Reflections on the Nature, Framing, and Testing of Historical Biogeographic Hypotheses

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Recent views on the goals and methods of historical biogeography have sought support in the distinctions between three phases of biogeographic study and between three aspects of biogeographical hypotheses that were made by Ian R. Ball in 1975 and 1990. Here it is shown that these recent perspectives on Ball’s philosophy concern misinterpretations of his views that, therefore, are incorrectly used in the development of a theoretical framework for the formation and testing of biogeographic hypotheses. This re-evaluation of Ball’s views also serves as a template for a critical appraisal of several recently published standpoints on the goals and methods of biogeography. Recent panbiogeographic studies postulate wide-spread ancestors in the explanation of present-day vicariant distributions. Wide-spread, even cosmopolitan, ancestral distributions also underlay early applications of taxon-cladistic biogeography, but this notion of primitive cosmopolitanism has been abandoned and replaced by the more realistic assumption that the ancestor had a more restricted distribution. The notion of primitive cosmopolitanism, or at least greatly widespread ancestors, has resurfaced in historical biogeographic hypotheses featuring in modern panbiogeographic studies. This explanatory model is combined with the concept of polymorphic ancestors, which may give rise to parallel evolution of descendant taxa through the process of recombination of ancestral characters. Ample parallelism is well-known in phylogenetic analyses, while it is known also from cases of relatively recent urban evolution. Recent insights into developmental genetics, character identity, and homology concur with hypotheses featuring in modern panbiogeographic studies. This re-evaluation of Ball’s views also serves as a template for a critical appraisal of several recently published standpoints on the goals and methods of historical biogeography.

Key Words: Ancestral distribution, area cladistics, cosmopolitanism, dispersal, panbiogeography, parallelism, philosophy, taxon-biogeography, vicariance biogeography.

Introduction

“Biogeography is a strange discipline. In general, there are no institutes of biogeography; there are no departments of it. There are no professional biogeographers—no professors of it, no curators of it.” With these lines Nelson (1978: 269) began his paper on the history of biogeography and he basically reiterated this point of view several years later (Nelson 1985). Although Nelson’s opinion has been acquiescently cited by others (e.g., Crisci et al. 2003; Morrone 2009), it is not fully correct. For example, when the Dutch ornithologist K. H. Voous (1960) published his “Atlas of European Birds”, he was at that time actually Professor of Zoogeography at the Free University of Amsterdam. And when Ian R. Ball was running his flatworm laboratory at the Zoological Museum of the University of Amsterdam, only a few years after he had published his landmark paper on biogeographic hypotheses (Ball 1975), he was Professor of Systematic Zoology and Zoogeography from 1980–1985. In point of fact, during the period 1928–2016 the University of Amsterdam had several other professors occupying a chair of Zoological Systematics and Zoogeography (L. F. de Beaufort, H. Engel, J. H. Stock, S. van der Spoel, F. R. Schram, and S. B. J. Menken; see https://www.uva.nl/onderzoek/onderzoek-aande-uva/hogleraren/album-academicum/album-academcum.html).

But probably it is true that when Nelson (1978) wrote his statement, these professors of animal biogeography in Amsterdam represented a small minority (but there are also botanical examples at the University of Leiden, The Netherlands). Since then, the field of biogeography in general and that of historical biogeography in particular has experienced vigorous debates on its goals, principles, and methods. Although this has not yet resulted in any coherence or general agreement, it has effectuated an increase in the number of academicians professionally dedicated to the science of biogeography as well as the number of biogeography departments, albeit that the latter usually carry labels such as, for example, macroecology, conservation biogeography, and biodiversity.

The dust of these, at times somewhat acrimonious, debates on subjects such as taxon-biogeography, area cladistics, panbiogeography, and dispersal biogeography has not yet settled. There is still a great deal of discussion going on between biogeographers on what are the best methods to use and even on the question of what should be the goal of historical biogeography. These controversies relate to the philosophy of science and to the scientific model used in historical biogeographic studies, subjects at the heart of Ball’s (1975) influential paper.

