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Author

Brignoli, Paolo Marcello

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A candid analysis of the tenets of the different biogeographical schools

PAOLO MARCELLO BRIGNOLI(*)

*Dipartimento di Scienze Ambientali, Settore Zoologico, Università di L'Aquila,
Piazza Regina Margherita 7, 67100 L'Aquila (Italy)*

SUMMARY

Notwithstanding the heated disputes between their supporters, the different biogeographic «schools» accept all the same basic principles. The differences between them are mostly methodological and quantitative (and sometimes even nearly purely semantic). The emphasis given to methods and the trend to accept only extreme points of view (specially about the possibilities of dispersals) have obscured the existence of a common basis.

One puzzling, but intellectually stimulating, peculiarity of biogeography, is the trend of its followers to form schools of thought separated by apparently insuperable barriers and between which exist frequent and heated disputes.

The most recent of these is that between the so-called clado-vicarianists and all the rest, Croizat (1982) included, who, in principle, should be a «prophet» of this school.

All the dispute turns around the problem of dispersal; the purpose of this paper is to discuss briefly the most controversial points. The conclusions may be surprising to most.

Unfortunately, whenever one examines problems of this kind it is unavoidable to touch some of the most basic questions of biology and to proceed on unstable ground, more similar to moving sands, than to solid rocks.

THE CENTER OF ORIGIN

Most authors (as Udvardy, 1969, for instance) maintain that any species is derived from comparatively few ancestors living in a definite place (e.g. a rather restricted range); if a species has actually a wide range, we must conclude from this that it has occupied the different parts of its actual range in different times.

(*) The manuscript of this paper has been sent to the Editor just the day before Paolo M. Brignoli died in L'Aquila on July 1986. These biogeographical speculations must be considered the latest scientific efforts of one of the foremost Italian taxonomists.

At the level of a supraspecific taxon, this entails that the different species which form it are derived from their ancestors either in the restricted primary range or in other regions successively occupied by their ancestor species (Croizat, Nelson and Rosen, 1974).

In itself there should be little to discuss on all this. Nobody, I believe, is anymore a follower of hologenesis, and even those who accept speciation models different from strict allopatry shall find little to criticize in the exposed theses.

Most biologists prefer to glide over the problem of the exact number of the necessary Adams and Eves, but usually we admit very, very few of them. The surely more or less limited range of these ancestors could well be called «center of origin», of the species derived from them: it is a simple, nice name, easy to remember and a concept familiar to us, as many human families or material or spiritual inventions have a well known «center of origin».

The migration/expansion from this center is also an attractive and easy concept for us: we could not explain in another way how, for instance, printing, invented in Germany (at least in Europe) in a few decades became known in all of Europe.

We all know that many animals and plants, before our eyes, are expanding their ranges: the names of *Streptopelia decaocto* or *Robinia pseudoacacia* are only two of hundreds of examples.

Why then, one may wonder, Croizat, Nelson and Rosen (1974) express themselves in a rather apodictic way: «we reject the Darwinian concept of the center of the origin and its corollary, dispersal of species, as a conceptual model of general applicability in historical biogeography»?

If, undeterred by the somewhat prophetic tone of these three authors (of which Croizat, 1982, manifested a strong dissent from the other two, just about the article of 1974), we try to understand what exactly they mean, we discover that they prefer to ignore the problem of the center of origin of a single species and that their wrath is more directed against another kind of center, not unheard of in the Old World, but which has enjoyed a considerable success specially in the New One: I mean the «evolution center».

Briggs (1981) by writing «a world without evolutionary centers to continually supply advanced, and presumably more competitive, organisms to other areas is far different than a world in which such dynamic changes are taking place» declares himself as a adept of this «damned and false theory».

An evolutionary center indeed, endowed with the properties suggested by Briggs has a smattering of metaphysics which does not appeal even to myself, but what about the «old» or «refugial» areas from which, according to the typical European biogeographers (as Holdhaus, Jeannel, Lindroth, de Lattin, La Greca, Gridelli, etc.) the fauna and flora should have dispersed on the «newer» lands or on those liberated by the glaciers? Should we also condemn this kind of centers, which we may also call «evolutionary»?

Unfortunately we can not answer to this question, principally because the clado-vicarianists prefer usually to ignore anything which has been written on biogeography in Europe.

