Juñent, F. Ronquist and M. Wetter for comments on the manuscript or parts of the manuscript, and M. Pabón and P. Marchionni for technical assistance. Valuable comments of Mike Crisp, Peter Linder and an anonymous reviewer resulted in improvement of the manuscript. Liliana Katinas provided an immeasurable amount of help and advice, her comments have undoubtedly made this paper of much higher quality that it would have been otherwise. My research on biogeography was supported by National Geographic Society (Grants no. 3966-88, 4662-91, 5776-96) and Consejo Nacional de Investigaciones Científicas y Tēcnicas (CONICET), Argentina.

JORGE V. CRISCI

Museo de La Plata, 1900 La Plata, Argentina.
E-mail: jcrisci@netverk.com.ar

REFERENCES

Avise, J.C. (2000) Phylogeography: the history and formation of species. Harvard University Press, Cambridge, Massachusetts.

Avise, J.C., Arnold, J., Ball, R.M. Jr, Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A. & Saunders, N.C. (1987) Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics*, **18**, 489–522.

Bremer, K. (1992) Ancestral areas: a cladistic reinterpretation of the center of origin concept. *Systematic Biology*, **4**, 435–445.

Brundin, L. (1966) Transantarctic relationships and their significance. *Kungliga Svenska Vetenskapsakademiens Handligar*, **11**, 1–472.

Caccone, A., Milinkovitch, M.C., Sbordoni, V. & Powell, J.R. (1994) Molecular biogeography: using the Corsica-Sardinia microplate disjunction to calibrate mitochondrial rDNA evolutionary rates in mountains newts (*Euproctus*). *Journal of Evolutionary Biology*, **7**, 227–245.

Cain, S.A. (1944) *Foundations of plant geography.* Harper & Brothers, New York.

Charleston, M.A. (1998) Jungles: a new solution to the host/parasite phylogeny reconciliation problem. *Mathematical Biosciences*, **149**, 191–223.

Condie, K.C. (1997) *Plate tectonics and crustal evolution*, 4th edn. Butterworth & Heinemann, Woburn.

Cox, C.B. & Moore, P.D. (2000) *Biogeography: an ecological and evolutionary approach*, 6th edn. Blackwell, Oxford.

Cranston, P.S. & Naumann, I.D. (1991) Biogeography. *The insects of Australia* (ed. I.D. Naumann), pp. 180–197. Melbourne University Press, Melbourne.

Craw, R.C. (1988) Continuing the synthesis between panbiogeography, phylogenetic systematics and geology as illustrated by empirical studies on the biogeography of New Zealand and the Chatham Islands. *Systematic Zoology*, **37**, 291–310.

Craw, R.C., Grehan, J.R. & Heads, M.J. (1999) *Panbiogeography: tracking the history of life*, Oxford biogeography series No. 11. Oxford University Press, New York.

Crisci, J.V. (1998a) Forma, espacio, tiempo: los métodos modernos de reconstrucción filogenética. Introducción. *Monographs in Systematic Botany from the Missouri Botanical Garden*, *Proceedings of the VI Congreso Latinoamericano de Botánica*, **68**, 443–444.

Crisci, J.V. (1998b) El cladismo y la biogeografía histórica. *Monographs in Systematic Botany from the Missouri Botanical Garden, Proceedings of the VI Congreso Latinoamericano de Botánica*, **68**, 459–463.

Crisci, J.V., Katinas, L. & Posadas, P. (2000) *Introducción a la Teoría y Práctica de la Biogeografía Histórica*. Sociedad Argentina de Botánica, Buenos Aires, Argentina.

Crisci, J.V., Posadas, P., Katinas, L. & Miranda Esquivel, D.R. (1999) Estrategias evolutivas para la conservación de la biodiversidad en América del Sur austral. *Biodiversidad Y Uso de la Tierra Conceptos Y Ejemplos de Latinoamérica* (eds S.D. Matteucci, O.T. Solbrig, J. Morello and G. Halffter), pp. 175–198. Colección CEA no. 24, EUDEBA-UNESCO, Buenos Aires, Argentina.

Croizat, L. (1958) *Panbiogeography*, Vol. I, IIa, IIb. Published by the author, Caracas, Venezuela.

Croizat, L. (1964) *Space, time, form: the biological synthesis*. Published by the author, Caracas, Venezuela.

de Candolle, A.P. (1820) Géographie botanique. *Dictionnaire des Sciences,* **18**, 359–422. FG Levrault, Strasbourg. Reprinted in *Ecological phytogeography in the nineteenth century* (ed. F.N. Egerton), 1977. Arno Press, New York.

Dickens, C. (1859) *A tale of two cities*. London.

Enghoff, H. (1996) Widespread taxa, sympatry, dispersal, and an algorithm for resolved area cladograms. *Cladistics*, **12**, 349–364.

Gatrell, A. (1983) *Distance and space. A geographical perspective*. Clarendon Press, Oxford.

Hausdorf, B. (1998) Weighted ancestral area analysis and a solution of the redundant distribution problem. *Systematic Biology*, **47**, 445–456.

Haydon, D.T., Crother, B.I. & Pianka, E.R. (1994) New directions in biogeography? *Trends in Ecology and Evolution*, **10**, 403–406.

Haydon, D.T., Radtkey, R.R. & Pianka, E.R. (1994) Experimental biogeography: interactions between stochastic, historical, and ecological processes in a model archipielago. *Species diversity in ecological communities: historical and geographical perspectives* (eds R.E. Ricklefs and D. Schluter), pp. 117–130. University Chicago Press, Chicago.