Ball (1975) distinguished between three phases of bio-
geographic study: (1) the descriptive phase, (2) the narrative phase, and (3) the analytical phase, the two last-mentioned ones belonging to the discipline of historical biogeography. Descriptive biogeography documents the ranges of the species or higher taxa. In narrative biogeography we develop a rational historical scenario that sketches how the members of a particular taxon evolved over space and time, and how that resulted in their present-day distribution. In the analytical phase, explanatory hypotheses of a particular biogeographic distribution are based on phylogenetic trees of the taxa and from these falsifiable statements can be derived that can be tested in future analyses.

Ball's distinction between these three phases continues to be invoked in support of particular views on the goal and procedures of analytical biogeography, and on the framing of historical biogeographic hypotheses and explanations. However, in their endeavor to support their viewpoints with Ball's notion of the three phases, some modern workers have extended his views beyond their original meaning. In this paper I comment on these recent perspectives on Ball's (1975, 1990) philosophy. In the context of this evaluation of current invocations of Ball's philosophy, the present critique simultaneously serves as a template for a critical appraisal of several recently published standpoints on the goals and methods of biogeography.

Misunderstandings

One misrepresentation of Ball's three phases—descriptive, narrative, analytical— is to consider these as representing phases of development in the science of historical biogeography, indicating a kind of historical progress in this discipline (e.g., Humphries and Parenti 1999; Crisp et al. 2011; Ebach 2017; Michaux 2020). This point of view may have been instigated by the following lines in Ball's paper (1975: 408): "As with any other discipline biogeography must pass through different stages of maturity..., and specialists .... may be working at different levels because of the nature of their respective subdisciplines...". Below I shall show that this passage, unwittingly, has led many biogeographers astray and that Ball actually meant quite something else with his three phases.

First of all, he wrote in the same paper (Ball 1975: 422): "I wish it to be understood that I am not suggesting that the different viewpoints of biogeography outlined throughout this paper are necessarily on trial." In the same paper he wrote also (Ball 1975: 411): "In criticizing narrative explanations,.... I do not wish to imply that all such explanations are worthless....I claim only that we should recognize their weaknesses and attempt to refine them sufficiently to make them true scientific hypotheses." And in the abstract, he wrote: "All biogeographical studies seem to pass through three main phases..." (Ball 1975: 407). Thus, first of all, the three phases concern individual biogeographic studies and not the entire discipline of historical biogeography.

In a paper published some years later, Ball (1983) provided some additional information on what he had in mind when he wrote his 1975 paper in Systematic Zoology. This is encapsulated in the following two quotations:

"What I tried to do...was to stimulate critical thinking so as to avoid what may be termed category errors" (Ball 1983: 422);

"...in distinguishing between descriptive, narrative, and analytical biogeography..., I was attempting to make...hierarchical distinctions for biogeographical statements with the intention of neutralizing pointless arguments that crossed, illegitimately, the boundaries within the hierarchy" (Ball 1983: 422).

In similar vein to this last quotation he had already written in his 1975 paper:

"What I am saying is that in advocating a hypothesis to account for observed distributional data we must be clear into what category our explanation falls and proceed accordingly" (Ball 1975: 422).

From these quotations it becomes clear that, according to Ball, there is not a single valid approach to historical biogeography. This interpretation of his views also emerges from the following two quotations:

"...deductive explanations, although perhaps to be preferred, are not the only modes of explanation used in the sciences, and we must be cautious about confining ourselves to one prevailing philosophical approach" (Ball 1983: 416);

"There may well be, indeed are, problems, methods, approaches appropriate to each level in the hierarchy" (Ball 1983: 423).

