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Radiation and adaptation, evolutionary biology and semantics

Edmund Gittenberger

National Museum of Natural History Naturalis, Institute of Biology, Leiden University, P. O. Box 9517, NL-2300 RA Leiden, The Netherlands

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Abstract

Radiations can be either adaptive or non-adaptive, resulting in a variety of niches occupied by sympatric species, or in hardly any niche differentiation and species showing largely mosaic distribution patterns. The terms are useful despite the fact that intermediate situations occur.

Keywords: Adaptation; Radiation; Non-adaptive

Points of view

Radiation, as discussed here, is restricted to cases of multiple speciation events within a relatively short period. By using the term more broadly, for example, by referring to the radiation of life on earth or an ecological radiation within a single species, the concept becomes even more vague than it inevitably already is due to the vagueness intrinsic to 'multiple' and 'relatively short'.

When radiation is combined with an epithet, such as adaptive or ecological, this suggests that there is more than one kind of radiation. Introducing either 'adaptive radiation' or 'ecological radiation' implies that there are also non-adaptive or non-ecological radiations. If in principle all radiations are the same then 'adaptive radiation' or 'ecological radiation' should be replaced by simply 'radiation' to avoid a tautology (Gittenberger 1991). It is illogical to reject the epithet adaptive but accept the combination 'ecological radiation'.

The meaning of an epithet is related to the object to which it refers. In 'adaptive radiation', adaptive refers to aspects of the multiple speciation events, i.e. to the radiation process as such. In this context adaptive has nothing to do with structures, which may or may not have a function in organisms. Instead at this higher level of abstraction it refers to species-specific niche differentiation. Species are adapted to their niches. In an adaptive radiation they diversify "to occupy a variety of habitats" (Futuyma 1979, p. iv).

No doubt, speciation may be triggered by differential adaptation to a variety of niches, resulting in adaptive radiation. This is most clearly, though not exclusively, so in sympatric speciation scenarios. However, when the speciation events occur in allopatry, genetic drift and founder effects may also result in divergence, and eventually there may be speciation in the absence of clear niche differentiation. In such a case, to be called non-adaptive radiation (Gittenberger 1991), the resulting species, whenever coming into secondary contact, show a mosaic pattern of distribution on the basis of competitive exclusion and extinction (Gause's rule). When, for example, the sea level drops, uniting a former group of islets to a single, larger island, this scenario becomes realistic. Species resulting from an adaptive radiation, occupying different adaptive peaks, can co-exist and, therefore, show fundamentally different distribution patterns. The species flocks of African

E-mail address: gittenberger@naturalis.nnm.nl (E. Gittenberger).

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cichlid fishes with many sympatric species occupying different niches illustrate this most clearly.

The issue is not whether all structures have a function but whether speciation, even when following the allopatry scenario, is always triggered or accompanied by niche specialisation. There is no good reason to embrace such a dogmatic point of view. A vicariance event, like islands originating when a rising sea level splits a large island into smaller ones, will not always result in substantial habitat differentiation between the various secondary islands. On the contrary, it is equally likely that those smaller islands remain more or less similar to each other. If the habitats are barely different then differential adaptation is unlikely to occur.

The real question is whether the radiation of, for example, dozens of cichlid fish species in an African lake differs from a radiation that has produced dozens of *Albinaria* species in southeastern Europe. The cichlid species may co-occur. The *Albinaria* species show a mosaic distribution pattern, with usually only one and hardly ever more than two species occurring sympatrically. The cichlid fishes occupy clearly different niches but the *Albinaria* do not, illustrating Gause's rule. In both cases there are multiple speciation events that can be jointly denoted as a radiation. For these extremes the epithets adaptive and non-adaptive are available and useful, emphasizing different aspects of the evolutionary process. Intermediate situations occur, but that should not prevent the use of different terms here. If indeed the allopatry scenario is the most common one applicable to speciation events, radiations might have at least an initial, non-adaptive stage, simply because the potential niches in the disjunct areas may still be largely similar if affected at all by the vicariant event. Upon secondary contact of the radiated species, adaptation with niche differentiation may still occur but does not necessarily do so.

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