Heisenberg, W. (1958) *The physicist's conception of nature*. Harcourt Brace, New York.

Hill, R.S. & Jordan, G.J. (1993) The evolutionary history of *Nothofagus* (Nothofagaceae). *Australian Journal of Botany*, **6**, 111–126.

Hovenkamp, P. (1997) Vicariance events, not areas, should be used in biogeographical analysis. *Cladistics*, **13**, 67–79.

Humphries, C.J., Ladiges, P.Y., Roos, M.C. & Zandee, M. (1988) Cladistic biogeography. *Analytical biogeography an integrated approach to the study of animal and plant distributions* (eds A.A. Myers and P.S. Giller), pp. 371–404. Chapman & Hall, London & New York.

Humphries, C.J. & Parenti, L.R. (1999) *Cladistic biogeography*, 2nd edn. Oxford biogeography series No. 12. Oxford University Press, New York.

Kuhn, T.S. (1970) *The structure of scientific revolutions*, 2nd edn. The University of Chicago Press, Chicago.

Linder, H.P. & Crisp, M.D. (1995) *Nothofagus* and pacific biogeography. *Cladistics*, **11**, 5–32.

Matthew, W.D. (1915) Climate and evolution. *Annals of New York Academy of Science*, **24**, 171–318.

Mickevich, M.F. (1981) Quantitative phylogenetic biogeography. *Advances in cladistics: proceedings of the first meeting of the Willi Hennig Society* (eds V.A. Funk and D.R. Brooks), pp. 202–222. New York Botanical Garden, Bronx, New York.

Morrone, J.J. (1993) Beyond binary oppositions. *Cladistics*, **9**, 437–438.

Morrone, J.J. (1994) On the identification of areas of endemism. *Systematic Biology,* **43**, 438–441.

Morrone, J.J. & Crisci, J.V. (1995) Historical biogeography: introduction to methods. *Annual Review of Ecology and Systematics*, **26**, 373–401.

Myers, A.A. & Giller, P.S. (eds) (1988) *Analytical biogeography. An integrated approach to the study of animal and plant distributions*. Chapman & Hall, London & New York.

Nelson, G. (1978) From Candolle to Croizat: comments on the history of biogeography. *Journal of the History of Biology*, **11**, 269–305.

Nelson, G. & Ladiges, P.Y. (1991) Three-area statements: standard assumptions for biogeographic analysis. *Systematic Zoology*, **40**, 470–485.

Nelson, G. & Ladiges, P.Y. (1996) Paralogy in cladistic biogeography and analysis of paralogy-free subtrees. *American Museum Novitates*, **3167**.

Nelson, G. & Platnick, N.I. (1981) *Systematics and biogeography: Cladistics and vicariance*. Columbia University Press, New York.

Nelson, G. & Platnick, N.I. (1984) *Biogeography*, Carolina Biology Readers No. 119. Biological Supply Company, Burlington, North Carolina.

Oakeshott, M.J. (1959) *The voice of poetry in the conversation of mankind*. Bowes & Bowes, London.

Page, R.D.M. (1987) Graphs and generalized tracks: quantifying Croizat's panbiogeography. *Systematic Zoology*, **36**, 1–17.

Page, R.D.M. (1994a) Maps between trees and cladistic analysis of historical associations among genes, organisms, and areas. *Systematic Biology*, **43**, 58–77.

Page, R.D.M. (1994b) Parallel phylogenies: reconstructing the history of host-parasite assemblages. *Cladistics*, **10**, 155–173.

Pascual, R. & Ortiz Jaureguizar, E. (1990) Evolving climates and mammal faunas in South America. *Journal of Human Evolution*, **19**, 23–60.

Popper, K.R. (1959) *The logic of scientific discovery*. Hutchinson, London.

Posadas, P. & J.J. Morrone (in press) Biogeografía histórica de la subregión Subantártica. *Biogeografía de América Latina y El Caribe* (eds J. Llorente Bousquets and J.J. Morrone), México.

Ronquist, F. (1994) Ancestral areas and parsimony. *Systematic Biology*, **43**, 267–274.

Ronquist, F. (1997a) Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, **46**, 195–203.

Ronquist, F. (1997b) Phylogenetic approaches in coevolution and biogeography. *Zoologica Scripta*, **26**, 313–322.

Ronquist, F. & Nylin, S. (1990) Process and pattern in the evolution of species association. *Systematic Zoology*, **39**, 323–344.

Rosen, B.R. (1988) From fossils to earth history: applied historical biogeography. *Analytical biogeography an integrated approach to the study of animal and plant distributions* (eds A.A. Myers and P.S. Giller), pp. 437–481. Chapman & Hall, London & New York.

Rosen, D.E. (1978) Vicariant patterns and historical explanation in biogeography. *Systematic Zoology*, **27**, 159–188.

Wegener, A. (1915) *Die Entstehung der Kontinente und Ozeane*. Vieweg & Sohn, Braunschweig.

Wiley, E.O. (1980) Phylogenetic systematics and vicariance biogeography. *Systematic Botany*, **5**, 194–220.

Wiley, E.O. (1987) Methods in vicariance biogeography. *Systematics and evolution: a matter of diversity* (general editor P. Hovenkamp), pp. 283–306. Inst. Syst. Bot, University of Utrecht.

Zandee, M. & Roos, M.C. (1987) Component-compatibility in historical biogeography. *Cladistics*, **3**, 305–332.

BIOSKETCH

Jorge V. Crisci is professor of botany at Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina. His professional interests include: biological classification, phylogenetics, multivariate analysis, biological education, historical biogeography and conservation of biodiversity.