Let us try to tackle in another way with the problem, by analyzing both concepts, that of the center of origin of a single species and that of the evolutionary center of a supraspecific taxon.

May we affirm scientifically that any species must have had a center of origin? For those addicted to Popper, the only way should be that of proving that this thesis is falsifiable. To admit that a species may have many centers of origin is the central thesis of hologenesis; in future maybe, by manipulating genes, an artificial new species could well be developed in many different places, but in nature this possibility can be excluded. The hypothesis of a species originating from nowhere seems at first sight a nonsense, but, playing a little with sophistry, we may equate a species with a material entity and conclude that, as the Universe (which is also a material entity) has been «born» from nowhere, we have falsified our thesis which is therefore ... scientific.

But let us leave by side these philosophical plays and «retournons à nos moutons»: the center of origin of a single species, even by those who avoid speaking of it and implicitly refuse to search for it, is not explicitly disputed.

The object of heavy criticism and even sarcasm is the evolutionary center. The somewhat metaphysical part of this concept is evidently questionable and does not deserve any discussion; but if we examine it as a whole with a more detached eye we may note some curious facts.

What are indeed the theses of the «spiritual father» of the clado-vicariants, Croizat, who against his «putative sons», as an angry Uranus expresses heavy criticism (1982)?

That the distribution/ranges of the living beings are not casual, but may be grouped together in a finite number of types. In other words, there are recurring types of distribution, common to very different groups of animals and plants. It should be noted that also other authors arrived independently to similar conclusions (in Italy, for instance, La Greca, 1964).

The most novel and complex point of the theses of Croizat is that of a kind of geographic «immanence» of the taxa, which is not immobility. As any taxon derives from a preceeding one, the actual range of a genus (for instance) corresponds roughly to that of the species from which the genus has been derived.

This thesis is repeated hundreds of times in the torrential volumes of Croizat; it is made unfortunately unclear by his only implicit acceptance of continental drift. The «tracks» he traces cross continents and oceans and appears at first sight completely senseless; they would be easily understandable if Croizat instead of using modern maps had used paleogeographic ones.

Croizat has never explicitly suggested that the range of the ancestor of a genus corresponded to the sum of the ranges of the species included actually in the genus; such a conclusion would be absurd, because it would imply that the ancestor had also an ecological and behavioural range corresponding to the sum of those of his descendants.

He does not deny in any way possible changes of range: very enlightening is the example he brings, of a rare plant of Northeastern Canada (*Solidago multiradiata*), which in nature has a very limited range, but which, cultivated in the botanic garden of Montreal, has developed in a pest, well able to extend its range. Roughly, because he his neither completely clear, nor very explicit, we may affirm that he believed that the range of a species was passively limited or, in other terms, that the external factors were those which confined a species to a certain range. I am unable to understand if he believed that any species, unless actively confined, had the tendency to expand indefinitely its range: this hypothesis, as far as I know, has been seldom discussed.

What Croizat rejects emphatically is the automatic conclusion that, if a species has «means of dispersal» (and all have some) it shall actually use them for changing its range (I shall discuss this point in brief); sometimes he uses himself the term of «center of dispersal» (1958, fig. 57, page 440) for certain geographic regions.

The theses of the clado-vicarianists (as Nelson and Platnick, 1981) are in principle the same: new species are «born» through allopatry, due to the fragmentation of the range of the parent-species and the appearance of (insuperable) barriers isolating the fragments.

And what about the theses of the (many) «enemies» of Croizat and of the clado-vicarianists? According to Croizat himself (1982) his opposers maintain that:

- a. the species are «born» in a center of origin;
- b. they migrate from this center;
- c. for migrating they use their own means or passive transport.

But neither Croizat nor the clado-vicarianists deny that:

- a. all species have been «born» in some place, even if it may be difficult (or useless) to decide what place it was;
- b. all species may change their range (migrate);
- c. all species, for migrating, use different methods.

A candid reader shall conclude, from this all, that no significant differences exist between the different «schools».

All maintain that all species have been «born», in different ways, in a definite and circumscribed place. From this «original range» (= center of origin) they expanded themselves (migrated) until they were blocked by barriers of different nature. Their ranges are fluctuating and may be fragmented successively. In the different fragments new species may be «born», which shall behave as their parent-ones.

