f29 Spatial or distributional elements in speciation < Mayr >

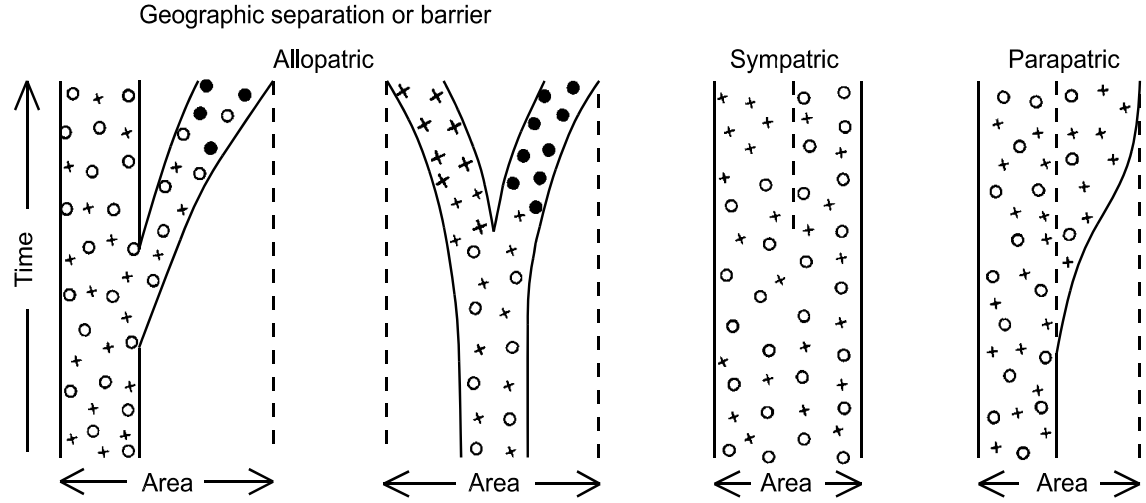
... there are few subjects where exists a greater diversity of opinion regarding practically everything than in paleontology. —Willem Anton Josef Maria van Waterschoot van der Gracht (1873-1943).[2]

In the diagrams: [3]

Time is the vertical axis, running from older to younger in the direction of the arrow.

Space is shown on the horizontal axis, which indicates only whether the area in question is continuous or discontinuous.

Variation in a population is suggested by circles and crosses for different characteristics and darkening of these for evolutionary change in the variant characteristics of the species involved.



Gradual speciation according to Mayr (1963) can be: [3]

Allopatric (means: separate or in another place)

Two possibilities are:

Allopatric branching: the ancestral population is perpetuated essentially unchanged (remains in stasis) but a geographically separating branch becomes progressively more distinct from that ancestry.

Allopatric bifurcation: geographically separating branches each evolve characteristics distinct from their common ancestry.

Types of allopatric speciation, are:

Vicariant speciation (by evolution following the appearance of a separating barrier)

Peripatric speciation (by evolution in an isolated colony)

Ernst Mayr himself has favored the view that speciation can occur only when geographical barriers enforce non-random mating while new species are emerging. And numerous documented examples of allopatric speciation (as say, squirrels but not birds on the north and south rim of the Grand Canyon are different species) support this orthodoxy. However, Anthony B. Wilson in 2000 reports on two examples of sympatric speciation:[4]

Sympatric (means: together or in the same place)

Sympatric speciation, in which differential inheritance tends to sort out ancestral variation and to produce two distinct stocks (demes or local populations) within the same general area; such groups become distinct species when they cease to interbreed, and they eventually also tend to evolve new and different characteristics:

Example 1: Isolated (4.15 and 0.6 km^2 in area) crater lakes in Cameroon harbor 11 and 9 endemic cichlid species, respectively. Genetic data show that in each lake the species are each other's closest relatives; implying that they speciated there. Ulrich K Schliewen and Barbara Klee note that the tiniest lake is only 14.5 m deep; making implausible that geographical barriers were involved.[5]

Example 2: Cichlid fish that differ in color (a "normal" morph and a "gold" morph) occur together in four lakes in Nicaragua. The mitochondria gene frequencies in different morphs within each lake are statistically more similar to each other than to those from different lakes. In two of the lakes, the nuclear and/or mitochondrial gene frequencies of the morph pairs are significantly different. Sympatric speciation is indicated. Alternative hypotheses are that allopatric speciation occurred on a local scale within each lake; or that parallel invasions of the lakes by two species that originated in different lakes were followed by hybridization between the two and the spread of mitochondria from one species to the other. As Mark Kirkpatrick points out: "These alternatives may be less likely, but they serve to show how hard it is to prove sympatric speciation conclusively, even with solid molecular data." [6]

Reprise

The geographical context in which allopatric and sympatric speciation occurs is different: Allopatric speciation occurs when populations become isolated, for whatever reason, and sympatric speciation is by lineage splitting within a single population. Hybridization (***Footnote f29.1***) and gene exchange is essentially absent in allopatry and is common in sympatry. In allopatry, divergence can be by chance when there are few individuals, or can be because in isolated populations natural selection acts on even very small differences. In sympatry, where there is substantial gene flow, only relatively strong natural selection can drive divergence.

