Darwin, historical biogeography, and the importance of overcoming binary opposites

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ABSTRACT

It is well known that Darwin and Wallace came to discover the phenomenon of evolution through a historical approach to the geographical distribution of organisms. Before Darwin, evolution was a mere speculation that could be invoked to explain some facts. Darwin's biogeographical argument for evolution is based largely on three main explanatory hypotheses. The first is that the geographical distribution of organisms is historically informative. The second hypothesis is that long-distance dispersal over barriers is one main force (extinction is the other) that modifies the distribution of organisms. The third of Darwin's biogeographical hypotheses is that the factors that shape the distribution of organisms are mainly historical (large, often global and long temporal scales) rather than ecological (small spatial and short temporal scales). From the time of Darwin until now, a wide spectrum of biogeographical schools have provided new insights that challenge the central role of space, dispersal and history as the main explanatory hypotheses for the distribution of organisms, generating three binary opposites: (1) the spatial dimension of evolution: geographical distribution of organisms as historically informative vs. historically uninformative; (2) the processes that modify the geographical distribution of organisms: dispersal vs. vicariance; and (3) the explanation of geographical distribution: history vs. ecology. We analyse these three binary opposites to show that the components of each are complementary rather than antagonistic approaches to the study of biogeography.

Keywords

Biogeography, Charles Darwin, dispersal, ecology, evolution, geographical distribution, history of science, vicariance.

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INTRODUCTION

It is well known that Darwin and Wallace came to discover the phenomenon of evolution through a historical approach to the geographical distribution of organisms. Before Darwin, evolution was a mere speculation that could be invoked to explain some facts. The fact that the general features of distribution can hardly be interpreted otherwise than as the result of evolutionary processes forms one of the strongest arguments in *On the Origin of Species* (Darwin, 1859). With Darwin's biogeographical synthesis, evolution became integral to a compelling system of explanatory theory (Darlington, 1959; Ghiselin, 1972; Richardson, 1981; Mayr, 1982). The importance of historical biogeography in the genesis of Darwin's evolutionary theory justifies a brief reflection on how the publication of the *Origin* has shaped historical biogeography.

Darwin's biogeographical argument for evolution is based largely on three main explanatory hypotheses. The first is that the geographical distribution of organisms is historically informative, that is, that space is a dimension of evolution, evidenced in the opening paragraph of the *Origin*:

> When on board of H.M.S. *Beagle*, as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species.
>
> (Darwin, 1859, p. 1)

The second hypothesis is that long-distance dispersal over barriers (e.g. oceans) is one main force (extinction is the other) that modifies the distribution of organisms. Many references to dispersal are found in the two chapters of the *Origin* dedicated to biogeography, for example:

… all the grand leading factors of geographical distribution are explicable on the theory of migration (generally of the more dominant forms of life), together with subsequent modification and the multiplication of forms. We can then understand the high importance of barriers, whether of land or water, which separate our several zoological and botanical provinces.

(Darwin, 1859, p. 408)

Hence, it seems to me, as it has to many other naturalists, that the view of each species having been produced in one area alone, and having subsequently migrated from that area as far as its powers of migration and subsistence under past and present conditions permitted, is the most probable.

(Darwin, 1859, p. 353)

The third of Darwin's biogeographical hypotheses is that the factors that shaped the distributions of organisms are mainly historical (large, often global and long temporal scales) rather than ecological (small spatial and short temporal scales). Darwin starts Chapter XI of the *Origin* by saying:

In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions.

(Darwin, 1859, p. 346)

The three hypotheses together are synthesized in Darwin's last chapter of the *Origin*:

Looking to geographical distribution, if we admit that there has been during the long course of ages much migration from one part of the world to another, owing to former climatal and geographical changes and to the many occasional and unknown means of dispersal, then we can understand, on the theory of descent with modification, most of the great leading facts in Distribution.

(Darwin, 1859, p. 476)

From the time of Darwin until now, a wide spectrum of biogeographical schools provided new insights that challenge the central role of space, dispersal and history as the main explanatory hypotheses for the distribution of organisms, generating three binary opposites, as follows.

1. The spatial dimension of evolution: geographical distribution of organisms as historically informative vs. historically uninformative.

