

Historical biogeography: A review of its basic concepts and critical issues

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Abstract

Biogeography (the study of the geographical distribution of organisms) ranges from descriptive to interpretative studies. Interpretative biogeography developed two research traditions named historical and ecological biogeography, respectively. The main difference between these research traditions is the time-scale one. The objective of this paper is to summarize the current state of historical biogeography.

We present a brief summary of the evolution of ideas in historical biogeography since its beginnings over two centuries ago. Also, we introduce the basic concepts of each of nine historical biogeographic approaches. Finally, we discuss the need for a new conceptual framework to solve some of the current critical issues in historical biogeography (i.e. the historical and ecological binary opposition in biogeography; the problem of methods; the inclusion of time in historical biogeography analysis; and the role of biogeography in biodiversity conservation).

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0. Introduction

Biogeography can be defined as the study of the geographical distribution of the organisms. This simple definition is accurate but it hides the complexity of the discipline (Crisci, 2001). Biogeography ranges from descriptive (basically, recognizing distributional patterns) to interpretative (basically, searching of causal explanations of such patterns) studies. Interpretative biogeographic studies have classically developed following one of two research traditions: Ecological or historical biogeography. These traditions were recognized as long ago as 1820 by the Swiss botanist Agustin Pyramus de Candolle. Each one of them has evolved independently, resulting in two completely different methodological and epistemological paths of thinking. The main difference between ecological and historical biogeography is the time-scale one. While ecological biogeography searches causal explanations of the distributional patterns in short temporal scales, historical biogeography concerns evolutionary processes over millions years (Crisci, 2001). In this way, ecological and historical biogeography, in an attempt to interpret the distribution of organisms in the geographic space, use different concepts. For example, ecological biogeography is concerned about functional groups of species and environmental constraints whereas historical biogeography focuses on taxonomic groups and historical biogeographic events (Crisci et al., 2006). Historical biogeography includes data from subjects as geology, geography, and biology to meet its aim. Consequently, the history of this discipline has been influenced by the evolving paradigms of these related fields.

More than 200 years since its beginning, historical biogeography is going through an extraordinary revolution in its foundations, basic concepts, methods, and relationships to other comparative biology disciplines (Crisci et al., 2003). For instance, despite some attempts to integrate historical biogeography and ecological biogeography, no such integration has been successfully achieved. This is a question that needs to be addressed since this divide between these two disciplines affects each in turn. Another issue is that there is a wide diversity of methods in historical biogeography, and that different methods may be appropriate in different circumstances. This conclusion may seem disturbingly inconclusive, but it reflects the nature of the problem. In the recent years, “time” has acquired a great relevance in systematic studies. There is currently a synergy between timing (e.g. fossils, molecular clock) and historical biogeography to generate hypotheses on the origin, evolution, and distribution of organisms. Finally, biodiversity conservation involves a biogeographic question, since one of the main tasks of conservation is to select the most appropriate areas for conservation. Even if some historical biogeographic methods have been applied to select conservation areas, it is still necessary to emphasize the role that historical biogeography could, and should, play in conservation when fully applied to the subject.

The objective of this paper is to summarize the current state of historical biogeography. Accordingly, we will: (1) review briefly the evolution of ideas in historical biogeography; (2) present a synthetic review of the basic concepts relative to historical biogeographic approaches; and (3) discuss some of the current critical issues in historical biogeography.

1. Evolution of ideas in historical biogeography

The origin of historical biogeography can be traced to XVIII century and was founded as a discipline of comparative biological science by George Louis Leclerc Comte de

Buffon. In his *Histoire Naturelle*, Buffon postulated that different areas were inhabited by different species and by comparing mammal faunas of America and the Old World concluded that under similar ecological conditions each area had its own particular fauna (Llorente-Bousquets et al., 2001).

Historical biogeography was an important substratum in which the evolutionary ideas of Darwin and Wallace were rooted (Llorente-Bousquets et al., 2001). Craw et al. (1999, p. 5) remark upon this link between historical biogeography and evolutionary theory when they wrote: “Darwin thought that biogeography was an interesting, indeed, a critical subject, otherwise he would not have introduced his evolutionary theory to the world through the medium of this distinct discipline.”

