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Form, Space and Time: Which Comes First?

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Source: *Journal of Biogeography*, Vol. 27, No. 1 (Jan., 2000), pp. 11-15

Published by: [Wiley](#)

Stable URL: <http://www.jstor.org/stable/2655978>

Accessed: 02/01/2014 09:08

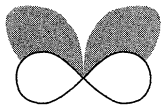
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MILLENNIUM
GUEST
EDITORIAL
NUMBER 3

Form, space and time; which comes first?

Keywords

Cladistics, dispersal, panbiogeography, vicariance.

INTRODUCTION

Despite considerable material progress in historical biogeography since Linnaeus (1781) first pronounced that species originated in Paradise (see Platnick & Nelson, 1978; Humphries & Parenti, 1986) there are still problems as to what constitutes a rational approach. Presently, widely different theories, methods and explanations prevail for assessing biogeographic patterns across the globe and for the last forty years, or so, the subject has moved in fits and starts with occasional revivals of interest (see for example Croizat, 1964; Nelson & Platnick, 1981; Hovenkamp, 1987; Cracraft, 1989; Craw, 1989; Ladiges, Humphries & Martinelli, 1991; Craw *et al.*, 1999; Humphries & Parenti, 1999). In summarizing this period of activity Nelson & Ladiges (1996) noted that developments in geology and biology (plate tectonics and systematics) did not render the facts of geographic distribution more clearly but heightened the expectation of putting that discovery in reach of empirical investigation. The manifestation of the problem is that in much the same way systematics harbours different and frequently unconnected sub-disciplines, the same is true of historical biogeography.

In their recent book, Craw *et al.* (1999) recognize four contemporary branches of historical biogeography; theories of faunal realms (Sclater, 1858; Wallace, 1876), centres of origin (Linnaeus, 1781; Darwin, 1859), island biogeography (Equilibrium theory in the sense of MacArthur & Wilson, 1967), vicariance (or cladistic) biogeography (Nelson & Platnick, 1981) and panbiogeography (Croizat, 1958, 1964; Avise, 1989). Morrone & Crisci (1995) made a slightly different cut by suggesting that since Nelson & Platnick's (1981) synthesis we should recognize five basic methods, all of which have some value in the scheme of things. These include: dispersalism from ancestral centres of origin (Bremer, 1992, 1995; Bremer & Gustafsson, 1997), phylogenetic biogeography (in the sense of Hennig, 1966; Brundin, 1966, 1972a, 1972b, 1981, 1988), panbiogeography (*sensu* Croizat, 1952, 1958), cladistic biogeography (in the sense of Nelson & Platnick, 1981; Humphries & Parenti, 1986, 1999), and parsimony analysis of endemism (Rosen & Smith, 1988). To this list I would also add the 'event-based' methods of Ronquist (1997), and Hovenkamp (1997) for diagnosing historical sequences, and, the most recent chimera of scenario building, phylogeography, synthesizing molecular techniques, population biology, genetics, phylogenetic theory and dispersal biogeography (e.g. Arbogast, 1999; Avise, 2000; Avise *et al.*, 1987). Thus, it seems hardly surprising to me that Tassy & Deleporte 1999 when reviewing the 1998 biogeography symposium of the Willi Hennig Society suggested that historical biogeography was in a mess, a subject looking for a method.

HISTORICAL BIOGEOGRAPHY

Maybe this problem stems from an inability to deconstruct the central aims and the essential components of historical biogeography. Throughout, the subject has been dogged by evolutionary narratives about fossils and ancestors, and serious attempts to cope with the modern 'three-fold parallelism', the relationship between form, space and time, seems an endless, circular struggle. Of the many published works, Darwin's (1859) *Origin of species*, Croizat's (1964) *Space, time, form; the biological synthesis*, Hennig's (1966) *Phylogenetic systematics*, and Nelson & Platnick's (1981) *Systematics and biogeography; cladistics and vicariance*, stand out as markers in the shifting, century-long, examination of the interplay between these three aspects.

Darwin considered space in a rather static way. His special theory of evolution by natural selection was embedded in ecology. He saw species originating slowly and successively in 'centres of creation' to then disperse over the globe due to changes of climate and availability of habitat. For Darwin, geography and geology are older than life and, although the earth evolved slowly and steadily, continents remained static on a globe of fixed dimensions. Consequently, new species were formed after migration from centres of origin across existing geographical barriers. Form was expressed as variation and selection, time as geological succession, and space, dispersal of organisms across the pre-formed landscape.

