



Cladistic biogeography: identity and place

Four papers published recently in this journal (Crisci, 2001; Brooks & Van Veller, 2003; Ebach *et al.*, 2003; Van Veller *et al.*, 2003) revised some concepts of historical biogeography. All of them deserve attention because they reflect the current state of science within the discipline. I believe, however, that some of their conclusions, particularly those referring to the scope of cladistic biogeography, may lead to misunderstandings. My objective is to comment on these contributions, in order to discuss cladistic biogeography alongside the other historical biogeographical approaches.

Crisci (2001) (see also Crisci *et al.*, 2000, 2003) analysed some of the current forces shaping historical biogeography, defined the biogeographical processes that modify the spatial distribution of taxa, and presented a classification of the biogeographical approaches and techniques. The author recognized nine basic approaches to historical biogeography: centres of origin and dispersal, panbiogeography, phylogenetic biogeography, cladistic biogeography, phylogeography, parsimony analysis of endemicity, event-based methods, ancestral areas and experimental biogeography. Problems with this classification that have been discussed elsewhere (Morrone, 2004; Van Veller, 2004) include that 'event-based' methods, those that postulate explicit models of the processes that may have had an effect on geographical distributions, are excluded from cladistic biogeography, being treated as a different approach.

Brooks & Van Veller (2003) presented a critique of parsimony analysis of endemicity (PAE), an approach originally developed by Rosen (1988), which classifies the study areas according to their shared taxa by means of the most parsimonious

solution (Morrone, 1994; Morrone & Crisci, 1995; Crisci *et al.*, 2000, 2003; Escalante & Morrone, 2003). The authors rejected PAE as an appropriate *a priori* method for cladistic biogeography. This is erroneous, as the method does not include phylogenetic information about the taxa analysed, so it cannot be a cladistic biogeographical method (Morrone & Crisci, 1995; Humphries & Parenti, 1999).

Van Veller *et al.* (2003) (see also Brooks & Van Veller, 2003) questioned the usually accepted idea that several cladistic biogeographical methods have been developed to implement the same research programme. They considered that *a priori* methods – those that allow modification of the taxon–area cladograms to deal with dispersal, extinction or duplicated lineages, in order to obtain resolved area cladograms and provide the maximum fit to a general area cladogram – are intended to implement cladistic biogeography; whereas *a posteriori* methods – those that deal with dispersal, extinction or duplicated lineages after parsimony analysis of a data matrix based on the unmodified taxon–area cladograms – are intended to implement phylogenetic biogeography. Thus, they restricted the field of cladistic biogeography to encompass only component analysis, reconciled tree analysis, three-area statement analysis and paralogy-free subtree analysis, and assigned Brooks' parsimony analysis and component compatibility to phylogenetic biogeography. I find this inappropriate, because 'phylogenetic biogeography' has been used for decades to refer to Hennig's (1966) and Brundin's (1966) cladistic implementation of the dispersalist approach (Morrone & Crisci, 1995; Humphries & Parenti, 1999). [In fact, Nelson (1969) initially tried to formalize Hennig's phylogenetic biogeography, but soon he (Nelson, 1974) rejected all *a priori* rules to resolve centres of origin and dispersal without reference to general patterns of vicariance.] In addition, the statement 'all methods used in historical biogeographical analysis aim to obtain resolved area

cladograms that represent historical relationships among areas' (Van Veller *et al.*, 2003: 319; see also Brooks & Van Veller, 2003) is not correct. Instead, it would be appropriate to refer to cladistic biogeography rather than to the whole field of historical biogeography, which also includes panbiogeography, that does not use area cladograms to represent relationships among areas but instead uses generalized tracks.

Ebach *et al.* (2003) noted the two meanings of 'phylogenetic biogeography', one, of Hennig (1966) and Brundin (1966), related to the search for centres of origin and the other more recent one, of Van Veller *et al.* (2003), related to a *posteriori* cladistic biogeographical methods. They accepted that phylogenetic biogeography *sensu* Van Veller *et al.* (2003) originates in Hennig's (1966) 'parasitological method', and that it was inappropriate as a cladistic biogeographical approach. In their effort to respond to Van Veller *et al.* (2003), these authors have implicitly accepted their restriction of cladistic biogeography.