During the XVIII and XIX centuries all ideas related to the geographic distribution of living beings were developed within a static concept of geography. In this geologic paradigm, disjunct distributions of organisms were explained as dispersal events (Fig. 1). Thus, the aim of the discipline at this time was the search for centre of origin.

In the second half of the XX century, historical biogeography evolved rapidly. Historical biogeography is strongly linked to other disciplines (e.g. systematic biology, geography, and geology) and consequently, the evolving paradigms of these fields have modelled historical biogeography. The evolution of the discipline is reflected in the great number of approaches (and corresponding techniques) to the subject that arose at this time (Table 1). The development of phylogenetic systematics and the emergence of global tectonics as the dominant paradigm in geosciences and, more recently, molecular systematics had shaped today historical biogeography (Crisci et al., 2000, 2003). The influence of these disciplines is reflected in the emergence of different approaches to historical biogeography, each of which constitutes an independent research program in its own right, and each approach has developed its own methods. Not always does the



Fig. 1. A dispersal explanation for the distribution of the plant genus *Nothofagus*. According to this hypothesis the actual distribution of *Nothofagus* species is explained by origin in Antarctica and subsequent dispersal events (e.g. Moore, 1972).

Table 1
Historical biogeographic approaches and techniques

Approaches	Techniques	Authors
Center of origin and dispersal	Center of origin and dispersal	Matthew (1915)
Phylogenetic biogeography	Phylogenetic biogeography	Brundin (1966)
Ancestral areas	Camin–Sokal optimization Fitch optimization Weighted ancestral area analysis	Bremer (1992) Ronquist (1994) Hausdorf (1998)
Panbiogeography	Track analysis Spanning graphs Track compatibility	Croizat (1958) Page (1987) Craw (1988)
Cladistic biogeography	Reduced area cladograms Ancestral species maps Quantitative phylogenetic biogeography Component analysis Brooks parsimony analysis Component compatibility Quantification of component analysis Three-area statement Integrative method WISARD Paralogy-free subtrees Vicariance events PACT	Rosen (1978) Wiley (1980) Mickevich (1981) Nelson and Platnick (1981) Wiley (1987) Zandee and Roos (1987) Humphries et al. (1988) Nelson and Ladiges (1991) Morrone and Crisci (1995) Engelhoff (1996) Nelson and Ladiges (1996) Hovenkamp (1997) Wojcicki and Brooks (2004)
Parsimony analysis of endemism	Localities Areas of endemism Quadrats	Rosen (1988) Craw (1988) Morrone (1994)
Event-based methods	Coevolutionary two-dimensional cost matrix Reconciled trees Dispersal–vicariance analysis Jungles Bayesian approach to cospeciation Combined method	Ronquist and Nylin (1990) Page (1994a, b) Ronquist (1997) Charleston (1998) Huelsenbeck et al. (2000) Posadas and Morrone (2001)
Phylogeography	Phylogeography Nested clade analysis	Avise et al. (1987) Templeton et al. (1995)
Experimental biogeography	Experimental biogeography	Haydon et al. (1994)

emergence of a new approach resulted in replacement of the previous one. In most cases, the approaches have different research goals (e.g. area versus taxon biogeography), or methodological perspectives (e.g. event-based versus pattern-based methods), or function under different hypotheses (e.g. dispersal versus vicariance explanations). Crisci et al. (2003, p. 17) presented a list of 31 methods corresponding to nine different approaches to historical biogeography.