Parapatric (means: connected or an adjoining place)

Parapatric speciation, which differs from sympatric speciation primarily in that the differentiating group, here more obviously a geographically definable deme, is marginal to the main body of the ancestral species. Interbreeding of the new with the old group lessens. Also, the differentiating, marginal group, becomes increasingly geographically isolated.

G. G. Simpson in *Fossils and the History of Life*, 1983, writes: [7]

> ... microevolutionary events at or below the species level are of primary interest to geneticists and systematists dealing with living populations. Consideration of them is interesting also to paleontologists for several reasons, some negative and some positive. One is that, when related species reach clear distinction in different areas, as in [say] (a) and (b) and to a lesser extent in (c), it is rarely possible to follow their exact courses in geologic time. That is because fossil-bearing strata of a precise age rarely are available over as large an area or for as long a time as speciation typically involves. That is a major element in the incompleteness of the fossil record. Another point is that, in a fossil sample of a population undergoing sympatric or parapatric speciation, it will usually be difficult and often impossible to determine objectively that speciation was in fact under way. A third (and, for paleontology, the most important) point is that any supraspecific group (a genus, a family, an order, and so on) for which the fossil record does often contain abundant and precise data almost certainly originated by simple speciation followed by long and frequent similar further speciational events. Thus the interpretation of the data that paleontologists have and the inferences about principles of evolution to be drawn from them should have a firm background in an understanding of speciation. Another point of special interest for paleontology is that species evolving sympatrically, or becoming sympatric after allopatric or parapatric evolution, generally are (or become) quite distinct without complete ecological duplication. Thus, if closely related fossils (such as those of organisms of the same genus) of the same age are found in the same local fauna, it is a reasonable assumption that they represent a single species unless two or more parts of the sample have definitely determinable distinctions not present in the other or others. This principle, called by the Argentinian paleontologist Angel Cabrera 'the law of ecological incompatibility,' has been repeatedly 'discovered' and often applied by paleontologists and neozoologists alike.

Microevolution is evolution *at* the species level. In 1997, David Jablonski, Michael J. Benton, Robert A. Gastaldo, Charles R. Marshall, and J. John Sepkoski, Jr. reintroduced *macroevolution* (formerly called "quantum" evolution)[8] which is the study of higher level (species, genera, and above) evolutionary patterns that transpire over thousands to millions of years.[9]

Non-speciation (stasis) even though the environment is changing indicates, Eldredge suggested in 1995, "habitat tracking" in which species migrate to follow the habitat they are adapted for. Different is "adaptation tracking" in which species adapt to an altering habitat through natural selection.[10]

Species selection

If you force me to be precise, of course I'll make mistakes.
—René Thom (when his audiences had urged him to more mathematical precision and then found mistakes in his formulas).

Stephen Jay Gould in 1982 [11]

Since we proposed punctuated equilibria to explain trends, it is infuriating to be quoted again and again by creationists—whether through design or stupidity, I do not know—as admitting that the fossil record includes no transitional forms. Transitional forms are generally lacking at the species level, but they are abundant between larger groups.
—S. J. Gould, (1983).[12]

In his last prolix book, *The Structure of Evolutionary Theory*, 2002, **Gould** describes the alternating fast-slow pattern of evolution, which is his familiar punctuated evolution theme, and then reaches for novelty by suggesting that a species is to be thought of as an "individual." [8] The semantics is that Darwinism is natural selection of individual organisms in a species, whereas Gould enlarges this to, natural selection of individual species with respect to others. This higher-level process he claims drives large-scale evolutionary processes and is irreducible to natural selection on organisms. However, neither punctuated evolution nor selection at the species level is contrary to orthodox Darwinism. Matt Ridley in his review of *Structure*, dryly points out that Frank H. Rhodes wrote a paper documenting how Darwin often said that evolution may be relatively rapid at speciation (punctuated evolution) and unsurprising are the additional factual claims of the individuality of species and of species selection. Nor does he "agree that the three are linked causally or conceptually." Ridley: [13]

> "According to Gould, the theory of punctuated equilibrium implies that species are individuals, not classes. But I do not see the logical connection. Evolution in general, not punctuated evolution in particular, is the reason species do not form classes. If anything, the relative constancy of species after their sudden origin would make them more like a class. Individual people lack defining attributes because they change as they develop and decay. If people were born fully formed and remained identical until death, it would be easier to define them by attributes in much the way we do for chemical elements.
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> "Then we have the theory of species selection. Some species have properties that enable them to last longer, making them less likely to go extinct. For example, species with sexual reproduction have lower extinction rates than species with asexual (or clonal) reproduction. So, over time they proliferate more than clonal species because they don't die off as fast. This species selection is analogous to natural selection between organisms."

In commenting upon *Structure*, David B. Wake informs that Gould's "study of species formation has made me question the reality of species as bounded entities, and I am wary of the perspective that species are individuals. I find clade (*see* Topic *f35*) selection an attractive and more general alternative to species selection." [14] ❑