Crisci (2001), Van Veller *et al.* (2003) and Ebach *et al.* (2003) have restricted the field of cladistic biogeography, whereas Brooks & Van Veller (2003) have expanded it, by assigning PAE to it. So, what is cladistic biogeography? Instead of giving a formal definition, I will present a classification of historical biogeographical methods (Morrone, 2004) and discuss its basis (Table 1):

1. The first dichotomy divides historical biogeography into dispersalism and vicariance biogeography. The former seeks to locate centres of origin/ancestral areas and then use dispersal out of them to explain the biogeographical histories of particular taxa. Phylogenetic biogeography (*sensu* Hennig, 1966 and Brundin, 1966), ancestral areas (Bremer, 1992) and intraspecific phylogeography (Avice, 2000) may be ascribed to the dispersalist approach because they basically concur in explaining distributions in terms of narrative dispersal

explanations, although they eventually accept vicariance explanations. Vicariance biogeography seeks to uncover patterns of biotas by comparing the distributional patterns of different plant and animal taxa. The ontology of this approach lies in biogeographical homology (Craw *et al.*, 1999; Humphries & Parenti, 1999; Morrone, 2001, 2004).

2. The second dichotomy divides vicariance biogeography into panbiogeography and cladistic biogeography. Panbiogeography (Croizat, 1964; Craw *et al.*, 1999) reconstructs ancestral biotic distributions by drawing individual tracks on maps (connecting localities of taxa by lines approximating to minimum spanning trees) and looking for coincidence among unrelated taxa, which leads to the recognition of generalized tracks. Morrone (2001, 2004) considered that panbiogeography – including PAE as a quantitative technique of this approach (Smith, 1992; Craw *et al.*, 1999; Luna *et al.*, 2000) – allows us to identify primary biogeographical homology, which represents a conjecture on a common biogeographical history. Cladistic biogeography (Nelson & Platnick, 1981; Humphries & Parenti, 1999; Ebach & Humphries, 2002) assumes a correspondence between the phylogenetic

relationships of the taxa under study and the relationships among the areas that they inhabit. Comparative phylogeography (Arbogast & Kenagy, 2001) may be ascribed to cladistic biogeography because its aim is to compare phylogeographical patterns of multiple co-distributed taxa, in order to recognize vicariant patterns. A cladistic biogeographical analysis basically comprises three main steps (Morrone & Carpenter, 1994): construction of taxon–area cladograms from taxon cladograms by replacing their terminal taxa with the areas of endemism that they inhabit; conversion of taxon–area cladograms into resolved area cladograms (if necessary); and derivation of general area cladogram(s). Morrone (2001, 2004) considered that cladistic biogeography deals with secondary biogeographical homology, namely the cladistic test of the primary biogeographical homology formerly recognized. Thus, panbiogeography and cladistic biogeography may be applied as two successive steps of a biogeographical analysis (Morrone & Crisci, 1995). [A similar distinction between these two steps has been made by Donoghue *et al.* (2001) and Hausdorf & Hennig (2003).]

3. Within cladistic biogeography, I was unable to find a satisfactory way to classify the

different techniques. Several features may be employed as demarcation criteria: pattern-based vs. event-based methods (Ronquist & Nylin, 1990), parsimony vs. tree manipulation methods (Humphries & Parenti, 1999), *a priori* vs. *a posteriori* methods (Van Veller *et al.*, 2000, 2002; Van Veller & Brooks, 2001), taxon vs. area biogeography (Crisci *et al.*, 2003) or cladogenetic vs. event-based methods (Van Veller, 2004). I believe that these criteria are inadequate because they do not consider all the complexities of this range of techniques. Furthermore, I consider the more pressing need at this moment to be for an evaluation of them in order to provide practitioners the means by which to choose the most appropriate technique.

With the taxonomy discussed herein I do not pretend to describe the ‘progress’ of historical biogeography from dispersal biogeography to cladistic biogeography. What I have attempted to do is to provide some bases to characterize the three basic research programmes in the field, each of which asks different questions. I fully agree that ‘the present plethora of techniques reflect a lack of scientific debate and agreement as to what constitutes the ontology (specification of conceptualization) of biogeography’ (Ebach & Humphries, 2003, p. 959). I hope this contribution furthers an

Table 1 Taxonomy of the methods of historical biogeography

Basic approaches	Techniques
Dispersalism	Manual reconstruction (Matthew, 1915) Phylogenetic biogeography (Brundin, 1966; Hennig, 1966) Ancestral areas (Bremer, 1992) Phylogeography (Avice, 2000)
Vicariance biogeography	
Panbiogeography	Manual reconstruction (Croizat, 1964) Connectivity and incidence matrices (Page, 1987) Track compatibility (Craw, 1988) Parsimony analysis of endemism (Rosen, 1988)
Cladistic biogeography	Reduced area cladogram (Rosen, 1978) Ancestral species map (Wiley, 1980) Quantitative phylogenetic biogeography (Mickevich, 1981) Component analysis (Nelson & Platnick, 1981) Brooks’ parsimony analysis (Wiley, 1988) Component compatibility (Zandee & Roos, 1987) Quantification of component analysis (Humphries <i>et al.</i> , 1988) Three-area statement analysis (Nelson & Ladiges, 1991) Reconciled tree analysis (Page, 1994) Paralogy-free subtree analysis (Nelson & Ladiges, 1996) Vicariance event analysis (Hovenkamp, 1997) Dispersal–vicariance analysis (Ronquist, 1997) Comparative intraspecific phylogeography (Arbogast & Kenagy, 2001)

understanding of the current approaches in historical biogeography and their techniques, in order to provide practitioners and others with a clearer perspective of this discipline.