Here we present examples of how phylogenetic systematics, global tectonics, and molecular systematics influenced historical biogeography:

- (a) *Phylogenetic systematics*: The accession of phylogenetic systematics in the second half of XX century resulted in the development of “phylogenetic biogeography”. It was developed by Hennig (1966) and Brundin (1966). Phylogenetic biogeography was the first historical biogeography approach to consider an explicit phylogenetic hypothesis (a cladogram) of a given taxon as the basis for inferring its biogeographic history. Currently, most accepted historical biogeographic methods require phylogenetic information (e.g. ancestral areas, Brooks parsimony analysis, paralogy-free subtrees, dispersal-vicariance analysis, reconciled trees) in their analysis.
- (b) *Global tectonics*: The emergence of global tectonics as a paradigm of geosciences changed the focus of historical biogeography. Originally, historical biogeography was developed in a static paradigm, which means that only two kinds of historical events (mechanisms) could be assumed as causal explanations for organism distributions: dispersal and extinction. In a mobilistic paradigm, the rearrangement of continental land masses and islands and the opening and closing of sea and ocean basins predicted by global tectonics have undoubtedly affected the distribution and history of organisms (Fig. 2). As was stated by Léon Croizat (1964): “Earth and life evolve together”. The influence of global tectonics turned the dispersalist paradigm in biogeography to a vicariant one. Among the first vicariant-based research programs in historical biogeography we can mention “cladistic biogeography”. Cladistic biogeography came into the biogeographic scene inspired by Hennig’s phylogenetic systematics (1966) and Croizat’s panbiogeography (see below). This approach is based on the idea that different taxon phylogenies and their distributions are potentially informative about patterns in the relation among areas of endemism, which may correspond to events in earth history (Crisci et al., 2003). Today, most approaches to historical biogeography consider dispersal, vicariance, and extinction as equally possible processes that affect the distribution of organisms.
- (c) *Molecular systematics*: The use of molecular characters in systematics is a source that exponentially increased the data available for phylogenetic estimations (Hillis et al., 1996). Molecular-based phylogenies are used as raw data for historical biogeographic methods, which require phylogenetic information (in the same way that morphological-based phylogenies are used). Also, in some cases molecular phylogenies allow us to infer molecular clocks that indicate the time of origination and the time of each cladogenetic event in a phylogeny. Such temporal information may help to support or to reject hypotheses of biogeographic-event causality. For example, if a defined tectonic event is hypothesized as the causal explanation of a taxon disjunct distribution, we can reject or accept such hypothesis using molecular clock timing. If molecular timing indicates that the taxon under consideration originated well before the last known connection between two currently isolated landmasses, a vicariant explanation based on such tectonic event is untenable, since timing indicates only minimum ages for cladogenetic events and not absolute ones (for a detailed explanation see Heads, 2005). Also, molecular systematics’ influence on historical biogeography resulted in a new research program that was named phylogeography (Avise et al., 1987, see below). According to Avise (see Fig. 2 in Avise, 1998) this approach tends to emphasize the influence of historical factors (mainly, dispersal and vicariants events) on geographic distributions of lineages.

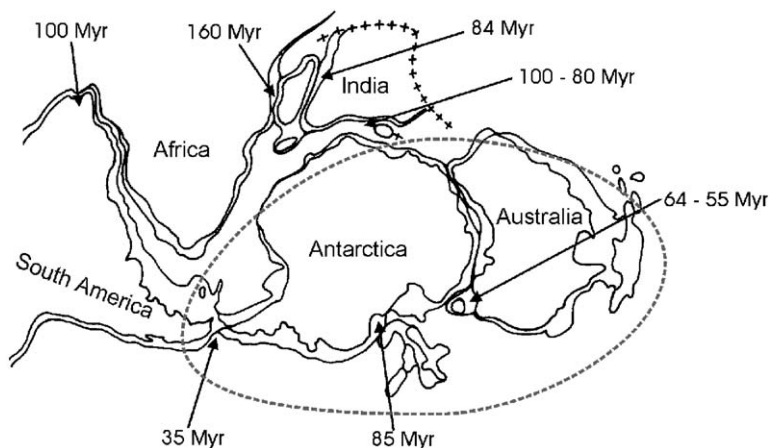


Fig. 2. A vicariance explanation for the distribution of the plant genus *Nothofagus*. According to this hypothesis the actual distribution of *Nothofagus* species results from vicariance events related to the break-up of Gondwana (e.g. Humphries, 1981).