2. The processes that modify the geographical distribution of organisms: dispersal vs. vicariance.

3. The explanation of geographical distribution: history vs. ecology.

In binary opposites (Eagleton, 1983), one term, concept or process is central to the discipline, privileged, freezing the play of the system, and marginalizing the opposite member of the pair. In other words, when one opposite becomes central, it attempts to exclude and, in doing so, ignores or marginalizes the other. The three biogeographical binary opposites mentioned above went through several transpositions where the once-central opposite became marginal, and the marginal opposite became central. We will see that the first of these binary opposites, the recovery of historical information only through the distribution of organisms, was relegated to the status of simple raw data by the use of modern tools such as phylogeny and the molecular clock. The second, the dispersal

vs. vicariance paradigm, fluctuated through history, with each process alternately given more importance, the dispersal paradigm being favoured by modern molecular biogeographical schools. And the third of the binary opposites, ecological vs. historical explanations for an organism's distribution, were and are equally emphasized in biogeographical studies, but are divorced from each other. We will briefly analyse these three binary opposites to show that the components of each are complementary rather than antagonistic approaches to the study of biogeography.

GEOGRAPHICAL DISTRIBUTION OF ORGANISMS AS A DIMENSION OF EVOLUTION

To Darwin, the distribution of organisms was sufficiently historically informative that it became central in his evolutionary theory. This belief prevailed until the arrival of modern methods of phylogenetic reconstruction, especially those using molecular data. In many current analyses, the empirical data on geographical distribution of organisms that were so useful to Darwin are commonly considered historically uninformative if they are not combined with a phylogenetic analysis. In other words, geographical distributions become informative, understandable and comparable only when combined with a genealogical hypothesis and expressed in an area cladogram. Area cladograms are branching patterns of areas as determined from phylogenetic information by substituting the names of taxa for the names of areas in which they occur. The construction of area cladograms assumes that the nodes of the cladograms, with their information about relationships among taxa, are the medium through which geographical distributions are conveyed in a historically informative way. One factor in support of the idea of combining geographical distribution and genealogy is that organisms move about, so their actual distributions are historically informative only if they are seen in a historical context such as phylogeny. Another route to presenting this position, although less emphatic, was taken by Mayr (1982) and Haydon *et al.* (1994), with the idea that those organisms that are less capable of moving from one area to another (for instance, snails) provide a better historical signal than those organisms that can disperse more easily (for instance, bats). This assertion has been countered by Craw *et al.* (1999), who demonstrated a biogeographical congruence between some genera of bats and some genera of snails, and concluded that differing dispersal abilities of different organisms do not necessarily result in fundamentally different distribution patterns.

Craw *et al.* (1999) stressed that many aspects of current distribution (geographical structure, distributional limits, spatial geometry, boundaries and range, taxa present in a region, taxa absent in a region, etc.) are all potentially evolutionarily informative. They attempted to reintroduce and re-emphasize the importance of the spatial or geographical dimension of life's diversity for the study of biogeography and for our understanding of evolutionary patterns and processes. Despite its partisan adoption of a particular method, this

attempt, which is based on the panbiogeographical approach of Croizat (1958, 1964), has two important assets for biogeography: (1) it focuses on the role of locality and place in the history of life, and (2) it considers that an understanding of locality is a fundamental precondition to any adequate analysis of historical biogeography. Another method that focuses on the distribution of organisms is parsimony analysis of endemicity (PAE; Rosen, 1988), which classifies areas (or localities or quadrats) according to their shared taxa, resulting in a hierarchical classification of the geographical units. According to Rosen (1988), PAE generates historical (hence geological) hypotheses even from modern distributions.

The following example shows that distributions themselves can be empirical data in historical biogeography. The application of parsimony analysis of endemicity and panbiogeography (track compatibility analysis) to Onagraceae in North America (Katinas et al., 2004) helped to find the historical explanations that led to the high diversity and endemicity of the plant family in this area. These analyses defined two broad biogeographical units based on the distribution of many taxa, eastern and western North America, with the biotas on each side sharing a common history. These results are correlated with major historical events in North America, including orogenic processes such as the uplifting of the Rocky Mountains and the Sierra Madre Occidental in the early Tertiary, which changed the biota of western North America to a remarkable degree by creating a barrier to floristic exchanges between eastern and western North America. In this way, the analysis of the distribution of taxa through the application of two historical biogeographical methods facilitated the recovery of the distributional history of Onagraceae in North America. Similar methods were used to analyse the distributional information of South American taxa (animals, plants and fungi). The results indicated that South America is biogeographically hybrid (Katinas et al., 1999), a conclusion confirmed by recent studies using phylogenetically based biogeographical methods (Sanmartín & Ronquist, 2004).