Even before plate tectonics and continental mobility became respectable, Croizat's (1964) critique of

Darwin reminded us that the earth and life were forever evolving together and history forever repeats. To Croizat, evolution of form (as expressed in the taxonomy of organisms) took place in changing space, and time represented the fusion of geography and biology expressed as panbiogeographic direction. For Croizat the only way to uncover biogeographic history was to examine wholesale distribution patterns (panbiogeography), and to ignore preconceived mechanisms explaining processes. *Craw et al.* (1999) showed that Croizat was interested in classifying areas of the globe in terms of their geological and biotic history. Croizat eschewed the somewhat arbitrary areas of endemism, or the major biogeographical regions as conceived by the former biogeographers, de Candolle (1820), Wallace (1876) and Sclater (1858). To him these geological and geographical conglomerates, indicating previous historical sutures, needed to be teased apart to reveal the natural geographic entities through analysis of biotas.

Croizat was looking for the biogeographical equivalent of homology. For him, the modern ocean basins provided the boundaries of former historical units (Croizat, 1952, 1958, 1961, 1964), and 'centres of origin', 'migrations' by 'casual means', 'stepping stones' and 'landbridges' could all be ignored as particular explanations for observed patterns. Croizat's greatest contribution was to show that time is central to an understanding of the interplay between form and space and that dispersalist or vicariant narratives are futile debate (see also *Craw et al.*, 1999 and Humphries & Parenti, 1986, 1999). Nevertheless it appears that Croizat's critique of Darwinian narrative was incomplete. It is clear on reading *Craw et al.* (1999), that panbiogeography even now has yet to shake off the impediment of ancestors as part of the explanations it avowed to replace.

Hennig (1966) is arguably the most important systematist of the 20th century. He exposed the shortcomings of conventional systematic methods and provided the most substantial method for reconstructing phylogenies in the framework of Darwin's evolution by common descent (Richter & Meier, 1994). To his everlasting memory, Hennig provided the means of recognising relationships of taxa, and clarifying the meaning of homology and monophyly into one rational system. To Hennig, form was phylogenetic systematics, time was phylogeny, and space meant dispersal. Thus, despite a revolution in how taxa are recognised, and relationships of organisms are revealed, Hennig's view of space was somewhat traditional and stuck in a Darwinian mould of tracing ancestors through some infinite regress. Nelson & Platnick (1981) capitalized on these earlier developments when they synthesized the systematics of Hennig and the panbiogeography of Croizat into vicariance biogeography, to provide a method that classified areas in terms of general area cladograms. To them area relationships were based on taxic relationships and the technique really clarified (for me at least) the notion that life and earth evolved together. To Nelson & Platnick (1981) form was comparative biology, time was ontogeny, phylogeny and palaeontology, and space was represented by repetitive disjunct (vicariant) distribution patterns. The problem of the Hennigian approach which appeals to ancestors for hypotheses of characters (homology), and groups (monophyly), was overcome by the realisation that ancestry is a matter of interpretation rather than inherent to any method. Pattern cladistics modifies the practicalities of empirical endeavour (e.g. Humphries & Parenti, 1999) such that form and space represent the measurable aspects, and ancestry and time are inferred. It follows that historical biogeography is about classification of areas amongst biological and spatial co-ordinates, and not about dispersal or individual historical scenarios for every group of organisms: 'The geographic distributions of organisms are coherent patterns related to, and explained by, historical processes of geographic change' (Nelson & Ladiges, 1996).

NARRATIVES

Readers might wonder why it should be important to reiterate old issues that should be so patently obvious to historical biogeographers. The reason is that despite four decades of analytical criticism, narrative biogeography still seems to persist and is indeed growing with renewed vigour amongst contemporary evolutionists. Fossils and ancestors still assume cardinal importance and centres of origin are alive and kicking. Phylogenetic biogeography as described by Hennig (1966) and Brundin (1966) attempted to determine centres of origin by invoking gradual progression and morphological deviation from proposed centres as depicted at the roots of branching diagrams. More recently Bremer (1992) revived the approach when he used an optimisation procedure based on gains and losses of areas on area cladograms to determine ancestral areas (and hence centres of origin). He provided dispersal scenarios to explain present-day biogeographic patterns for particular groups of organisms as if uninterested in the relationships of areas (for a critique see Ronquist, 1994, 1995). The outcome of such an approach is that it represents yet another reworking of the idea that the 'tracks of life' (*Craw et al.*, 1999) are independent from geography and each group of organisms has its own story to tell. It should have been possible to let the matter rest but dispersal scenarios are being published at a rate

faster than ever before. Papers published under the rubric of phylogeography, defined as—the study of biogeography as revealed by a comparison of estimated phylogenies of populations or species with their geographic distributions—are widespread amongst investigations of particular groups of organisms² (e.g. Avise *et al.*, 1987; Avise, 2000; Bakker *et al.*, 1995; Mustrangi & Patton, 1997; Oppen *et al.*, 1994; Wooding & Ward, 1997). It seems that these contributions are revitalised descendants (through cladistics and molecular biology) of the ‘new systematics’ (Huxley, 1940), which, now as then, blur the boundaries of ecology, population biology, genetics and systematics, the distinction between pattern and process (Rieppel, 1988) and hence the relationship of space with form. The two aspects are considered to be separate rather than both part of the same system.