2. Basic concepts relative to historical biogeographic approaches

Historical biogeography methods and approaches could be classified using different criteria, which then result in different taxonomies (see for example: Andersson, 1996; Humphries, 2000; Lieberman, 2000; Van Veller et al., 2000). Some of these taxonomies have been the subject of recent discussions (see Ebach, 2001; Brooks and McLennan, 2002; Ebach et al., 2003, and literature cited therein).

In this section, we will briefly summarize the taxonomy of historical biogeographic approaches published previously by Crisci et al. (2003). The aim of this section is to introduce the reader to the diversity of approaches to the field of historical biogeography. For each of the abovementioned approaches we will mention primary literature sources, also a more detailed treatment of each of them can be found in Crisci et al. (2003) and literature cited therein.

2.1. Center of origin and dispersal

Among the most prominent exponents of this approach we can mention William Matthew (1915). This is a pre-tectonic approach based on the Darwin–Wallace tradition. Its focus is the distributional history of individual groups in a dispersalist conceptual framework. According to this approach species originated in one center of origin, from which some individuals subsequently dispersed by chance, and then changed through natural selection. This approach considers that dispersal and extinction are the only historical events involved in the distribution of taxa. It has been defined as an ad hoc discipline that requires external causes to explain the patterns analysed (Croizat et al., 1974; Platnick and Nelson, 1978; Humphries and Parenti, 1986). The center of origin and dispersal approach had fallen into discredit due to the acceptance of global tectonics and that its dispersal explanations tended to reside in narrative frameworks, resulting in

irrefutable hypotheses that do not provide a general theory to explain distributional patterns. In recent years, center of origin concept and dispersalist explanations have been retaken in biogeography as is reflected, for example, in the development of the ancestral areas approach (see below).

2.2. *Phylogenetic biogeography*

This approach evolved through the ideas of Willi Hennig (1966) and Lars Brundin (1966). It is defined as the study of the history of monophyletic groups in time and space. Phylogenetic biogeography emerged also in a pre-tectonic paradigm. As in the case of the center of origin and dispersal approach, phylogenetic biogeography considers dispersal and extinction as the only processes involved in species distributions. As we mentioned before, 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). The same arguments against center of origin and dispersal approach are used against phylogenetic biogeography. Notwithstanding, it is interesting to note that many papers have been published in the last few years (especially, with molecular-based phylogenies) that explicitly (e.g. Knox and Palmer, 1998) or implicitly apply this method or its assumptions in part. It is common to find in this type of literature molecular cladograms in which the terminal taxa have been replaced by the areas that they inhabit in order to postulate dispersal events, which are hypothesized to have a direction from the base to the top of the cladogram.

2.3. *Ancestral areas*

This approach, originally formalized by Kare Bremer (1992), retakes the ideas of center of origin and phylogenetic biogeography approaches and therefore it assumes the possibility of dispersal and extinction. Bremer considered that understanding ancestral areas for an individual taxon is a valid part of the study of the natural history of a given group. The main focus of ancestral areas approach is to postulate hypotheses of the distributional history of individual groups. Accordingly, the ancestral area of a group could be delimited using the topological information of its cladogram. There are three formalized cladistic procedures based on this dispersalist approach (see Bremer, 1992; Ronquist, 1994, 1995; Hausdorf, 1998). The ancestral areas approach has been criticized by Ebach (1999).

2.4. *Panbiogeography*

This approach was proposed by Léon Croizat (1952, 1958, 1964) and is based on the idea that earth and life evolve together. It was a completely new research program with the aim “to reintroduce and reemphasize the importance of the spatial or geographical dimension of life’s diversity for our understanding of evolutionary patterns and processes” (Craw et al., 1999, p. 4). Panbiogeography allows us to identify ancestral biotas. This approach assumes the possibility of dispersal, vicariance, and extinction, and its main focus is the history of biotas. Panbiogeography has been criticized by several authors, for various reasons such as the uncritical use of systematics treatments (Patterson, 1981;

Seberg, 1986); the use of geographical proximity, and disregard of cladistic information (Platnick and Nelson, 1988).

