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SYNTHESIS

Track analysis beyond panbiogeography

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ABSTRACT

Aim Panbiogeography, as originally formulated by Léon Croizat, assumed that vicariance and range expansion are the only biogeographical processes needed to explain general biotic distributions. This was in opposition to the prevailing paradigm at the time, known as dispersalism, which postulates that organisms evolve in 'centres of origin' from pre-existing species and then randomly cross barriers to occupy new areas, where they adapt and evolve into new species. The panbiogeographic approach is implemented through track analysis, which consists of three basic steps: constructing individual tracks for two or more different taxa, obtaining generalized tracks where two or more different individual tracks coincide, and identifying nodes in the areas where two or more generalized tracks intersect. In this synthesis I discuss some criticisms that have been directed at panbiogeography and track analysis.

Location Global.

Methods I evaluated the papers with track analyses that have been published in the last few decades and the critiques provided by several authors.

Results Most of the critiques have been directed at the original panbiogeographic approach, with its complete or almost complete reliance on vicariance explanations. Track analyses published in the 1980s and 1990s usually applied a strict vicariance explanation; however, most of the analyses published in the last 10 years or so consider both vicariance and dispersal to explain the observed patterns.

Main conclusions Although Croizat's metaphor 'Earth and life evolve together' may be a useful guide to understanding broad, general patterns, the relationships between Earth history and life are more complex because biotic history is reticulate. To reduce our explanations exclusively to vicariance or dispersal is misguided. We should integrate both processes into a dispersal–vicariance model that allows us to understand the evolution of biotic distributions, incorporating the dating of the lineages and the identification of the cenocrons (sets of taxa that share the same biogeographical history) that coexist within biotas. In the framework of this model, panbiogeographic track analysis is a useful method for identifying biotas, and may constitute the first step of an evolutionary biogeographical analysis.

Keywords

Biotas, cenocrons, dispersal, evolutionary biogeography, generalized tracks, historical biogeography, nodes, panbiogeography, track analysis, vicariance.

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INTRODUCTION

Panbiogeography originated with Croizat (1958, 1964) and was developed subsequently by other authors (e.g. Craw, 1988a,b, 1989a,b; Henderson, 1989, 1991; Craw *et al.*, 1999; Heads, 2012a, 2014). It has had a mixed reception. It has been portrayed by some partisans as the only appropriate biogeographical approach or as a revolutionary new paradigm (Craw, 1978; Zunino, 1992; Colacino, 1997; Grehan, 2001a,b, 2009; Heads, 2005a). Other authors (Crovello, 1981; Nelson & Platnick, 1981; Cox & Moore, 1993; Humphries & Parenti, 1999; Parenti & Ebach, 2009) have argued that the significance of panbiogeography is that it led to the emergence of cladistic or vicariance biogeography. Some commentators denounced its idiosyncrasies (Seberg, 1986; Mayden, 1991; Cox, 1998; Humphries & Parenti, 1999), or have argued 'that—as it stands—panbiogeography is not a useful approach for evolutionary biology' (Waters *et al.*, 2013, p. 496). Other critics have commented that it 'reached its peak of popularity in 1989–1990 and then began to fade' (Briggs, 2007, p. 273) or that it 'can now be decently laid to rest' (McGlone, 2005, p. 739). In addition, several authors have applied track analyses under approaches that may be considered not strictly panbiogeographic.

Why should biogeographers of the 21st century care about panbiogeography? Are there any questions about biotic patterns that track analysis can address and which hold relevance? In order to answer these questions, I analyse some basic issues, discussing the criticisms that have been directed at panbiogeography and track analysis, to determine the utility of track analysis in biogeography and to discuss its place among other approaches and methods.

PANBIOGEOGRAPHY

Panbiogeography was created by Léon Croizat, during the second half of the 20th century. Biographical information on Léon Croizat (1894–1982) has been provided by several authors (see Appendix S1 in Supporting Information). Croizat published *c.* 300 scientific papers and seven books (Heads & Craw, 1984), dealing with plant systematics and biogeography. Croizat (1958) assumed that range expansion ('mobilism' or 'dispersion') and vicariance ('immobilism') are the only biogeographical processes needed to explain general biotic distributions. During phases of mobilism, geological changes lead to range expansion and overlap; during phases of immobilism, geographical barriers fragment ancestral biotas. Croizat rejected chance dispersal as a relevant process, positing instead that all significant dispersal involved range expansion through normal dispersal. The panbiogeographic approach is summarized in the metaphor 'Earth and life evolve together' (Croizat, 1958, 1964).

As originally proposed, panbiogeography was in opposition to the prevailing paradigm at the time, known as dispersalism, which originated with Darwin (1859) and Wallace (1876). In order to explain disjunct distributions, namely those where two related taxa are distributed in two or more widely separated areas, pre-Darwinian authors had postulated the existence of 'centres of multiple creation'. Darwin (1859) and Wallace (1876) interpreted disjunct distributions as a result of evolution or descent with modification. After evolving in 'centres of origin' from pre-existing species, organisms randomly cross barriers to occupy new areas, where they adapt and evolve into new species. This approach is known also as CODA – centre of origin–dispersal–adaptation model (Lomolino & Brown, 2009; Heads, 2014) – or evolutionary biogeography I (Lomolino *et al.*, 2010). Croizat (1958) analysed the geographical distribution of several taxa, finding that the same patterns were shared by relatively vagile organisms (such as birds) and extremely sedentary organisms (such as wingless insects) connecting widely separated areas. He concluded that it was unnecessary to postulate separate long-distance dispersal events for particular taxa to explain these disjunctions, and that phases of vicariance and range expansion produced the general patterns. Curiously, although Croizat (1964) insisted that panbiogeography was not a theory but a strictly comparative and statistical method, he implicitly interpreted data under a theoretical paradigm.