To affirm that to search for the center of origin is pointless and non-informative is more typical of the clado-vicarianists than of Croizat; this way of thinking is principally due to the blind acceptance of Popper's methodological system. A more pragmatic observer shall naturally appreciate the

suggestion to be more prudent in the search for the centers or in the methods for finding them but shall refrain, I think, from denying in absolute the possibility of individuating them.

The center of origin may be indeed difficult to find, at least that of a single species, but what about the secondary centers, the «centers of form-making» in the sense also of Croizat? Everybody knows that of the actually emerged lands, some were submerged until recently and that some, on the contrary, are emerged since long; the same happened with the glaciers, in rather recent times. The traditional European biogeographers are very interested in these «secondary centers»: is the search for them also pointless?

I find this hard to believe, as on many of these «secondary centers» we have so many informations of different kind (geological, geographical, palinological etc.) that we know their recent history fairly well. We are not always building castles with sand.

DISPERSION AND DISPERSAL

If the quarrel about the centers of origin is heated, that about dispersal is truly fiery. The different dispersalists (which may be divided in an American group — with Matthew, Simpson, Darlington, Mc Arthur and Wilson, Simberloff etc. — and an European one, including most of the already quoted authors) usually trace on maps «dispersal routes», in which a species X, departing from its center of origin, migrates to the areas A, B, C, which may be separated (from the center and between themselves) by barriers of different kind, passing them by different and even accidental means. Whenever the barrier becomes insuperable, by allopatry a new species may be «born».

All this is anathema to Croizat and the clado-vicarianists. Why?

All turns around, evidently, with what is meant by «barrier». For Croizat (and the clado-vicarianists) a barrier is always insuperable; we may believe that something is a barrier, but not after a species has crossed it.

The ability of a species to cross a — supposed — barrier would mean that for this species the barrier does not exist. One may answer to this that, as some human beings are able to cross the Channel by swimming, the Channel is no barrier for our species.

I doubt very much that Croizat or even the most extreme clado-vicarianists held over this unquestionably naive view of the barriers; our species is not at all exceptional in its variable ability to cross barriers.

In any species some individuals are more enduring or stronger than the rest (and some less enduring or weaker); few barriers are absolute, most are indeed filters. Specially the botanists, who have a large experience on the seeds, would have much to say about this.

The real, basic, question is about the hypothesis of an «urge to migrate», which indeed gleams through the pages of some of their «enemies».

As I have already noted, few have openly discussed this problem and some, as Mc Arthur and Wilson, have implicitly admitted that any species is potentially expanding its range.

Those species indeed which use passive means of dispersal/dispersion appear to adopt this strategy, but what about the rest? May we affirm that also the species with active means are doing the same?

It may be interesting to pay some attention to our own species. In most (if not all) human cultures we find two opposite trends: one who «pushes» some individuals from their birth place and one instead who «nails» them to this place. Curiously enough, these two counterposed views appear to be ubiquitous in most fields of human activity. Everywhere, in commerce, politics as well as in ... biogeography, there are some who explain/solve all by moving from a place to another and some who prefer static solutions (and accept even easier the movement of the soil on which they stand than that of themselves).

I think we may explore the hypothesis of the existence, at least in some groups, of a kind of behavioural polymorphism; of two groups, distinguished by what may be called «exploring behaviour». Biologically, this polymorphism could be of considerable selective value in ensuring the discovery of new suitable habitats, without bringing to the giving up of the habitats already «used» by the species. Very specialized species should have a very low percentage of «explorers», as the suitable habitats for species of this kind are rare or hard to find and the search for them would bring to a high mortality of the «explorers» (e.g. the biological investment would be high and coupled with high risks).

The usual «r» and «k» models are probably too stereotyped. Many intermediate situations possibly exist, but could be discovered only by very careful auto- and synecological studies.

If we return now to the two opposed theses we must conclude that they differ indeed more quantitatively than qualitatively: one is more optimistic on the superability of the barriers than the second. What the dispersalists call «barrier» is only in some instances a barrier for Croizat and the clado-vicariants; we may speak therefore of true barriers and pseudo-barriers. The dispersalists in my opinion magnify too often occasional events («jumps»); their opposers underestimate the importance of intermediate situations («filter bridges») which seem to me very common.

And what about the «dispersal routes»? The quarrel here is threefold; the dispersalists trace arrows on maps, Croizat only lines («tracks»), the clado-vicariants refrain from both and use only area-cladograms.