The next quotation from his 1983 paper is specifically directed against cladistic vicariance biogeographers, who are solely interested in area biogeography, maintaining that historical biogeography should examine only the interrelationships between areas and their biotas. During the 1970s, 1980s, and 1990s workers like Gareth Nelson, Norman Platnick, Christopher Humphries, and Lynne Parenti argued that this was the only true historical biogeography. These days this view is propagated by, for example, Lynne Parenti, Juan Morrone, and Malte Ebach. They have all published one or more books advocating cladistic vicariance biogeography, although they may call it differently, such as evolutionary biogeography, comparative biogeography, area classification or area taxonomy (see Morrone 2009; Parenti and Ebach 2009; Ebach 2017). This is Ball's view on this approach to historical biogeography:

"In the light of current stress on vicariance biogeography..., I emphasize my agreement that it is the vicariant components alone that, within limits, will enable us to make predictions concerning earth history, but such predictions are not the only, or even the principal, objectives of a science of biogeography" (Ball 1983: 423).

I believe that these quotations show that Ball’s notion of historical biogeography was not that the entire discipline progressed on a ladder of scientific perfection—from descriptive to narrative to analytical—but that each individual study may have its own appropriate approach. The only requirement is that the hypotheses are expressed as falsifiable statements.
The nature of historical biogeographic hypotheses

That the hierarchical distinction between the three phases applies to individual studies and does not represent an ascending three-step scale going from lesser to greater scientific and philosophical perfection is illustrated by the following example. In the analytical phase of a botanical historical biogeographic study it appeared that the time-calibrated area cladogram did not correlate with plate tectonic events and presumed areas of endemism. Therefore, the authors resorted to the descriptive and narrative phases in an attempt to account for present-day distributional patterns, presumably resulting from non-vicariant speciation events involving phenomena such as different dispersal capability, habitat specialization, adaptation to pollinators, and edibility of fruits (van Welzen et al. 2015).

Ball’s “method”

My sketch of Ball’s vision completely contradicts Ebach’s (2017: 19) interpretation given in his recent book “Reinvention of Australian Biogeography”: “Together these three phases form a procedure, or steps, within the reformation of a scientific discipline.” In his book Ebach (2017) put at center stage Ball’s (1975) three phases and in particular the preferred three aspects of a biogeographical hypothesis that the same worker formulated many years later (Ball 1990). Reading Ebach’s book one gets the strong impression that he attributes to Ball the construction of a kind of method for testing biogeographic hypotheses and that it is “…one that moves biogeography forward to an evidence-based science” (Ebach 2017: 132; italics in original). I offer two comments on this. First, Ball never claimed to have formulated a method and he was quite explicit about this when he wrote “…[the] inference that I proposed a distinct methodology for solving problems of historical biogeography I find somewhat embarrassing, in that this is something that I have never myself claimed” (Ball 1983: 421). Second, evidence is not the crucial arbiter in formulating historical biogeographic hypotheses, as “No one deliberately erects an hypothesis that is discordant with the facts to be explained, thus,…concordance with the facts is not a measure of truth” (Ball 1980: 1285).

One other misapprehension by Ebach (2017) concerns the three items that Ball (1990) lists as important aspects of biogeographical hypotheses, viz., clarity, comparability, and rigour. Ebach considers Ball’s (1990) three aspects to be criteria for testing biogeographic hypotheses; the same misunderstanding can be found in Crisci et al. (2003). However, Ball did not at all promote these aspects as potential testing criteria. He merely suggested that clarity, comparability, and rigour should form three “facets” in the framing of biogeographic hypotheses. Clarity refers to the notion that the units of study should be clearly denoted and have the philosophical, logical status of individuals. In biogeography this relates, for example, to the definition and recognition of areas of endemism. Comparability should be achieved by presenting the hypothesis “... in such a way that direct comparison with hypotheses derived for other organisms in the same area can be made” (Ball 1990: 5). In a modern context one could think of time-calibrated phylogenies for several taxa inhabiting a particular portion of the globe, in which the taxa and their distributions are mapped at the tips of the phylogeny. Such trees may profitably be compared, as they are constructed in a similar way, and thus it may be assessed whether or not they have been subjected to the same geological drivers in space and time. Rigour in the formulation of biogeographical hypotheses means that these should be presented in such a way that future data on systematic characters, geographic distribution or on geological events may be evaluated as potential falsifiers of the hypothesis. Thus, these three facets play a role in the framing of biogeographic hypotheses by promoting their testability, but they are no tests themselves, as mistakenly argued by Crisci et al. (2003) and Ebach (2017).