Croizat's panbiogeography was not generally accepted in the decades after its proposal, and most English-speaking biogeographers did not take it seriously (Llorente-Bousquets *et al.*, 2000; Heads, 2005a). Simpson privately wrote to Gareth Nelson: 'Study of Croizat's voluminous work has convinced me that he is a member of the lunatic fringe' (Nelson, 1977, p. 451). Ernst Mayr added: 'Neither Simpson nor anyone else has affected my treatment of Croizat, but only his totally unscientific style and methodology. Time is too short to argue with such authors and one cannot simply refer to Croizat without detailed analysis. I am prepared to be criticized for this, but any scientist has to make the decision where to draw the line' (Nelson, 1977, p. 452). Some authors, however, provided positive comments on Croizat's contributions (Corner, 1959; Good, 1959; Brundin, 1966; Löve, 1967). Croizat published some of his books privately, and also found editorial support in continental Europe (Heads, 2005a).

In the late 1960s and 1970s, Gareth Nelson, Donn E. Rosen and Norman Platnick, of the American Museum of Natural History of New York, concluded that panbiogeography was a useful approach and synthesized it with Hennig's phylogenetic systematics, thereby initiating vicariance or cladistic biogeography (Nelson, 1969, 1973, 1978; Rosen, 1975, 1978; Platnick & Nelson, 1978; Nelson & Platnick, 1981). Cladistic biogeography assumes a correspondence between the phylogenetic relationships of the different taxa inhabiting the studied areas and the relationships between such areas, comparing area cladograms derived from different taxa in order to detect a general pattern of area fragmentation (Humphries & Parenti, 1999; Parenti & Ebach, 2009). This synthesis was unacceptable to Croizat, because it involved the use of *a priori* identified areas of endemism, and because he did not accept phylogenetic systematics (Croizat, 1978). In one of his last contributions, Croizat stated: 'Under the ill-fitting name "vicariance biogeography" stand today confused two very different streams of thought and praxis, that is, panbiogeography of Leon Croizat, and "vicariance biogeography" by Gareth Nelson as its principal author and promoter… [P]anbiogeography is a method, Nelson's vicariance biogeography is a theory…' (Croizat, 1982, p. 299). This reflects Croizat's belief that his approach was inductive (see Haddon, 1984).

Robin Craw, Michael Heads, John Grehan and other New Zealand biologists adopted Croizat's original approach in the late 1970s and 1980s (e.g. Craw, 1978, 1984; Grehan, 1989; Page, 1989). Soon supporters of panbiogeography and cladistic biogeography initiated a debate about their relative merits (Craw, 1982, 1988a,b; Platnick & Nelson, 1984, 1988; Heads, 1985; Humphries, 1985, 2000; Seberg, 1986; Page, 1987, 1990; Craw & Page, 1988; Humphries & Seberg, 1989; Mayden, 1991; Humphries & Parenti, 1999). This debate referred, among other issues, to the primacy given by panbiogeographers to 'space' (distribution) over 'form' in analysis ('form' taken in a broad sense, including all aspects of morphology, physiology and behaviour; Craw, 1988b). It is interesting to note that in recent contributions, Heads (2012a, 2014) has relied on molecular phylogenies as the basis for track analyses.

In the 1990s, some Latin American authors applied panbiogeographic and cladistic biogeographical methods to biogeographical problems and, in the process, raised some theoretical issues (e.g. Morrone & Crisci, 1990; Llorente-Bousquets & Espinosa-Organista, 1991; Crisci & Morrone, 1992a,b). Morrone & Crisci (1995) suggested that panbiogeography and cladistic biogeography could be treated as complementary within a more integrative approach, with the former used to discover general distribution patterns and the latter using phylogenetic hypotheses to falsify these patterns (see also Crisci *et al.*, 2000, 2003; Crisci, 2001; Morrone, 2001). This integrative approach is known as evolutionary biogeography (Morrone, 2009) or evolutionary biogeography II (Lomolino *et al.*, 2010).

Several books contain empirical analyses or theoretical treatments of panbiogeography. For a list see Appendix S2.

TRACK ANALYSIS

Track analysis (Craw, 1988a,b, 1989a,b; Morrone & Crisci, 1995; Craw *et al.*, 1999; Grehan, 2001b, 2011; Crisci *et al.*, 2000, 2003; Morrone, 2004a,b, 2009; de Carvalho, 2011) consists of three basic steps (Fig. 1):

1. Constructing individual tracks for two or more different taxa, by connecting the localities of each taxon according to their geographical proximity.