DISPERSAL AND VICARIANCE

Prior to Darwin's work, naturalists had vigorously discussed the question of whether species were created at one or more points on the Earth's surface. When Darwin began his studies on the species question, the accepted opinion of naturalists was that animals and plants had each been created separately, that the needs of each had been provided for at the beginning, and that each was incapable of variation beyond certain predetermined, fixed limits. Darwin found a lack of congruence between the theory of special creation and the observable facts of biogeography. It was obvious to Darwin (1859, p. 351) that: '… several species of the same genus, though inhabiting the most distant quarters of the world, must originally have proceeded from the same source, as they have descended from the same progenitor'. In this way, Darwin (1859, p. 351) gradually introduces the centre of origin concept (in the Darwinian sense; see Croizat et al., 1974): 'It is also obvious

that the individuals of the same species, though now inhabiting distant and isolated regions, must have proceeded from one spot, where their parents were first produced …'. Darwin called these the 'single centres of creation' from which the species migrated to other regions. Darwin constructed a model involving mechanisms of dispersal, and was one of the first to study the effects of seawater on seeds. These experiments constituted an integral part of the argument in the Origin. He tested, for example, how long seeds could resist the injurious action of sea-water and found that out of 87 kinds, 64 germinated after an immersion of nearly 1 month, and a few survived an immersion of 137 days. Darwin showed also that seeds may be occasionally transported by drift timber, carcasses of birds floating on the sea, and in the intestines of living birds.

With the appearance, in the middle of the 20th century, of a formal method of phylogenetic reconstruction, the logical principle of Darwin's reasoning became generalized as the progression rule (Hennig, 1966), that is, to circumscribe a centre of origin from phylogenetic trees (Nelson & Ladiges, 2001). The progression rule, as applied for example by Brundin (1966) and Ross (1974), states that primitive members of a taxon are found closer to its geographical centre of origin than are more apomorphic ones, which are found on the periphery of the taxon's distribution. Their method assumes that taxonomic groups have centres of origin from which members dispersed (Humphries & Parenti, 1999). The idea that distributions of taxa in the most basal branches of a cladogram indicated the centre of origin was then evoked by one of Bremer's (1992) criteria for determining the ancestral area of a given taxon (Crisci et al., 2003) and by the current widespread way of optimizing the geographical distribution of taxa onto cladogram nodes.

The theory of continental drift postulated by Wegener (1915), and by others, and its general acceptance during the 1960s and 1970s, supported the idea that disjunct biotic patterns and corresponding geological patterns are due to common events in Earth history. The track approach of Croizat's panbiogeography was then joined with cladistics to produce cladistic biogeography. Cladistic biogeography (Nelson, 1973; Rosen, 1976; Nelson & Platnick, 1981) tries to explain the relationships of areas through discovery of biotic patterns favouring vicariance over dispersal. The main criticism of the emphasis of others on dispersal made by cladistic biogeographers is that such an emphasis does not provide a general theory of Earth history, but rather explains only particular case histories for particular taxonomic groups. Cladistic biogeographers accept the reality of dispersal in nature, but believe that it is useless for finding patterns. Heads (2005a) made the interesting observation that in the past 150 years, vicariance never occupied the dominant explanatory position over dispersal. Even when panbiogeography and cladistic biogeography (both approaches that favour vicariance over dispersal) became available, they were never popular. Using dispersal in biogeography was always so ingrained in biogeographical thinking that the vast majority of biogeographers simply assumed it (Heads, 2005a).

One hundred and fifty years after the publication of the *Origin*, there is a revival of dispersal explanations, occasioned in part by the development of molecular systematics and molecular clocks. Molecular dating of lineage divergence favours oceanic dispersal over tectonic vicariance as an explanation for disjunct distributions in a wide variety of taxa (de Queiroz, 2005). The molecular clocks mostly indicate that divergences in phylogenetic trees occurred too recently to be explained by vicariance. de Queiroz (2005) pointed out that although mismatches between area cladograms and tectonic fragmentation do not necessarily imply oceanic dispersal, in many cases dispersal is the most plausible explanation. Thus, in the past few years there has been an increase in the number of molecular studies that support oceanic dispersal (e.g. Calsbeek & Smith, 2003; Howarth *et al.*, 2003; Heinicke *et al.*, 2007; Vidal *et al.*, 2008). Therefore, dispersal hypotheses have claimed a new-found respect, with molecular clock theory providing decisive evidence. But there are those who strongly question the precise estimate of divergence events by molecular clocks (e.g. Graur & Martin, 2004) and their attributed evidence in favour of dispersal (e.g. Heads, 2005b; Grehan, 2007; Nelson & Ladiges, 2009).

