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.
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.

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).


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. 2).

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.
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 endemcity 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-Esquível, 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
Croizat’s ‘formal taxonomy’ merely refers to nomenclatural
onomy/classification from phylogenetics/evolution’ (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 taxa-
onomy/classification from phylogenetics/evolution’ (Craw, 1979, p. 105). I find it difficult to accept this claim, because
Croizat’s efforts to show that ‘[a]ttempts to extrapolate from
the former to the latter as a general historical biogeographi-
ical explanation have done much to hinder the development
of a genuine science of biogeography’ (Craw, 1979, p. 102).

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 empha-
sis given to vicariance as the only relevant biogeographical
process, and what he saw as the secondary role given to dis-
persal and extinction. He also found the claim that dispersal-
ists did not work under a hypothetico-deductive framework
to be incorrect, postulating that even in the 1940s dispersal-
ists evaluated alternative hypotheses in terms of their predic-
tions. He considered that vicariance biogeographers ‘subscribe to a rigid dogma and . . . their whole endeavour is
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 Cro-
izat, 1977).

Croizat & Weston (1984) provided a comparative analysis of
panbiogeography, cladistic biogeography and dispersalism in
the framework of Lakatos’ (1978) ‘scientific research pro-
grammes’. They considered that only panbiogeography and
cladistic biogeography can be considered as progressive
research programmes, because they generate novel predic-
tions 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 bi-
ological 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 bio-
geography concerns their ‘hard cores’ (sensu Lakatos),
because the former rejects the possibility of random distribu-
tional patterns (clearly a major shortcoming) and the latter
investigates the possibility that they may exist. Craw & West-
ton (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 panbiogeog-
raphy as the inspiration for cladistic biogeography and dis-
cussed 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 Cro-
izat’s views on orthogenesis are similar to those held by Dar-
win, Mayr, Gould and others. Seberg (1986) also criticized
Croizat’s (1978) critique of phylogenetic systematics, in particular his
approach to analyse biogeographical approaches in the epistemological framework of Lakatos
(1978), by their redefinition of Croizat’s concepts and cita-
tion of extracts from Croizat’s works. In particular, he con-
considered that Craw & Weston (1984) reinterpreted some of
Croizat’s writings criticizing Hennig’s phylogenetic systemat-
ics 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, par-
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 deci-
siveness of geographical data followed from his particular
view of evolution, as ‘the fortuitous recombination of char-
acters 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 panbiogeogra-
phy considering that two factors hindered Croizat’s ideas: his
extreme rejection of chance dispersal as a possible mecha-
nism under any circumstances and his particular terminol-
ogy, which differs from that used in any other
biogeographical approach. According to Cox (1998), Cro-
izat’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 ‘vicariantists’ 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 \textit{et al.}, 2013).

Waters \textit{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 \textit{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 ‘northeast andsouthward dispersal of \textit{Eucyclops} in the Americas’ (Mercado-Salas \textit{et al.}, 2012, p. 457). It is unclear to me whether Waters \textit{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 \textit{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.

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’,
The different methods and soft-
ware 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 clad-

istic 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 formu-

lated without any phylogenetic information. Secondary bio-


geographical 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 bio-

geographical analysis.

Once biotas have been identified (track analysis) and

tested (cladistic biogeographical analysis), dating the vari-
cance 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 (Mor-

rone & 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 cri-
tique 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 pro-
vide 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 criti-
cized 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 hypothe-
ses on dispersal and vicariance and to distinguish cases of

pseudo-congruence (Donoghue & Moore, 2003). Addition-

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).

Figure 3
ally, 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, 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 tions. The vicariance model assumes a widespread ancestor, 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, restricted origin of the ancestor of a group, followed by dispersal, arrival to new areas and adaptation to new conditions.

ACKNOWLEDGEMENTS

I thank Claudio de Carvalho, Malte Ebach, Michael Heads, Liliana Katinas, Adriana Ruggiero and two anonymous referees for useful comments on the manuscript. Both anonymous referees kindly read revised versions of the manuscript, helping me to formulate my ideas more clearly.

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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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Editor: Liliana Katinas