2. Obtaining generalized tracks based on the superposition of two or more different individual tracks.

3. Identifying nodes in the areas where two or more generalized tracks intersect.

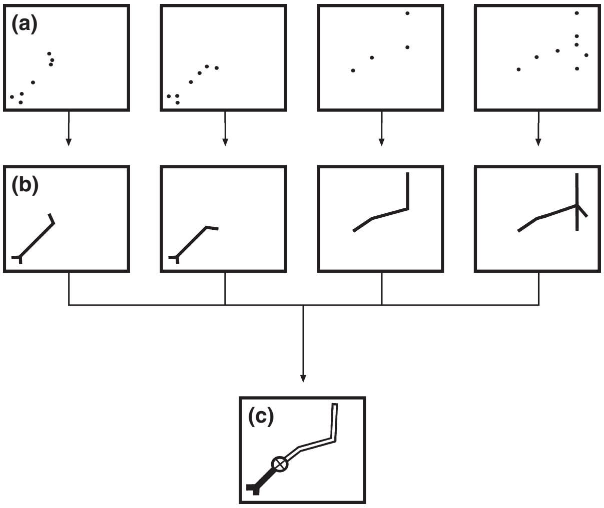

Figure 1 Diagrammatic representation of a track analysis: (a) localities of four different taxa, (b) four individual tracks, and (c) two generalized tracks and one node.

Individual tracks

An individual track provides 'the primary coordinates…in *space*, and opens thus the way to an inquiry into factors of *time* and *form*' (Croizat, 1964, p. 7, italics in the original) and has been defined as 'a line on a map connecting the disjunct populations of a species or the disjunct species of a monophyletic group' (Rosen, 1975, p. 432). An individual track represents graphically the distribution of a taxon on a map by a line graph that connects the different localities according to their geographical proximity (Henderson, 1989). Craw (1988a) and Cox (1998) suggested that the concept of individual track is not original to Croizat but had been proposed earlier by van Steenis (1934–35), and Craw *et al.* (1999) noted other predecessors.

Page (1987) conceptualized an individual track as a minimum-spanning tree that for n localities contains $n - 1$ connections (although Croizat did not always use the minimum distance criterion). In order to draw it, after choosing any locality, the nearest one to it is identified, and they are connected by a line; then, this pair of localities is connected with the nearest locality to any of them; the nearest locality to any of the three is united, and so on (Fig. 2). In the resulting graph the sum of all the segments connecting the localities is minimal (Morrone, 2009). There is an alternative formalization (Zunino *et al.*, 1996), based on minimum Steiner trees, where hypothetical localities are added in order to reduce the length of the tree (Fig. 2f).

Minimum-spanning trees are unrooted graphs, but they may be oriented by formulating a hypothesis on the sequence of the implied disjunctions. The most common way to orient an individual track is designating a baseline, which represents a geological feature, such as an ocean or marine basin on a global scale, or a river or mountain chain

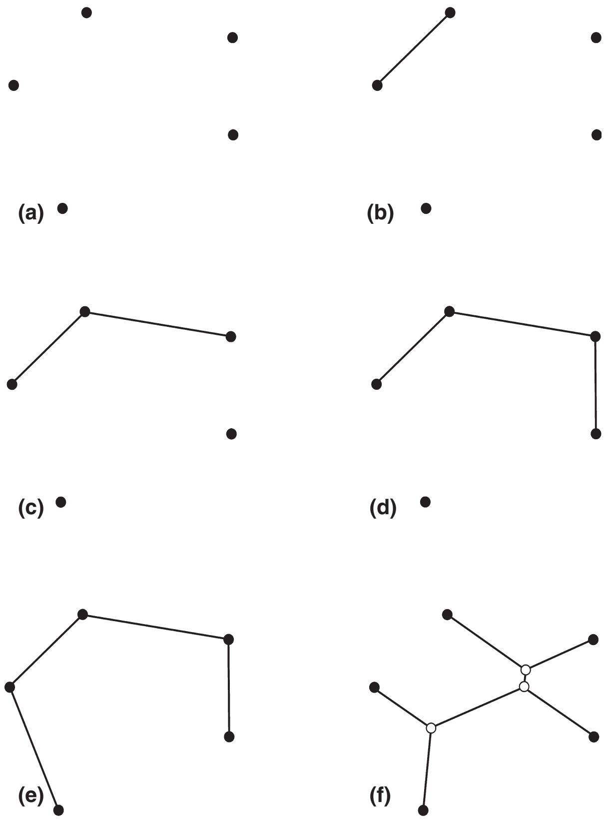

Figure 2 Drawing of an individual track: (a) localities of a taxon, (b)–(d) successive connection by the criterion of minimal distance, (e) resulting minimum-spanning tree, and (f) alternative Steiner tree that can be obtained from the same data.

on a continental scale (Page, 1987; Craw *et al.*, 1999). Page (1987) suggested that phylogenetic information could be used to orient individual tracks (see also Craw, 1988a; Henderson, 1989; Grehan, 1991). A third criterion for orienting individual tracks is the location of a main massing, which is defined as the greatest concentration of biological diversity in the range of the taxon, measured by the number of species (in a supraspecific taxon) or genetic diversity (in a species). Main massings represent areas of numerical, genetic or morphological diversity of a taxon (Page, 1987), which may be identified by a grid analysis (Craw *et al.*, 1999). These criteria are rather problematical (see below), so most of the published analyses do not orient individual tracks (Morrone, 2009).

Recent developments regarding the construction of individual tracks include their combination with ecological niche modelling (e.g. Ramírez-Barahona *et al.*, 2009; Delgadillo *et al.*, 2012). In order to draw the tracks taking into account the area topography, digital elevation models were incorporated by Barrera-Moreno *et al.* (2011).