2.5. Cladistic biogeography

This approach was originally developed by Donn Rosen (1978), and Gareth Nelson and Norman Platnick (1981). Cladistic biogeography is an “area biogeography” research program. Its aim is the search for a pattern in the relations among areas of endemism that arises repeatedly in different taxon phylogenies, which may correspond to events in earth history (Crisci et al., 2003). The ultimate objective of cladistic biogeography is to interpret the history of the areas by means of the distributional and phylogenetic information of taxa. To do that, cladistic biogeography assumes that the correspondence between phylogenetic relationships and area relationships is biogeographically informative. Comparisons between area cladograms derived from different taxa that occur in a certain region allow general patterns to be elucidated. Such patterns are most likely caused by allopatric speciation originated in vicariance events. On the other hand, ambiguity related to these patterns could be due to sympatric speciation, taxa that do not speciate in allopatry, or dispersal events. This approach assumes the possibility of dispersal, vicariance, and extinction. Crisci et al. (2003) have identified at least 12 methods within this approach, perhaps the most widely applied of these methods are Brooks parsimony analysis (Wiley, 1987), three-area statements (Nelson and Ladiges, 1991), and paralogy-free subtrees (Nelson and Ladiges, 1996). Cladistic biogeography has been criticized by Donoghue and Moore (2003) because its methods ignore absolute timing of diversification on the component lineages. These authors argued that ignoring temporal information obscures the connection between biogeographic patterns and their underlying causes.

2.6. Parsimony analysis of endemism (PAE)

This approach is based on the ideas of Brian Rosen (1988). PAE classifies localities, quadrates or areas (analogous to taxa, if compared with the analysis of phylogenetic systematics) according to their shared taxa (analogous to characters) by means of the most parsimonious solution (parsimony principle). The aim of this approach is to elucidate the history of areas or localities. Crisci et al. (2003) distinguished three PAE variants which they named as: PAE based in localities (Rosen, 1988), PAE based in areas of endemism (Craw, 1988), and PAE based on quadrats (Morrone, 1994). It is important to note that the method proposed by Morrone (1994) has a different aim than the other two methods. The PAE variants of Rosen and Craw both have the aim of elucidating the history of the areas, while Morrone’s method aims to identify areas of endemism on the basis of shared presences of taxa. Despite that, PAE methodology is analogous to cladistic systematics, this approach is not related to cladistic biogeography because its aims and assumptions are quite different. Some authors have postulated that PAE methodology is conceptually related to panbiogeography (e.g. Craw et al., 1999). Major criticism against PAE is that it ignores cladistic (i.e. phylogenetic) relationships among taxa, considering only their distributions (Humphries, 1989, 2000). Such criticism is only applicable to PAE variants which have the aim of elucidating the history of the areas.

2.7. *Event-based methods*

This approach postulates explicit models of the processes that have an effect on the geographic distribution of living organisms (Ronquist, 1997). Its main focus is the distributional history of particular taxa. However, recent applications of event-based methods to area biogeography problems have been published (e.g. Sanmartín et al., 2001; Sanmartín and Ronquist, 2004). The different types of processes (dispersal, extinction, and vicariance) are identified and assigned values of benefit-cost. Consequently, the distributional history of a taxon is inferred on the basis of its phylogenetic information and applying the criterion of maximum benefits and minimum costs respecting the biogeographic processes (for example, maximizing vicariance and minimizing dispersal and extinction). The main argument against approaches with explicit cost assignments has been the possibility of an infinite combination of costs (Siddall and Kluge, 1997; Grant and Kluge, 2003).