This last position is consistent with their methodological (Popperian) approach and evidently related with the refusal of discussing the center of origin (or dispersal) problem. In a way it is an application of the Pyrrhonian «epoché», a suspension of judgment. To affirm that species X, living in A, is nearer to species Y, living in B, than to species Z, living in C, does not imply anything about movements (of species, at least).

But to affirm that it is methodologically preferable not to advance hypotheses on the direction of a movement, is quite another thing from denying a movement. And I would not conclude from their writings that the clado-vicarianists suppose that the ranges of the species are fixed.

They simply elude any answer to a very common question: the (geographic) origin of the fauna and flora of a certain region, of which we know, through other sources, that it is geologically more recent than the surroundings lands or that its climate has radically changed in recent times. No inquisitive biologist shall easily accept rather naive theories on «mass migrations», following more or less the same routes taken by many human peoples or even on «evolutionary centers», acting like magic horns of plenty in providing the less privileged regions with fauna and flora, but, at the same time, in too many instances, it is rather obvious that the species of a region actually came (with different means) from another land.

Tracks and dispersal routes differ in a similar way: Croizat is more prudent and usual refrains from suggesting that a group has migrated from A to B; he is right in denouncing many rash hypotheses but is unable to demonstrate that all the hypotheses of the dispersalists are wrong.

CONCLUSIONS

«What is in a name? ... That which we call a rose by any other name would smell as sweet» (Shakespeare, «Romeo and Juliet», act II). In writing this, Shakespeare demonstrated little respect for semantics. For many human beings, a «nomen» is also an «omen».

Most of the disputes between biogeographers recall the Byzantine ones like that about «homoiusios» and «homiousios». From what I have shown, the greatest differences between the opposed theses are methodological and not conceptual, quantitative and not qualitative.

All biogeographers indeed affirm that:

- a. all species have been «born» somewhere from other species;
- b. allopatry is the principal speciation mechanism;
- c. the distribution of species is not casual, but due both to historical and ecological factors;
- d. the ranges of the species change in time.

These four generally accepted facts are the actual bases of biogeography. All the rest is speculation. I feel that it is exceptionally unfortunate that many biogeographers have believed it necessary, in proposing a new method, to ignore deliberately other methods or to slight their opposers, without discussing exhaustively their theses. This working method (if it may be called so) is rather unusual in science and would be better left to our humanistic colleagues.

To continue in this way shall bring only discredit to biogeography and confuse its ultimate goals and purposes.

This situation is due to the coexistence in biogeography not only of the two already spoken of trends («static» and «dynamic») but also of two «souls», ecological and historical, which in truth are inseparable. But whereas the first is strictly linked with the natural sciences, the second has a very close affinity with history, a typically humanistic branch of knowledge. This duality explains probably much. Those biogeographers who, unknowingly, are repelled by humanism, avoid all untestable hypotheses; many others, on the contrary, give interpretations of past events based, as many historians do, on incomplete facts linked together by suppositions and intuitions.

To cry anathema at this working method because it is different from that used in other branches of knowledge is at the same time naive and intolerant.

Historical biogeography, e.g. the reconstruction of past events, shall never be an «exact science», through obvious reasons. As already noted, to suppose that all species shall react in the same way to factors influencing their ranges, is a sort of mechanicalism and excludes internal factors which, at least in *Homo sapiens* (which is part of nature) do exist. A careful study of an actually living species does not enable us to conclude that its ancestors behaved (biogeographically) in the same way. We may learn something methodologically from our humanistic colleagues, the historians and

- a. firstly examine very carefully the facts we have at hand
- b. build on them probabilistic hypotheses.

Luckily enough, we do not have to do with ideological problems. Most evidently, we must be ready to abandon nice looking hypotheses, if new facts come at light.

Ecological biogeography is in my opinion correct if we limit ourselves to study modern species and ecosystems. But to presume that everything which is happening now has always happened in the same way is an undue extension of Lyell's theses on geology. It is the same way of thinking which brings Marxist economists in trouble when dealing with a post-capitalistic society or a zealous Christian priest in difficulty when contacting «savages». The biological world is always changing: we should not forget this.

On the other hand, the study of modern ecosystems and their evolution is possible and may bring to testable hypotheses. In a way, biogeography should be more a science concerned with the future than with the past, but few (specially between the zoogeographers) seem to have understood this.

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