Generalized tracks

Generalized or standard tracks result from the significant superposition of different individual tracks: 'If a given type of distribution (individual track) recurs in group after group of organisms, the region delineated by the coincident distributions (generalized track) becomes statistically significant and invites explanation on a general level' (Croizat *et al.*, 1974, p. 266). They have been typically interpreted as indicating the pre-existence of ancestral biotas that were fragmented by geological (often tectonic) or climatic events (Morrone, 2009). When we compare oriented individual tracks, we consider that they belong to the same generalized track when they agree in both their structure and direction (Craw, 1988a). Nihei & de Carvalho (2005) suggested that generalized tracks should be recognized only when there is phylogenetic evidence supporting them (e.g. they consist of sister clades); however, I find this problematical, because generalized tracks should reflect the existence of ancestral biotas (assemblages of different taxa) and sister taxa represent a putative vicariance event (in a single taxon).

There are different methods that have been used to identify generalized tracks. Although Croizat did not give any indication of how to construct generalized tracks, the minimum-spanning tree method has been considered as the first formalization (Page, 1987; Craw, 1988a,b; Morrone, 2004b), and it has been the most widely applied. Page (1987) formalized a method using connectivity and incidence matrices. Craw (1988a, 1989a) formalized track compatibility, a quantitative method based on character compatibility, where the largest set of compatible tracks ('clique') is used to construct the generalized track. A method combining spatial analysis by geodesic distance calculation, connectivity matrices and minimum-spanning trees was proposed by Liria (2008). Parsimony analysis of endemicity or PAE (Rosen, 1988; Morrone, 2014) was proposed as a method for identifying generalized tracks (Echeverry & Morrone, 2010). The analysis of published contributions (Appendix S3) shows that the most popular methods were the minimum-spanning tree method applied manually (146, 71.9%), PAE (25, 12.3%) and track compatibility (8, 3.9%).

Three software packages implement the minimum-spanning tree method for identifying generalized tracks: Trazos2004 (Rojas-Parra, 2007), Croizat (Cavalcanti, 2009) and MartiTracks (Echeverría-Londoño & Miranda-Esquivel, 2011). They draw individual tracks efficiently, but unfortunately they consider any overlap between parts of two or more of them as a generalized track. This results in a substantial modification of the original concept of a generalized track, which required a significant superposition of two or more individual tracks, not just of *parts* of them (Morrone, 2014). Ferrari *et al.* (2013) compared the performance of MartiTracks with PAE and track compatibility, finding that MartiTracks does not provide reliable results, because of unclear congruence criteria, subjective parameter definition and obscure analytical procedures. For the moment, PAE has been considered to be the best method (Ferrari *et al.*, 2013; Morrone, 2014). It is interesting to note that the problem of finding generalized tracks where only parts of individual tracks overlap has been found also in some manual analyses (e.g. Nihei & de Carvalho, 2005; Gallo *et al.*, 2007, 2010), where the number of generalized tracks found is larger than that expected (≤ *n*/2, where *n* is the number of individual tracks).

Nodes

Nodes are areas where two or more generalized tracks intersect (Morrone, 2009). Nodes are particularly interesting from an evolutionary biogeographical viewpoint, because they allow us to speculate on the existence of compound or complex areas. They may be characterized by the location of endemism, high diversity, distributional boundaries, disjunction, anomalous absence of taxa, incongruence and recombination of characters, and unusual hybrids; these features are found together only in the most important nodes (Heads, 2004). Fontenla & López Admirall (2008) considered that endemism might not be a relevant feature of all nodes, because rather than their exclusive species they are characterized by the species shared between two or more generalized tracks. Miguel-Talonia & Escalante (2013) suggested that the presence of the features defined by Heads (2004) depends on the scale and taxa analysed, and even on the available data.

Nodes correspond to points with high density of terminal track 1° vertices, namely endpoint vertices that only have one connecting link to another point, so they should be situated at the periphery of a minimum-spanning tree (Henderson, 1989; Fontenla & López Admirall, 2008; Morrone, 2009). Henderson (1991), however, warned that some points with high number of terminal vertices can be expected from random data. The highest density of 1° vertices occurs where different individual tracks come into contact (Grehan, 1991; Craw *et al.*, 1999) and thus they represent the dynamic boundaries between different biotas (Morrone, 2004b). Miguel-Talonia & Escalante (2013) postulated that nodes identified in areas that represent the overlap of 2° or 3° vertices may reflect ecological rather than historical processes.

Counting the number of species present in grid-cells has been presented as an alternative method to identify nodes by Craw *et al.* (1999) and was applied by Heads (2001, 2002). Henderson (1989) discussed the possibility of submitting nodes to statistical tests, by analysing the distribution of nodes under a null hypothesis of random distributions.

Nodes are often represented graphically by an 'x' enclosed in a circle, to represent biotic overlap (Fortino & Morrone, 1997). Miguel-Talonia & Escalante (2013) considered this graphical convention to be 'totally inexact', but they did not provide any alternative to replace it.

Some authors (Henderson, 1989; Craw *et al.*, 1999; Grehan, 2001c) also consider as nodes the localities of intersection of two or more individual tracks, which would represent the boundary between two sister species (Henderson, 1989). In order to avoid any confusion, these latter may be called 'individual nodes' and the ones found at the intersection of generalized tracks, 'generalized nodes'.