2.8. *Phylogeography*

This approach was originally proposed by John Avise et al. (1987) and can be defined as the study of the principles and processes governing the geographic distribution of genealogical lineages at intraspecific level using mitochondrial DNA (mtDNA) in animals and chloroplast DNA (cpDNA) in plants. Its aim is to understand the distributional history of populations, and subsequently the history of areas. In this approach the individuals are genotyped and assigned to maternal lineages and the resulting phylogeny is related to patterns of geographic distribution. This approach assumes the possibility of dispersal and vicariance, and implicitly extinction. Statistical approaches that incorporate demographic-phylogenetic methods into phylogeography have been developed. Among them, is the nested clade phylogeographic analysis (NCPA, Templeton et al., 1995). Among the criticisms of this approach, some authors consider phylogeography as an insular and blinkered approach in an integrated and interdisciplinary field (biogeography) which fails to consider historical context (Ebach et al., 2003).

2.9. *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. Experimental biogeography 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 concern of this approach is the history of areas, and to date only theoretical applications have been done.

3. *Critical issues in historical biogeography*

The main issue to be addressed in historical biogeography is the need of a new conceptual framework. This conceptual framework should cover several items such as:

(1) the historical and ecological binary opposition in biogeography; (2) the problem of methods; (3) the inclusion of time in historical biogeography analysis (or timing); and (4) the role of biogeography in biodiversity conservation. These issues are discussed below.

3.1. *Ecology versus history? Or ecology and history?*

Perhaps one of the most critical issues in biogeography is the lack of integration between historical and ecological biogeography. As long ago as 1820, the Swiss botanist Agustin P. de Candolle posed this problem when he wrote “the confusion of these two classes of ideas [meaning historical and ecological approaches] is one of the causes that have most retarded the science [biogeography] and that have prevented it from acquiring exactitude”. Nearly two centuries later this problem has not been resolved. Ecology and history are indissolubly tied together, and therefore, the long established division between ecology and history is an obstacle to the progress of biogeography. Some efforts have been carried out to overcome this duality between historical versus ecological biogeography, such as Haydon et al. (1994), Avise (2000), Grehan (2001), and Crisci et al. (2006).

3.2. *The problem of methods*

One important area of the new framework is the issue of methods. Crisci et al. (2000, 2003) have listed and revised up to 30 methods responding to the aforementioned nine historical biogeographic approaches, and since then some new methods have been developed (e.g. PACT, Wojcicki and Brooks, 2004). Any attempted conceptual framework for biogeography will have to deal with two problems that could be labelled as “plurality” and “disowning”.

3.2.1. *Plurality*

Any attempt to define historical biogeography in terms of a distinctive and unique method is doomed to failure. Some authors, based on the plethora of methods currently available in the discipline, have suggested that historical biogeography is a “mess” (Tassy and Deleporte, 1999). However, other authors see this proliferation of methods as the result of competing articulations (e.g. panbiogeography versus cladistics; event-based versus pattern-based methods) that are shaping biogeography (Crisci and Morrone, 1992). Furthermore, Crisci et al. (2003) have postulated that the proliferation of historical biogeographic methods in the last two decades is a symptom of the scientific revolution (in the sense of Kuhn, 1970) in which the field is involved. Accordingly, it could testify the health of the subject, but more promisingly, it may presage major advances in the field. In fact, as was mentioned before, each one of the historical biogeographic methods has been developed within a defined approach. Each approach implies a defined central core of concepts and assumptions and has different aims. That is, not all historical biogeographic methods have the same objectives, for example reconstruction of the distributional history of a taxon versus reconstruction of the history of areas of endemism. Therefore, certain methods are more appropriate in different situations. Despite this lack of a unique method, the increased precision and rigor of the latest methodological developments offer the possibility of removing biogeographical theories from a non-testable narrative status to one in which testable hypotheses of general significance may be generated.

3.2.2. *Disowning*

In not a few cases, molecular trees are used in the context of a phylogenetic study to make further assumptions on dispersal and vicariance without an explicit application of a historical biogeographic method. Probably, the better description of the disowning of methods problem could be presented as an analogy from a field so far away from biogeography as literary theory: “Many literary critics dislike the whole idea of method and prefer to work by glimmers and hunches, intuitions and sudden perceptions. It is perhaps fortunate that this way of proceeding has not yet infiltrated medicine or aeronautical engineering; but even so one should not take this modest disowning of method altogether seriously, since what glimmers and hunches you have will depend on a latent structure of assumption often quite as stubborn as that of any method” (Eagleton, 1983).

