

Frustrating facts about area cladistics and species individuality

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Abstract

Area cladistics suffer from the fact that areas have various "histories", as such dictated by different groups of taxa. Consequently, a generalized area cladogram has not or hardly any biological meaning. Conflicting area cladograms may be derived from even the same species, when their ranges in different geological periods are used. This is a consequence of the individuality of species.

Résumé

L'approche connue sous le nom d'"Area cladistics" souffre du fait que les aréaux semblent avoir des histoires différentes, dictées par l'existence de différents groupes de taxa. Par conséquent, les "generalized area cladograms" n'ont pas (ou ont à peine) une signification biologique. Des "area cladograms" contradictoires peuvent être construits même en utilisant les mêmes espèces, si leurs distribution dans des périodes géologiques différentes est prise en considération. Tout ceci est une conséquence de l'individualité des espèces.

Introduction

The present wealth in biogeographic theoretics and modelling (see e.g. Myers & Giller (1988) and various articles in *Systematic Zoology* 37 (3-4)) can be envisaged as token of a flourishing science, as well as illustrative of Edington's rule that the number of different hypotheses erected to explain a given biological phenomenon is inversely proportional to the available knowledge. The actual development seems to be parallelized by an increasing dog-

matism. Sometimes not the individualistic biological properties of a (group of) species existing in nature seem to be decisive for the biogeographer who has to explain a certain pattern, but his favorite explanatory model. There are vicariantists, dispersalists and several other kinds of biogeographers with a biased look at nature, influenced primarily by the dogmas of their school instead of by the facts of nature. As I tried to show before (Gittenberger, 1984), our objects of research, the biological species, should be looked upon as either vicariantists, dispersalists, or something in between. In science there should be simply biogeographers. In a way object and subject have to be interchanged again.

Good and bad species

The present situation results in doomed species, those neglected by the adherents of a certain school, because they fit better into the model of the competing biogeographers. Another consequence is the tendency to neglect weird distributional patterns that do not fit nicely into any model. Apparently, there should be law and order in nature, good species and bad species, those illustrating general patterns and those only aberrant. The latter category is condemned to obscurity by those who consider narratives inferior to scientific law.



Fig. 1. Miocene (M), Pleistocene (P), Holocene (H) and recent (dots) records of *Platyla polita* (Hartmann) (after Boeters et al., 1989: Fig. 149 and Shikov, 1984: 245).



Fig. 2. Pleistocene (squares) and recent (dots) records of *Platyla similis* (Reinhardt) (after Boeters et al., 1989: Fig. 161).

Phylogenetics versus area cladistics

There is a fundamental difference between phylogenetics and area cladistics. A group of species has phylogenetic relationships, but at least from the

point of view of biologists equalizing history with biological history, areas have nothing comparable. Recently Cracraft (1988: 221) made a start in undermining the foundations of area cladistics, emphasizing that “areas can have multiple histories, but taxa cannot”. There is only one single phylogenetic tree for a group of taxa, the one that represents their phylogenetic history correctly. There are several area cladograms for a group of fragments of earth crust, depending upon the taxa with common histories used to derive them. It can be of biological and geological interest to trace these cladograms, because they tell parts of a real story. However, constructing a generalized area cladogram by simply putting everything together and calculating the mean, is only a mathematical exercise.

General and special biogeography

In fact, general biogeography, applying to the distributional patterns of a large part of the organic world, came to an end long ago, with the unraveling of main biogeographic regions and few subdivisions. What remains at a lower level, are groups of more or less common patterns, resulting from common histories of collections of taxa that are closely related with regard to certain biological, not necessarily systematic or phylogenetic characters (migratory capacities, ecological characteristics, species longevity, etc.).

According to terrestrial snails, for example, there is a close relation between the Greek islands of Antikythira and Crete, and between the island of Kythira and the Peloponnese (Boettger, 1894; Gittenberger, in prep.). Comparable to Wallace’s line there is “Boettger’s line” between Antikythira and Kythira, based upon patterns in non-marine gastropods. One could expect to find Boettger’s line in other non-marine organisms as well, as far as these have at least similar migratory capacities and about the same way and speed of speciation. It is not surprising that for example birds or butterflies do not show Boettger’s line; according to these organisms, the southern Peloponnese, Kythira, Antikythira and Crete are all equally closely related. It would be absurd to ask for the “true relations” between

these areas. Such a “true relation” has neither a biological nor a geological meaning.