Interpretation of generalized tracks and nodes

Generalized tracks are interpreted as ancestral biotas, formerly widespread and now fragmented by tectonic or climatic changes (Craw *et al.*, 1999; Morrone, 2009). Most of the track analyses (especially those published in the 1980s and 1990s) have applied a strict vicariance explanation (97, 47.7% of the publications in Appendix S3). Five analyses have used a dispersal explanation (2.4%). Many analyses consider both vicariance and dispersal to explain the observed patterns (52, 25.6%), with a notable increase recently (1980s: 3, 1990s: 8, 2000s: 20, 2010s: 41). This might represent a general trend in biogeography towards using a combination of vicariance and dispersal explanations, which has been noted for papers published in the *Journal of Biogeography* (Posadas *et al.*, 2013). Additionally, there are several published track analyses that do not emphasize any particular biogeographical process, presenting the patterns identified and focusing mostly on biogeographical regionalization (49, 24.1% of the publications).

Nodes are interpreted as complex areas that result from the 'hybridization' of two or more ancestral biotas (Heads, 2004; Morrone, 2004b, 2009), with a tectonic explanation usually explicit. Miguel-Talonia & Escalante (2013) considered that ecological processes might also be relevant explanations for some nodes. The relevance of nodes for biodiversity conservation has been discussed by Grehan (1993, 2001b), Morrone (1998), Morrone & Espinosa-Organista (1998), Contreras-Medina *et al.* (2001) and Luna-Vega *et al.* (2010). Because of their complex biotic composition, several empirical analyses have identified nodes as candidate areas for conservation (see Appendix S3).

CRITIQUES

McDowall (1978) argued that panbiogeography is a flawed approach, involving some assumptions that were neither logical nor justified. He criticized Croizat's failure to recognize the relevance of phylogenetic relationships for biogeography, because 'only when phylogenetic patterns are understood (and these are hypotheses only) can vicariance events be identified' (McDowall, 1978, p. 88). McDowall's opinion contrasts with that of Rosen (1975), who stated that generalized tracks can be tested with phylogenetic relationships. Additionally, McDowall argued that assuming that vicariance was the only explanation of a generalized track was a guess, and that there was no way to falsify it. McDowall (1978) highlighted the relevance of dispersal, arguing that track analyses tend to provide an all-exclusive explanation (vicariance) for complex patterns, and that there is a need to give also consideration to dispersal. Craw (1979) responded by referring to his own arguments on the falsifiability criterion, the role of dispersal and the relationship between phylogenetic systematics and biogeography. Craw (1979) considered that McDowall confused falsifiability and verifiability, and that he discussed them in the framework of 'logical positivism' instead of using Popper's 'hypothetico-deductive' epistemological approach. McDowall (1978, p. 92) wrote: 'the belief that similar distribution patterns are the result of the same causal process – common patterns have common causes…may be true in some instances, false in others, and there is no way of determining how many of each'. Craw (1979) argued that this neglects Popper's (1972) view that practical action is hardly conceivable without believing in the existence of regularities. Concerning dispersal, Craw (1979) criticized McDowall (1978) for confusing dispersion or range expansion and chance dispersal, and for not appreciating Croizat's efforts to show that '[a]ttempts to extrapolate from the former to the latter as a general historical biogeographical explanation have done much to hinder the development of a genuine science of biogeography' (Craw, 1979, p. 102). Finally, Craw referred to Croizat's alleged failure to recognize the relevance of phylogenetics for biogeographical analyses, stating that 'Croizat has repeatedly distinguished formal taxonomy/classification from phylogenetics/evolution' (Craw, 1979, p. 105). I find it difficult to accept this claim, because Croizat's 'formal taxonomy' merely refers to nomenclatural ranking, as evident in the example given by Craw (1979).

Mayr (1982) reviewed Nelson & Rosen's (1980) book and referred to vicariance biogeography as being in opposition to dispersalism. He considered that '[c]onsistent with a current fashion, no opportunity is missed to denigrate Darwin and Darwinism' (Mayr, 1982, p. 618). Mayr criticized the emphasis given to vicariance as the only relevant biogeographical process, and what he saw as the secondary role given to dispersal and extinction. He also found the claim that dispersalists did not work under a hypothetico-deductive framework to be incorrect, postulating that even in the 1940s dispersalists evaluated alternative hypotheses in terms of their predictions. He considered that vicariance biogeographers 'subscribe to a rigid dogma and…[their] whole endeavour is to prove the validity of that dogma instead of simply trying to find the truth' (Mayr, 1982, p. 620). Mayr's criticisms are quite reasonable, and his perception of Croizat's treatment of Darwinism is evident in Croizat's writings (e.g. see Croizat, 1977).

Craw & Weston (1984) provided a comparative analysis of panbiogeography, cladistic biogeography and dispersalism in the framework of Lakatos' (1978) 'scientific research programmes'. They considered that only panbiogeography and cladistic biogeography can be considered as progressive research programmes, because they generate novel predictions about Earth history, although I find this unnecessarily limiting, because predictions may refer also to factors that influence dispersal, such as wind and ocean currents or biological features of the organisms. Additionally, dispersalism was judged as being unscientific in Lakatos' sense, because it excludes the possibility of generating novel predictions. The basic distinction between panbiogeography and cladistic biogeography concerns their 'hard cores' (*sensu* Lakatos), because the former rejects the possibility of random distributional patterns (clearly a major shortcoming) and the latter investigates the possibility that they may exist. Craw & Weston (1984) concluded that cladistic biogeography was 'still in its infancy', and it cannot be expected to have progressed as far as panbiogeography. I agree with this latter comment, and consider that a fair comparison between cladistic biogeography and panbiogeography is still missing.