3.3. *Timing*

The relevance of time when dealing with historical biogeographic problems lead [Hunn and Upchurch \(2001\)](#) to advocate the necessity of a “chronobiogeographical paradigm”. These authors postulated that this change of paradigm in biogeography represents a logical elaboration rather than a replacement of the current paradigm. In a recent paper, [Donoghue and Moore \(2003\)](#) have emphasized that cladistic biogeographic methods remain susceptible to confound effects of historical events on the distribution of organisms due mainly to the fact that these methods do not take into consideration absolute timing of lineages diversification. In other words, to ignore the temporal information obscures the connection between the biogeographic patterns and their possible underlying causes (i.e. vicariant and dispersal events).

In the last years, more and more historical biogeographic papers consider temporal information and molecular clocks has become the regular source for dating nodes (points of lineages diversification). However, [Heads \(2005\)](#) considered that the use of dated nodes on phylogenies as absolute ages is incorrect and that such datings only indicate minimum ages of phylogenetic events. Then, according to this author, only geological events younger than the dated nodes can be irrelevant to the phylogeny while those geological events which are earlier than dated nodes could not be discarded as having influence on the history of the analysed taxa. [Heads \(2005\)](#) focuses his statements in the way in which molecular clocks are calibrated and he pointed out that: “whether or not a strict clock is assumed, at least one node on a tree must be calibrated to give the tree a time dimension”. Data source for calibration (mainly, age of the earliest known fossil for a group or allied group) only allows to define minimum ages, since oldest known fossil not necessarily means time of origination of a taxon. Literature is plenty of examples in which dated nodes are considered as absolute ages and then earlier geological events are discarded as causal events of biogeographic patterns, which in many cases resulted in preferring dispersalist explanations against possible vicariance ones (for a detailed discussion see [Heads, 2005](#)).

Currently, there are two main sources of temporal information of taxa: the fossil record and the molecular clocks. Unfortunately, the relevance of the fossil record has been underestimated by most neontologists. Fossils have been relegated to calibrations tools for molecular clocks. However, fossils could bring more than only chronological information. For example, they could be used to reconstruct paleoenvironments and to infer paleoclimatic conditions. The paleoecological evidence together with the geological

knowledge could be used in turn to frame the biogeographic evolution of extant taxa. In this way, this core of independent evidence could help to postulate hypotheses concerning the physical and paleoenvironmental causes which have shaped distributional patterns of living beings. An example of how fossil and geological evidence could be used in this sense was published by Donato et al. (2003). In the future, historical biogeography would consider not just the distributional patterns of taxa but their temporal patterns too.

3.4. *Biogeography and conservation*

The impoverishment in global biodiversity is the result of its complex response to several changes in global environment. Sala et al. (2000) consider that most of these changes are human-induced ones. Also, they consider that the magnitude of the change in biodiversity is so large and so strongly linked to ecosystem processes and human's use of natural resources, that biodiversity impoverishment is currently seen as an important global change in its own. In this scenario, new strategies to conserve biodiversity are required. One of the perspectives that new strategies need to tackle ought to focus on where species currently live, have lived in the past, and would live in the future. This perspective is clearly a biogeographic one. At present, several historical biogeographic methods are used to define strategies for conservation. Among them, we can mention PAE, panbiogeography, and phylogeography (for a detailed discussion on conservation applications of these methods see Crisci et al., 2003). Similarly, ecological approaches to biogeography, as the theory of island biogeography, have been proposed as useful to design reserve networks. However, biogeography will be fully useful in conservation only if a new conceptual framework arises. This conceptual framework must highlight how humans affect the drivers of organism distributions. That is, changing of ecological factors as climate change, changes in land-use and creating of new historical events as human-mediated dispersal events resulting in biological invasions.

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