I take the opportunity of pointing out another remarkable aspect of Ebach’s (2017) philosophy of science and one that, as he argues, emanates also from Ball’s views. This is Ebach’s notion that “…biogeographic methods falsify proposed…hypotheses” (Ebach 2017: 133). In the context of Popper’s philosophy of science, with its emphasis on testability and potential falsification, it eludes me how a method can test an hypothesis, as the latter can be corroborated or falsified only by new observational data. Popper’s philosophy of science was adopted early in the development of modern systematic biology and analytical biogeography (Williams and Ebach 2008 and references therein) and was also favoured by Ball (cf. Ball 1975).

Polytopic origins

Ball (1975) applauded the work of Léon Croizat (1958, 1962), who developed a biogeographic method and philosophy that became known as panbiogeography (see Crisci et al. 2003; Lomolino et al. 2016 and references therein). One of the basic principles of panbiogeography is that the current distribution of taxa reflects the geological events that they have been subjected to during their evolution. Croizat categorically rejected long-distance dispersal as an explanation for present-day vicariant distributions. Soon thereafter, panbiogeographic principles were integrated with the, then new, discipline of phylogenetic systematics or cladistics and thus a new method of historical biogeography was created, viz., vicariance biogeography (see Morrone 2015a; Lomolino et al. 2016 and references therein), known also under the name cladistic biogeography (see Humphries and Parenti 1999).

Strict cladistic biogeographers maintain that there is only one kind of historical biogeography and that is the version that focuses on the historical relationships of areas and their biotas (cf. Parenti and Ebach 2009; Morrone 2009). Strict cladistic biogeographers denounce the historical biogeographic study of individual taxa. In contrast, taxon-cladistic biogeographers are interested in resolving the history of a particular taxon, that is, of a particular phylogenetic lineage. For each of these two analytical fields several methods have
been developed (see Lomolino et al. 2016 and references therein), but these need not concern us here. For now, the only important point to consider is that certainly taxon-biogeographers use their taxon-area cladograms to reconstruct ancestral distributions, which feature in hypotheses on the evolution through space and time of their taxa of interest. Although strict cladistic biogeographers eschew the reconstruction of ancestral areas, their areagrams, nevertheless, rest on the premises that “…biotic areas…share a history…” (Parenti and Ebach 2009: 244) and that thus “…areagrams can be used to evaluate…hypotheses of timing…” (Parenti and Ebach 2009: 184). Although strict cladistic biogeographers go to great lengths and complex arguments in order to deny that they are interested in ancestral areas or that the nodes on areagrams could be used as first approximations of such ancestral ranges (cf. Humphries and Parenti 1999; Parenti and Ebach 2009), it is inevitable that notions of common history of areas pervade their texts. And this need not surprise us, as strict cladistic biogeographers first and for all are systematists, specializing on particular groups of organisms. Where “…histories of areas [are] derived from biological…data…” (Humphries and Parenti 1999: 120–121) it is inevitable that a node in an area cladogram signals a shared history of biotas and/or areas, irrespective of the interpretations that different methods or researchers attach to these nodes. For example, nodes may be hypothesized as representing ancestral areas (e.g., Hausdorf 1998) or as vicariant events (Hovenkamp 1997, 2001; Heads 2014), or in first instance only as junctions of components. Generally, strict cladistic biogeographers purportedly only subscribe to the third interpretation, albeit that secondarily the nodes or junctions are interpreted as denoting close relationship of biotas and/or areas (Parenti and Ebach 2009; King and Ebach 2017). Evidently, when strict cladistic biogeographers would refrain from assigning, even secondarily, any causal and historical notion to the nodes of their area cladograms it would be futile to strive for “natural area classifications” (Ebach 2017: 145) and to determine “relationships” among biotic areas (King and Ebach 2017: 501), since in that case any classification or relationship would be equally valid. However, the fact that strict cladistic biogeographers assign ontological reality, either explicitly or implicitly, to their biotic areas and biogeographic regions (Morrone 2015b) implies an underlying hypothesis on the causality behind these areas and regions. Clearly, this hypothesis relates to geological and ecological events during the history of the earth (Corral-Rosas and Morrone 2016).