Seberg (1986) acknowledged the relevance of panbiogeography as the inspiration for cladistic biogeography and discussed several critical issues and inconsistencies in Croizat's writings. For example, Croizat's (1952, 1964) nodes seem to be almost impossible to distinguish from 'centres of origin'. Additionally, Seberg (1986) considered that Croizat's (1958, 1964) evolutionary ideas, which were interpreted by Rosen (1974) as orthogenetic (progressive evolution due to internal causes, not driven by natural selection), should be considered with great care; however, some panbiogeographers (Craw, 1984; Gray, 1989; Heads, 2005a) have postulated that Croizat's views on orthogenesis are similar to those held by Darwin, Mayr, Gould and others. Seberg (1986) also criticized Craw & Weston's (1984) attempts to analyse biogeographical approaches in the epistemological framework of Lakatos (1978), by their redefinition of Croizat's concepts and citation of extracts from Croizat's works. In particular, he considered that Craw & Weston (1984) reinterpreted some of Croizat's writings criticizing Hennig's phylogenetic systematics and Wegener's continental drift, in order to make his ideas more acceptable. [In this respect, I find Croizat's (1978) critique of phylogenetic systematics, in particular his attempt to show that Hennig plagiarized Danielle Rosa, particularly aggressive and ill-founded.] Seberg (1986, p. 378) concluded that 'the generalized track is still a useful concept, pointing out research areas where a more rigorous analysis is needed'.

Platnick & Nelson (1988) criticized panbiogeography, which they preferred to call 'spanning-tree biogeography', because it allows relationships between areas to be resolved even when no phylogenetic information is available, as it only considers geographical proximity. Platnick & Nelson (1988) hypothesized that Croizat's high regard for the decisiveness of geographical data followed from his particular view of evolution, as 'the fortuitous recombination of characters that renders systematics helpless and incapable, by itself, of arriving at the details of the truth in any particular case' (Platnick & Nelson, 1988, p. 415). Croizat's dismissal of phylogenetics is problematic, especially when considering that Heads, who is an orthodox panbiogeographer, proposed molecular panbiogeography, as explicitly phylogenetically-based.

Cox (1998) provided a general critique of panbiogeography considering that two factors hindered Croizat's ideas: his extreme rejection of chance dispersal as a possible mechanism under any circumstances and his particular terminology, which differs from that used in any other biogeographical approach. According to Cox (1998), Croizat's rejection of dispersal made him explain every disjunct distribution in terms of ancient vicariance events, even if this contradicts the accepted time of origin of the taxa; for example, assuming that the ancestor of Asteraceae was already in Australia between the Permian and the Triassic. Cox then proceeded to evaluate panbiogeographic concepts, concluding that '[t]he whole methodology is so erratic and variable that it is confusing and unreliable' (Cox, 1998, p. 824). Grehan (2001a) replied to Cox (1998), basically stating that Croizat never rejected dispersal and that his new terminology reflected a conceptual framework completely different from both dispersalism and cladistic biogeography. According to Grehan (2001a), panbiogeography incorporates neither dispersal nor vicariance in its methodology. Croizat's approach was to compare hundreds of distributional maps, where the 'recognition of shared patterns of dispersal led Croizat to propose a general vicariant form-making mode of dispersal where the "centre of origin" is represented by the combined range of all vicariant members of a taxon' (Grehan, 2001a, p. 415). With respect to terminology, Grehan argued that the introduction of graph theory to panbiogeography by Page (1987) provided new analytical tools, but tracks, nodes and baselines are still compatible with Croizat's earlier definitions.

Briggs (2007, 2009) reviewed the history of panbiogeography, from Croizat to the present century, referring to the reception of Croizat's ideas in New Zealand and the USA, and the development of cladistic biogeography. Briggs (2007, p. 273) considered that panbiogeography 'reached its peak of popularity in 1989–1990 and then began to fade'; that by the 1980s, some 'vicarianists' began to backslide and admit dispersal; and that the development of phylogeography led to a 'dispersalist counterrevolution'. I find that there is no empirical basis for this statement, and I wonder whether Briggs ignored publications from non-English-speaking countries or whether he restricted his analysis to 'classical' panbiogeography. According to Briggs (2007), it is now established that the bulk of the biota of Madagascar, the West Indies and New Zealand certainly arrived by dispersal in the Tertiary, so they can no longer be considered to have a significant number of Cretaceous relicts. Some recent analyses support this claim (Hedges, 2006; Wallis & Trewick, 2009; Samonds *et al.*, 2013).

Waters *et al.* (2013, p. 494) argued that panbiogeographic analyses 'are detrimental to the progress of biogeography as a discipline' and warned that 'some editorial and review processes continue to allow this misleading approach to be promulgated as a useful scientific method'. They noted especially the absence of quantitative methods and claimed that 'we have yet to see an empirical panbiogeographic study that argues for anything other than the primacy of some ancient vicariant process to explain distributional data' (Waters *et al.*, 2013, p. 495). This is not correct, as many papers use quantitative methods (see Appendix S3) and even one of the papers criticized by the authors refers to the 'northward and southward dispersal of *Eucyclops* in the Americas' (Mercado-Salas *et al.*, 2012, p. 457). It is unclear to me whether Waters *et al.*'s (2013) intention was to criticize all the researchers undertaking track analyses or only those rigidly adhering to Croizat's views. The proposal of scenarios that seemingly dismiss other data regarding the history of life, which the authors illustrated with Grehan & Schwartz's (2009) and Heads (2010) analyses, led them to state that '[w]hen panbiogeographic hypotheses of ancient vicariance conflict with data from geology, palaeontology, and molecular genetics (as they almost inevitably do), panbiogeographers tend to dismiss these other information sources as unreliable' (Waters *et al.*, 2013, p. 495). A similar critique is provided by de Queiroz (2014). Although these claims might seem quite reasonable, it should be noted that this is not a general feature of all track analyses, especially when they are undertaken under an evolutionary biogeographical framework. Waters *et al.* (2013, p. 496) conclude their critique by expressing concern over the tacit support provided by those journals that publish panbiogeographic contributions of an 'approach that is biased and misleading'. I find this comment disturbing, because it seems that the authors would like to have a sort of *Index librorum prohibitorum* for panbiogeographic papers. In case a ban on panbiogeographic papers is proposed, it should first be demonstrated that they are not scientific contributions.