Sanmartín & Ronquist (2004) showed how both dispersal and vicariance played a significant role in explaining the distribution of taxa in the Southern Hemisphere. They used the event-based tree-fitting method, which incorporates dispersal patterns while accounting for the vicariance events predicted by a geologically based area cladogram. They found that biogeography in southern South America is characterized by significant hierarchical distribution patterns, but these patterns are different in plants and animals. Among animals, the distribution patterns largely conform to the geological breakup of Gondwana and appear to have been generated by geologically induced vicariance. In plants, however, the hierarchical patterns are incongruent with the commonly accepted sequence of geological events and have apparently been shaped by concordant dispersal and extinction events.

HISTORY AND ECOLOGY

Darwin emphasized the role of historical explanations in the distribution of organisms, despite the fact that 39 years earlier, de Candolle (1820) had differentiated the role of ecological (= 'stations') and historical (= 'habitations') factors in biogeography. Since then, biogeographers have recognized two traditions, ecological biogeography and historical biogeography, both of which grew actively but separately, even in Darwin's time. The explanations for ecological biogeography depend on physical causes that are acting in the present time, whereas the explanations for historical biogeography depend on causes that existed in the past. Thus, ecological biogeography studies how the ecological processes that happen in short periods of time affect the distributional patterns of living beings, whereas historical biogeography studies how those processes (such as evolution or tectonics) that happen over long periods of time – often million of years – influence distributional patterns (Crisci *et al.*, 2003). Although both ecological and historical biogeography have the same objective, namely understanding the distribution of species in space and time, they use different epistemological approaches in addition to focusing on different spatio-temporal scales. Despite this fact, ecological and historical biogeography can be integrated in the context of spatial analysis (Gatrell, 1983) into a common framework for understanding distributional patterns, as shown by Crisci *et al.* (2006) and Posadas *et al.* (2006).

The initial phase of historical biogeographical studies consists of the analysis of geographical distributions of individual species based primarily on major biogeographical processes or events occurring over long spans of time. Changes in environmental factors are continually occurring at both ecological and evolutionary temporal scales. The historical setting has enormously influenced the geographical distribution of species. The non-random distributional congruence of two or more species implies the recognition of areas of endemism and ultimately of biogeographical regions. The interactions between the different space–time processes and spatial arrangements suggest the historical causes leading to the current distributional patterns of species. On the other hand, the ecological approach is based primarily on abiotic constraints and secondarily on other ecological constraints. Ecological niches that describe the range of conditions within which a species grows and reproduces are recognized. Clusters of species with similar niches can be recognized as a functional type, sharing a common ecological role with similar morphological and physiological characteristics. The overlap of the geographical distribution of abiotic factors with the requirements of functional types yields the geographical distribution of vegetation types or ecoregions, which correspond to the distributional patterns of their component species. Finally, distributional patterns of organisms are the result of ecology and history and represent the ultimate and common objective of historical and ecological biogeographical approaches. Consequently, distributional patterns cannot be fully understood without an integration of both subdisciplines. Crisci *et al.* (2006) showed an example of integration applied to conservation issues where a historically based approach serves as a primary source of information to identify target areas for conservation (identifying distributional patterns at present) and, in a second step, an ecologically based approach determines whether or not to invest conservation efforts according to future scenarios of global change (distributional patterns in the future).

CONCLUSIONS: OVERCOMING BINARY OPPOSITES

The spatial or geographical dimension of life's diversity is fundamental for our understanding of evolutionary processes and patterns. In particular, this means that geographical distributions, in and of themselves, are historically informative. Consequently, the analysis of the distributions of organisms is a valid historical biogeographical enterprise, independent of the application of phylogenies and the use of molecular clocks.

This is not meant to disparage the use of geographical distribution as raw data for phylogenetically based biogeographical methods.

Regarding the dispersal–vicariance opposition, no one, regardless of the biogeographical modern school to which he/she adheres, denies that both dispersal and vicariance have occurred in the past and are occurring now (the reality of extinction as the third process that modifies geographical distribution has never been challenged). Dispersal and vicariance are not mutually exclusive, and the two processes have probably contributed jointly to biogeographical patterns the world over.

Finally, an integrated approach using history and ecology could help to address conservation challenges, to design strategies to control biological invasions and vectors of human diseases, to provide information about the former distribution of species, and to guide development of ecological restoration initiatives, among other applications.

It is absolutely clear that the practice and philosophy of biogeography depends on a coherent and comprehensive conceptual framework for handling the distribution of organisms and events in space–time. We believe that an appropriate conceptual framework should, among other things, overcome the binary opposites by de-emphasizing their implied opposition and generating a free play of the opposites in a non-hierarchical way.

ACKNOWLEDGEMENTS

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Editor: Robert Whittaker