ANALYTICAL METHODS

Both cladistic biogeography and panbiogeography address the present and historical debate of pattern before process. Problems of dispersal and vicariance have dogged historical biogeography since the early 19th century. Panbiogeography sees itself as a subject that utilises a form-making model which recognizes that both ‘dispersal and vicariance as important processes by which organisms achieve their geographic distributions’ (Craw *et al.*, 1999). Its strength, is to recognize that it is the distributions of the organisms themselves that diagnose the areas to be classified. By using track analysis and the coincidence of tracks into generalized tracks it is considered possible to reconstruct ancestral biotas which have become fragmented through time by geographical change. This has considerable concordance with cladistic biogeography but the biggest drawback I see is that it does not make a clear statement as to what constitutes relationship between different areas on the earth. Rather than provide material evidence for homology it still clings to the mysteries of ancestry to hypothesise relationships of areas.

Cladistic biogeography is about classification of areas of endemism with a clear-cut analogy to systematics about how areas and the relationships of areas are recognised. Thus, by assuming clear correspondence between systematic relationships in different taxa in similar areas it provides biogeographically informative relationships of the biotas in those areas. Relationships of areas are identified from the internal nodes of cladograms with the geographic distributions of taxa placed at the terminal nodes. The historical relationships of the areas are inferred through congruence of pattern among two or more groups of taxa, and common history is represented in branching diagrams, area cladograms—hierarchical relationships of areas derived from cladograms of taxa.

The subject is complicated by the apparent lack of congruence amongst different taxa (see Humphries & Parenti, 1999 for details). There have been a number of attempts to separate signal from noise and to simplify incongruent patterns, including parsimony analysis of endemism (PAE) which classifies areas by their shared taxa. As with any shortcut method that tries to dispense with taxic homology and area paralogy PAE is a parody of systematic biogeography because it has corrupted the meaning of area homology. Nevertheless, it does raise the question of how to deal with biogeographical relationships rendered equivocal by widespread taxa across areas of endemism and by different patterns among different taxa brought about by a range of processes from extinction to different responses to earth history events.

Although others would argue, I still consider that the greatest success in solving this problem has come from component analysis (Nelson & Platnick, 1981; Humphries, 1989). Anomalies due to a variety of historical reasons can be catered for without assuming any dispersal, vicariant or extinction events, and recently, the problem of area paralogy has been greatly simplified by sub-tree sampling of area cladograms rife with geographic duplication (Nelson & Ladiges, 1996). However, there is a growing realization that a number of problems have yet to be solved. For example Hovenkamp (in prep.) suggests that it is not necessary to predefine ‘areas of endemism’, with all its associated problems (Axelius, 1991; Harold & Mooi, 1994; Morrone, 1994, Humphries, in prep.). Also, the widespread species should be considered on equal footing with less widespread or endemic ones, when evaluating their contribution to geographical and geological boundaries.

CONCLUSION—THE FUTURE

Although there is still a very long way to go in uncovering biogeographic patterns I believe that there is just one underlying sequence of geographical and geological evolution. Ecological biogeography

²See *Journal of Molecular Phylogenetics and Evolution*.

considers that diversity is in some equilibrium with the environment (e.g. MacArthur & Wilson, 1967). Historical biogeographers consider that non-equilibrium patterns due to historical singularities are not separated out or identified enough. When the historical components are adequately investigated most, if not all, the large-scale distribution patterns will be explained. Of the varied forms of methodology on offer I would suggest that to uncover a workable underlying theory of change of form in space and time will be based on an exhaustive analysis of biological and geological cladograms (Humphries & Parenti, 1999). Hopefully, this would have a more fruitful outcome than the supply of individual stories for every different group of taxa. Naturally, there are problems with combining taxa into general area patterns, in the delineation and recognition of areas, and the problem of optimizing multiple simple sequences derived from cladograms (Hovenkamp, 1997, in prep.). Nevertheless, I consider cladistic biogeography takes us one step further down the road to a solution than the panbiogeography programme which ultimately sees 'biodiversity ... made up of ... tracks and nodes of life' (Craw *et al.*, 1999). To me this represents only half of the equation—the recognition of the need for geographic homology. If ultimately the aim is to provide a general system of classification for all of the places on earth there needs to be a precise idea of what constitutes the relations (area homologies) and the things being related (areas) in the analyses.

ACKNOWLEDGMENTS

I am grateful to Peter Hovenkamp for allowing me to see his unpublished manuscript, to Darrel Siebert and David Williams for reading a draft of the text, Gary Nelson for his interesting insights and Philip Stott for inviting me to write this article.

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