The majority of the previous criticisms are directed at panbiogeography as a general approach, which in a few cases may be an expression of a lack of scholarship and in others may reflect the perception that panbiogeography is a single, unified approach (the same situation occurs with dispersalism, see Savage, 1982; Morrone, 2002). In fact, there are different approaches, as varied as Croizat's original panbiogeography (followed mostly by New Zealand's authors), evolutionary biogeography, and molecular panbiogeography that differ in terms of the processes considered (vicariance or vicariance–dispersal), the relationship with phylogenetic systematics and cladistic biogeography, the possibility of falsifying their hypotheses, and the methods used. These different approaches qualify as panbiogeography if we equate panbiogeography with track analysis, but we may postulate that evolutionary biogeography – using track analysis as a first step of a multi-stage protocol – is a different biogeographical approach, with some overlap with the 'classical' versions of dispersalism, panbiogeography and cladistic biogeography (Fig. 3).

Other criticisms refer more specifically to methodological weaknesses of track analysis. Although it is clear what individual and generalized tracks do represent, they way the former are drawn and oriented, and how the latter are identified have raised some concerns. With respect to individual tracks, Platnick & Nelson (1988) considered that if phylogenetic information shows that the nearest geographical neighbours are not nearest phylogenetic relatives, the spanning-tree approach should be abandoned. Several authors criticized the criteria for orienting individual tracks. For example, Croizat referred in different works to baselines as 'centres of dispersal', 'places of origin', 'centres of emergence', 'centres of origin', 'centres of gravity', 'centres', 'ancestral centres of radiation', 'ultimate centres of origin', 'distal centres of origin', 'original cradles',

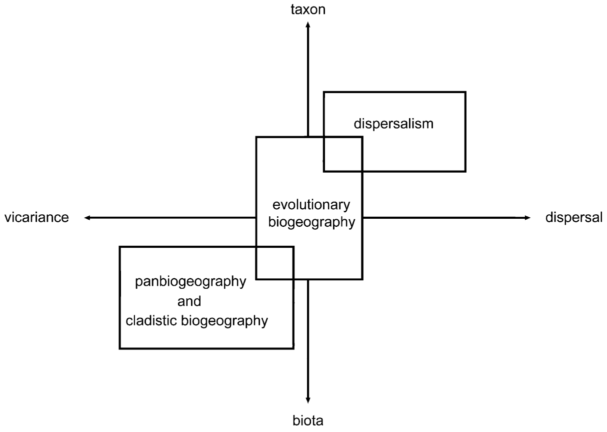

Figure 3 Comparison of approaches of dispersalism, panbiogeography, cladistic biogeography and evolutionary biogeography with reference to the entities analysed (taxa versus biota) and the processes invoked (vicariance versus dispersal).

'primary cradles' and 'distal cradles' (Platnick & Nelson, 1988). Page (1990) admitted that the concept of main massing was 'horribly vague'. Baselines have been considered as equivalent to 'centres of origin' (e.g. Grehan, 1994; Craw *et al.*, 1999) or the 'spatio-temporal sector of the Earth in which certain biological (and geological) distributions have evolved' (Grehan, 1990, p. 690).

McDowall (1978) discussed the possibility of testing generalized tracks, noting the problem of using phylogenetic criteria to construct the individual tracks on which they are based. Platnick & Nelson (1988) considered that the phylogenetic criterion is analogous to Hennig's progression rule. If generalized tracks represent hypotheses of primary biogeographical homology, which may be falsified in a cladistic biogeographical analysis (Morrone, 2001), it seems problematic to orient the individual tracks on which they are based using phylogenetic information, which would imply the use of circular reasoning (Morrone, 2009). Finally, if a track is oriented from the main massing towards the periphery, the inference would be similar to that from some dispersal hypotheses (Platnick & Nelson, 1988; Crisci *et al.*, 2000). Of the three criteria, the least problematic would be the baseline, but when analyses are undertaken on a continental scale, the use of geological characteristics is somewhat more difficult to carry out (Morrone, 2004a). Because of these critiques, the majority of the published track analyses (even those by panbiogeographers that consider track orientation as a fundamental procedure; e.g. Craw *et al.*, 1999) present unrooted individual tracks.

McDowall (1978) also questioned the statistical basis of generalized tracks. He considered that it was not clear how many individual tracks should coincide in order for a generalized track to be identified, how good the coincidence must be for an individual track to be considered part of a generalized track, and how non-congruent or conflicting generalized tracks should be interpreted. The different methods and software packages currently available are aimed at identifying generalized tracks more objectively, and I hope that in the future more efficient methods will be developed.