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Parsimony analysis of endemism: time for an epitaph?

Historical biogeography is a broad discipline, encompassing different areas of research, such as systematics, evolutionary biology, ecology, geology and palaeontology. A central goal in biogeography is to find reliable answers to the problem of 'Why organisms are distributed the way they are today' (Platnick & Nelson, 1978, p. 1), as recently pointed out by many authors (Ebach & Humphries, 2003; Ebach *et al.*, 2003; McDowall, 2004). Since the first evolutionary studies of Charles Darwin and Alfred Wallace [and even long before, with the works of George-Louis Leclerc Comte de Buffon, Alexander von Humboldt, Alphonse P. de Candolle, Carl von Linné and others (Nelson & Platnick, 1981; Humphries, 2000; Ebach *et al.*, 2003)], biogeography has attempted to establish the paths that have led to the current spatial distribution of life on the Earth's surface. Accordingly, historical biogeography aims to explain the distribution of taxa as elements of form, space and time (Ebach & Humphries, 2003), involving historical reconstruction based on geographical and phylogenetic patterns (McDowall, 2004). In other words, the reconstruction of the history of the use of space by species strictly depends on phylogeny.

It would be rather trivial, then, to assert that historical biogeography is deeply rooted in the history of organisms, and hence, inseparable from time. Even those who firmly believe that present events, such as non-random dispersal are more important for biogeography than vicariance events (the latter being well represented in Croizat's statement that earth and life evolved together), would agree that strategies to infer historical connections among areas or biotas should be grounded on a temporal perspective. Indeed, whatever the method employed, it does not make sense to perform historical biogeographical analysis without this focus.

Under such constraints, some currently and commonly employed methods used in historical biogeography should be reviewed or somehow modified. One of these is parsimony analysis of endemism (PAE; Rosen, 1988). In a recent paper, Brooks & van Veller (2003) criticize the validity of PAE as a procedure for historical biogeographical inferences. They claimed that PAE is 'the least defensible and least desirable of all *a priori* methods' (Brooks & van

Veller, 2003, p. 823). In this short comment, I wish to deepen their criticisms, reinforcing the view that PAE, at least in its usual sense, should be avoided as the main method in biogeographical studies, even in very specific cases.

PAE was first proposed in a palaeontological context (Rosen, 1988; Morrone & Crisci, 1995), and is supposed to classify areas or localities based on shared taxa according to the most parsimonious solution. The sampled localities, usually quadrats drawn over a map of the region to be analysed, are taken as analogous to synapomorphies (shared derived characters) in phylogenetic analysis. Shared areas in the distribution of species are assumed to indicate shared unique biological history (Rosen & Smith, 1988; Rosen, 1988; Morrone & Crisci, 1995; Brooks & van Veller, 2003). PAE data are composed of area *vs.* taxon matrices, in which character states are presence/absence of 'terminal areas' in the distribution of species.

PAE does not consider phylogenetic relationships of groups for the construction of area relationships. This clearly contradicts current methodological practices of historical biogeography, especially those related to cladistic biogeography [there are many reviews of the methods used in biogeographical inferences, such as Crisci (2001), Humphries & Parenti (1999), and Morrone & Crisci (1995)]. As stated above, biogeographical reconstruction depends on phylogeny, or at least depends on hypotheses of monophyly of given taxa.

The disconnection between phylogenetic procedures and PAE lead Humphries (1989) and Humphries & Parenti (1999) to disregard it as a historical biogeographical method. Nevertheless, Brooks & van Veller (2003) recently gave the method some authenticity in very specific cases. They assert that PAE 'produces correct historical relationships among areas when species became distributed over these areas by a particular combination of vicariance and of non-response vicariance events' and that PAE 'can also produce correct historical relationships among areas when species distributions result from a particular combination of extinction events affecting widespread species' (Brooks & van Veller, 2003, p. 820). Those authors explain both cases with a hypothetical example (their Fig. 1a,b). However, the two special cases listed by Brooks & van Veller (2003) are based on *a priori*