In cladistic biogeography, either strict or taxon-based, the preferred historical explanation for present-day organizational distributions is the fragmentation of the ranges of once continuously distributed taxa, thus resulting in presently vicariant ranges. However, some cladistic biogeographers and panbiogeographers have offered an alternative explanation of major vicariant biogeographic patterns. In that model a polytopic and polytypic origin is postulated for taxa exhibiting major disjunctions, instead of hypothesizing a uniform ancestral population living in a single geographic area that eventually did break up and thus gave rise to vicariant sister taxa. This notion of polytopic and polytypic origins recently has been most explicitly advanced by Heads (2012, 2014). However, the roots of this notion lie further back in time and go back to Croizat (e.g., 1962; see also Cain 1944) and probably even further (Williams and Ebach 2008). I will here restrict myself to the views expressed by Croizat (1962) and Heads (2012, 2014).

Croizat (1962) described this important aspect of his panbiogeography under the term “wing dispersal”. It refers to a group of phylogenetically related (“consanguineous”; Croizat 1962: 13) taxa in which certain closely related (“al- lied”; Croizat 1962: 285) members occur at the very opposite ends of a wide-ranging group, distributed over a major portion of the globe. For the sake of clarity I do here point out that Croizat used the term dispersal for a different notion than commonly understood, that is, for what he called “translation in space plus form-making” (cf. Ball 1979: 387); for the present discussion this does not need to concern us here any further. Presence of closely related taxa in the “wings” is not due to chance dispersal by an ancestor from one end of the distributional range to the other, but is explained by fragmentation of the range of a once wide-spread ancestor and by the so-called recombination of ancestral characters. This last-mentioned notion is also an important aspect of Croizat’s panbiogeography. Through recombination of ancestral characters in geographically different portions of the ancestral range new taxa evolve in situ. This may result in a situation that taxa in the “wings” acquire sets of similar characters that are absent in taxa located at more central portions of the group’s distributional range. A few quotations from Head’s books suffice to show that he endorses Croizat’s notions of “wing dispersal” and recombination of ancestral character states:

“It seems that lineages do not necessarily evolve in a linear or hierarchical way and that phylogeny may develop through the recombination of ancestral characters, rather than the evolution of any new, uniquely derived characters” (Heads 2012: 36);

“The New World, Macaronesian, and Old World genera each evolved in situ out of a widespread ancestor by recombination of ancestral characters” (Heads 2012: 36–37);

“In this model, polymorphic ancestral complexes already occupied ancestral landscapes, and aspects of modern biogeography and biodiversity were already established, long before the extant groups or their landscapes existed. Parallelisms concentrated in a particular area are often thought to be responses to particular needs imposed by the environment, but are just as likely to reflect ancestral polymorphism” (Heads 2014: 407).

This model of polytypic evolution combined with the concept of recombination of ancestral characters, has two implications that warrant some further discussion, viz., the evolution of parallelism (see last-mentioned quotation from Heads given above) and the assumption of a kind of primitive cosmopolitanism.
Parallelism

The polytopic biogeographic model depends on the parallel evolution of similar, homologous characters ([I shall here short-circuit the argument that under a cladistic framework there is no difference between convergence and parallelism (see Williams and Ebach 2008 for an historical overview of this discussion; see also Sluys 1989a) and simply accept that true parallelisms concern the expression of similar evolutionary modifications based on a common foundation]. Recurrent evolution of homologous features in different, separate branches of the phylogenetic tree is a phenomenon that frequently emerges when one phylogenetically studies in detail a group of organisms, either based on morphological features or on molecular characters (Sluys 1989a and references therein; Meyer 1999). This may even go so far that in some groups it is very difficult or impossible to recognize uniquely derived, apomorphic characters. It has been argued that in such cases cladistic analysis does not necessarily grind to a halt, but that repeatedly evolved, parallel characters may be profitably used to resolve portions of the phylogenetic tree when they function as non-universal derived character states or underlying synapomorphies (Sluys 1989a and references therein).