Species dynamics and individuality

A phenomenon that has not yet received much attention in the biogeographical literature, at least partly for reasons just mentioned, concerns the individualistic shifts in distributional pattern of certain species during their geological history. The fact that the elements within an ecosystem may react more or less independently to for example climatic changes, has consequences for the easiness of reconstructing ancient biotas. This is also relevant for our views concerning area cladistics.

Erkamo (1956), Huntley & Birks (1983) and several other authors noticed that climatic changes did not simply induce shifts in entire vegetations, but affected the ranges of various plant species in different ways. Thus species compositions and, as a consequence, ecological interactions, were altered as well, which implies much more dynamic events than would be expected at first sight. Similar observations have been published for the ranges of animal species by e.g. Coope (1979) and Graham (1986).

While revising the systematics and distribution of the terrestrial prosobranch gastropod family Aciculidae, species of which may be found in the fossil record unchanged for several millions of years, some additional data on individual distributional shifts could be gathered (Boeters et al., 1989).

Platyla polita (Hartmann, 1840) is known from central Europe since the Miocene; its actual distribution encompasses northern and, more fragmentary, southern Europe. In warm periods during the Pleistocene the species occurred from central Europe northwestward to Great Britain (Fig. 1), where it became extinct afterwards (although it survived in southern Denmark and southern Sweden).

The congeneric *Platyla similis* (Reinhardt, 1880) (Fig. 2) was sympatric with *P. polita* during warm parts of the Pleistocene. However, afterwards the former species became completely extinct in central and northern Europe. Its actual disjunct range, far

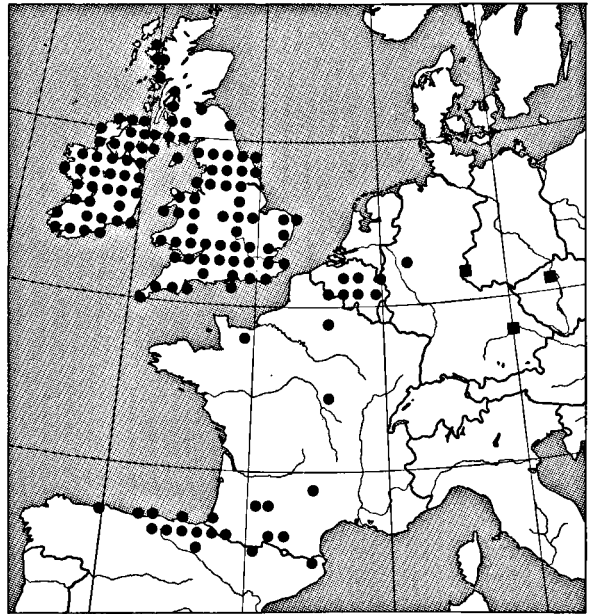


Fig. 3. Miocene (squares) and recent (dots) records of *Acicula fusca* (Montagu) (after Boeters et al., 1989: Fig. 48).



Fig. 4. Miocene (square) and recent (dots) records of *Acicula limbata* Reuss (after Boeters et al., 1989: Figs. 37, 58).

away from the Pleistocene records, extends in Italy and southeast Europe, where it occurs partly outside the actual range of *P. polita*.

Acicula fusca (Montagu, 1803) (Fig. 3) is known from Miocene and Pliocene deposits in central Europe, next to its strictly western European actual range. *Acicula limbata* Reuss, 1860 (Fig. 4), is also known from Miocene deposits in central Europe; at one site the two species are even found together.

However, the present range of *A. limbata* is in the Caucasus, which implies a shift opposite to that in *A. fusca*.

Thus the Pleistocene ranges of *Platyla polita* and *P. similis* contribute to an area cladogram that differs considerably from the one supported by the recent ranges of the same species. The fossil and the recent ranges of *Acicula fusca* and *A. limbata* do also illustrate this problem. Maybe we should conclude that the principles of area cladistics cannot be fruitfully applied in Europe because of the environmental changes in that part of the world, which are not unique, however. Maybe we should neglect groups of taxa with individualistic shifts in distributional patterns, but how do we recognize such taxa if fossils remain unknown? Should we use the disjunct ranges of a single species in various geological periods to derive another (? “vertical”) kind of area cladogram, highly dependent again from the species involved?

The present author concludes that area cladistics is of a limited value. Only with regard to vast biogeographic realms one could argue that these have meaningful generalized relationships. However, these biogeographic relationships became known even before the term area cladistics was invented.

Acknowledgements

Although Hengeveld (1988) is not cited in this short contribution, his paper was a valuable introduction to the literature, which I would like to acknowledge here.

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