EVOLUTIONARY BIOGEOGRAPHY

I have previously proposed that track analysis is aimed at recognizing primary biogeographical homology, whereas cladistic biogeography is aimed at secondary biogeographical homology (Morrone, 2001, 2004a). Primary biogeographical homology represents a hypothesis about a common biotic history based on distributional congruence, which is formulated without any phylogenetic information. Secondary biogeographical homology refers to the cladistic biogeographical test of the previously recognized homology, thus requiring phylogenetic evidence (Morrone, 2009, 2014). The idea that track analyses can be tested with cladistic biogeography has been discussed in several published analyses (e.g. Linder, 1987; de Carvalho *et al.*, 2003; Nihei & de Carvalho, 2005). Here is where I identify the most basic distinction between molecular panbiogeography and evolutionary biogeography. Molecular panbiogeography uses molecular phylogenetic data as basic information, thus precluding their use to falsify its hypotheses, whereas evolutionary biogeography undertakes track analyses without previous phylogenetic considerations, allowing the test of a track analysis through a cladistic biogeographical analysis.

Once biotas have been identified (track analysis) and tested (cladistic biogeographical analysis), dating the vicariance events that isolated them seems the next logical step. Molecular dating of divergences between lineages has been suggested as a possible way to achieve this objective (Morrone & Crisci, 1995; Morrone, 2009, 2011; Posadas *et al.*, 2013), while fossil data may also be used (Morrone, 2009). Heads (2004, 2005b,c, 2009, 2011, 2012b) has provided a critique of fossil-based calibration of chronograms, considering that fossil ages given as minimum are 'transmogrified' into maximum ages. He proposed, instead, that lineages should be calibrated with tectonic events, using fossil data to provide minimum, not maximum, clade ages. He argued that 'this approach combines the best of molecular biology with hard-rock geology and avoids the many problems of fossil calibration' (Heads, 2011, p. 214). This idea has been criticized by Swenson *et al.* (2012), who found that 'calibrating molecular phylogenies *a priori* on sister relationships as if they represent alleged vicariance events…is inappropriate' (Swenson *et al.*, 2012, p. 530). They used as an example Heads' (1999) analysis of *Abrotanella*, finding that assuming a molecular clock and extrapolating the dates based on his tectonic calibrations, the origin of Asteraceae would be 511 Ma (a date that precedes the split between plants and mosses) or even 1.5 billion years! [Interestingly, this echoes one of Cox's (1998) criticisms.] In spite of the problems detected by Heads, I think molecular dating is a promising area for biogeography, because it allows us to refine hypotheses on dispersal and vicariance and to distinguish cases of pseudo-congruence (Donoghue & Moore, 2003). Additionally, molecular dating analyses can be used to identify cenocrons, which represent sets of taxa that share the same biogeographical history, constituting identifiable subsets within a biota by their common biotic origin and evolutionary history (Morrone, 2009). Cenocrons incorporate a temporal dimension that implies explicitly or implicitly a different time of the dispersal of taxa into the biota.

Currently, there are three general models in historical biogeography: centre of origin–dispersal–adaptation (CODA), vicariance and dispersal–vicariance. The first assumes a restricted origin of the ancestor of a group, followed by dispersal, arrival to new areas and adaptation to new conditions. The vicariance model assumes a widespread ancestor, which differentiates due to the appearance of barriers that isolate the populations. The dispersal–vicariance model contemplates alternating episodes of vicariance and dispersal. CODA and vicariance represent extreme, ideal situations, and it is unrealistic to choose one process and discard the other; the same point has been made previously by several authors (Savage, 1982; Brooks, 2004; Lieberman, 2004; Sanmartín & Ronquist, 2004; Riddle *et al.*, 2008; Crisci & Katinas, 2009; Morrone, 2009, 2011; O'Grady *et al.*, 2012; de Queiroz, 2014). In fact, some decades ago, Cracraft (1975, p. 237) postulated that 'when analysing the history of biotas we must first attempt to understand the general patterns of vicariance, and then, following this, consider whether it is necessary to invoke dispersal to explain the composition of the biota'. A few years later, George Gaylord Simpson admitted: 'A reasonable biogeographer is neither a vicarist nor a dispersalist but an eclecticist' (Simpson, 1980, p. 253) and Croizat added: 'I do agree, but with the understanding that a biogeographer must be a vicarist in principle and a dispersalist in detail, case by case according to the merits of each case' (Croizat, 1982, p. 297).

Although panbiogeography's metaphor 'Earth and life evolve together' may provide a useful guide to understanding broad, general patterns, the relationships between Earth history and life are more complex because biotic history is reticulate (Brooks, 2004). Vicariance may be treated as the default explanation for general patterns, whereas dispersal later modifies the distribution of particular taxa. To reduce explanations exclusively to vicariance or dispersal is misguided. We should integrate these different explanations in order to understand the evolution of biotic distributions, incorporating the dating of the lineages and the identification of the different cenocrons. In the framework of this dispersal–vicariance model, track analysis is a useful method for detecting general patterns, and may constitute the first step of an evolutionary biogeographical analysis. Identifying biotas and the processes that led to their evolution is fundamental for other, more elaborate analyses.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Publications including biographical aspects of Léon Croizat.

Appendix S2 Books dealing with panbiogeography, including Croizat's major works, edited books and textbooks.

Appendix S3 Publications including track analyses by authors other than Croizat, the methods applied (and software, when used) and the processes postulated by the authors.

BIOSKETCH

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