In the present context it is not relevant how such underlying synapomorphies might be used in cladistic analyses or to argue whether or not this is feasible or valid under current philosophies and methods of systematics. It is only important to realize that it depends on the notion that there are causal biological mechanisms giving rise to these patterns of parallelism. The same notion underlies the polytopic biogeographic model and has been presumed to be based on the hints that parallel development of homologous characters may be due to retention of genes or gene interactions, developmental constraints, embryonic pathways (Meyer 1999), incomplete lineage sorting (Heads 2012, 2014), or ancestral polymorphism (Heads 2012, 2014). It is particularly the last-mentioned presume case that has been invoked as giving rise to the recombination of ancestral characters, which, in turn, results in the parallel and polytopic origin of genealogically related taxa (Croizat 1962; Heads 2012, 2014). Although Heads (1985) noted the resemblance between the notion of recombination of ancestral characters (see Croizat 1962: 208), and concepts such as unique inside parallelism (see Brundin 1981) and underlying potential or underlying synapomorphies, there is a difference. This resides in the fact that underlying synapomorphies are seen as newly evolved, derived characters (Sluys 1989a), whereas ancestral characters are plesiomorphic by definition.

In a biogeographic context an important question to ask is: how plausible is it to assume that closely related taxa with similar combinations of features originate at different locations from a widespread common ancestor? A parallel of this phenomenon may be found in recent studies on so-called urban evolution. The quickened pace of evolution in cities has made it possible to study in real time the evolution of parallel features and adaptations in urban life forms (Schilthuizen 2018). A showcase example is the blackbird Turdus merula Linnaeus, 1758. After originally having been a forest bird, blackbirds started to colonize European cities in the beginning of the nineteenth century, each city being stocked by local forest birds. Thereafter, each separate city population evolved shorter and stubbier bills, different songs, earlier breeding and non-migratory habits, as compared with rural birds (Schilthuizen 2018 and references therein). In this way a new kind of blackbird evolved independently, in parallel, in each city. The city birds do not yet form one urban gene pool because blackbirds hardly disperse between different cities, but eventually their genes might homogenize. Thus, this kind of ecological speciation indeed may give rise, perhaps, to new species through a diffuse process of speciation more or less at the same time at different locations.

One might be inclined to consider such ecological speciation as irrelevant in the explanation of broad-scale biogeographic patterns and argue that the temporal and genomic scales of this process are of a different order of magnitude than those required for the independent polytypic and polytopic differentiation of taxa in widely separated parts of an ancestral distributional range. Nevertheless, recent insights in developmental genetics and modern concepts of character identity and homology support the notion that dormant ancestral features or alleles can be independently re-activated in portions of a lineage that occur at different periods at different geographic locations (see Wagner 2014).

Primitive cosmopolitanism

The notion of the polytopic and polymorphic origin of taxa is linked to the assumption that the ancestor of a group “…was always already widespread…” (Heads 2012: 41). The same assumption underlay early applications of taxon-cladistic vicariance biogeography, in which ancestral areas were estimated by summation of the ranges of the taxa at the tips of the area cladogram (Nelson 1975). However, in a group with a wide distribution, in this way one always quickly ends up with ancestral areas that comprise a major part of the globe or even that the range of the ancestor has been cosmopolitan (e.g., Sluys 1989b: fig. 314). But this automatic consequence of an ancestral cosmopolitan range is difficult to reconcile with the fact that presently species generally have much more restricted geographic distributions. Probably, ancestors also had more restricted ranges. Several pointers have been suggested as being indicative of the extent of presumed ancestral ranges, such as (1) “Areas that are positionally plesiomorphic in the area cladogram are more likely parts of the ancestral area than are positionally apomorphic areas” (Bremer 1992: 440), and (2) “Areas represented on numerous branches of the cladogram are more likely parts of the ancestral area than are areas represented on few branches” (Bremer 1995: 256). A related indicator was suggested by Enghoff (1993: 527): “…the degree of cladistic subordinateness (=positional apomorphy) of the underlying taxon is a measure of the relative probability of disper-
sal”. On the basis of such assumptions over the years several methods have been developed, and refined, for the reconstruction of ancestral distributions, such as DIVA (Ronquist 2001) and S-DIVA (Yu et al. 2010).

Nevertheless, strict cladistic vicariance biogeographers and also panbiogeographers have always strongly voiced their objections against the notion of ancestral areas and presumed areas of origin of particular taxa (e.g., Croizat et al. 1974) and have resorted to “the principle of primitive cosmopolitanism” (Nelson 1973: 315), assuming that the “ancestor was always already widespread” (Heads 2012: 41), thus “emphasizing a widespread ancestral range” (Craw et al. 1999: 15). However, in practice this axiom is superseded by the biological reality that taxa generally are not cosmopolitan and that, therefore, it has to be acknowledged that “every taxon has a particular center of form-making” or “an initial center of form-making” or that a particular region is “a major center of form-making, and origins” (Croizat 1962: 121, 711, 49, respectively); this again comes close to the concept of ancestral areas of origin (see also Ball 1975: 420).

It is noteworthy that in their biogeographic vicariance models for the evolution in space and time of particular taxa, panbiogeographers (Craw et al. 1999; Heads 2012, 2014) in practice resort to the reconstruction of such primal centers of form-making or the ranges of widespread (mostly non-cosmopolitan) ancestral complexes or “centre[s] of differentiation” (Heads 2014: 402), despite their disparagement of such notions, through the summation of the distributions of all presently known taxa, a technique that earlier was considered unrealistic and, therefore, was abandoned by taxon-biogeographers (see above).

The way forward

In my monograph on the marine triclads (Sluys 1989b) I argued that although taxa may have evolved at different time periods, their biogeographic patterns, area cladograms, nevertheless may be similar. Greatly similar branching patterns in the area cladograms of several taxa or similarities between the topologies of area cladograms and those of the sequence of continental drift, for example, do not necessarily imply an identical underlying cause. Causal congruence is only to be expected when taxa evolved roughly in the same temporal, geological time frame. Therefore, meaning-ful historical biogeographic comparisons can be made only between taxa and their area cladograms when the organisms diversified during more or less the same period. Strict cladistic vicariance biogeographers generally have never been bothered by the absence of an absolute time frame in their area cladograms, to the contrary (see Humphries and Parenti 1999; Parenti and Ebach 2009). However, others have seen this as a major drawback, potentially leading to wrong conclusions (see Lomolino et al. 2016 and references therein). From that perspective, the arrival of molecularly-based timetrees represented the long-awaited breakthrough in the discipline of historical biogeography, irrespective of the practical difficulties involved in their calibration (Crisp et al. 2011; de Queiroz 2016).

As biogeography in general, and historical biogeography in particular are multidisciplinary fields of study (Morrone 2009; Ebach 2015; Ebach et al. 2016) unification is not the proper framework for future progress. However, theoretically recognizing this multidisciplinarity of biogeography is one thing, but accepting its implications may be more difficult in practice. For example, although Ebach (2015) and Ebach et al. (2016) argued that biogeography and historical biogeography are multidisciplinary disciplines that “not need to be integrated into other fields” (Ebach 2015: 79), Ebach (2017: 138) posited that “discovering natural areas is the main problem” to be tackled in biogeographic studies and that the sole purpose of an “integrative” biogeography is the construction of area classifications. This does not give the impression of an unbiased, multidisciplinary vision of biogeography. However, a pluralistic approach is required, as already argued by Ball (1983); but then it is paramount that the boundaries of various biogeographical hypotheses are clearly demarcated in order to determine the applicability of potentially falsifying observations (see also Ball 1982). That is the way forward, which has been chosen already by a good number of recent analytical biogeographic studies (e.g., van den Ende et al. 2017).

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