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Why are there so many cichlid species? On the interplay of speciation and adaptive radiation

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The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems.

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The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physicochemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

Two examples illustrate this assertion. Although Darwin's publication of "The Origin of Species" sparked off the whole evolutionary revolution, oddly enough, the population genetic framework underlying the modern synthesis holds no clues to speciation events. A second illustration is the more recently appreciated issue of jump increases in biological complexity that result from the aggregation of individuals into mutualistic wholes.

These and many more problems possess a common source: the interactions of individuals are bound to change the environments these individuals live in. By closing the feedback loop in the evolutionary explanation, a new mathematical theory of the evolution of complex adaptive systems arises. It is this general theoretical option that lies at the core of the emerging field of adaptive dynamics. In consequence a major promise of adaptive dynamics studies is to elucidate the long-term effects of the interactions between ecological and evolutionary processes.

A commitment to interfacing the theory with empirical applications is necessary both for validation and for management problems. For example, empirical evidence indicates that to control pests and diseases or to achieve sustainable harvesting of renewable resources evolutionary deliberation is already crucial on the time scale of two decades.

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Why are there so many cichlid species? On the interplay of speciation and adaptive radiation

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The problem: haplochromine diversity

The explosive speciation of cichlid fishes in the great African lakes has intrigued biologists for many decades. Interest was revitalized last year after the publication in *Science* of geological data¹ which indicate that the youngest lake, Lake Victoria, must have been completely dry during the ice age perhaps as late as 12,400 years ago. This implies that the approximately 500 haplochromine cichlid species must have evolved within this extremely short time span from a single ancestral species². Even with lower estimates of species number and higher estimates of the age of the species flock, the haplochromine cichlids still present one of the most dramatic examples of speciation and diversification in vertebrates.

An old hypothesis on the importance of temporary geographical isolation of cichlid fishes in satellite lakes around Lake Victoria for speciation of cichlid fishes³ is no longer much in favour^{4,5}. Such satellite lakes only have very few species of cichlids and can therefore not explain the bulk of the speciation events in Lake Victoria. More specifically, this hypothesis cannot explain the large diversity of rock species since there are no rocky islands in these satellite lakes and each group of rock islands in Lake Victoria has its own species assemblage.

The mate recognition system underlying speciation

Seehausen et al. in *Science*⁶ have now put forward a persuasive hypothesis explaining the high frequency of speciation events that must have occurred. They show how sexual selection could be the driving force behind speciation in the haplochromine cichlids of Lake Victoria in that mate choice of females for differently coloured males maintains reproductive isolation between sympatric species and colour morphs. Females do have a strong preference for males of a particular colour when light conditions are sufficiently

good⁷. Males of sympatric, closely related species always differ in colour: one species having blue males, the other red or yellow males (females are usually inconspicuously coloured). This colour dichotomy of blue versus red/yellow also holds for conspecific male color morphs which abundantly occur in the lake. The colours of the males coincide well with the visual sensitivity of cichlids. Cichlid eyes have three retinal cone pigments and the greatest sensitivity is either for blue or for red and yellow. In deeper water red/yellow is better visible than blue. Small evolutionary changes can modify the maximum sensitivity of the eye from red/yellow to blue and vice versa (polymorphism in colour vision is e.g. known in guppies⁸). Changes in colouration of the males happen frequently, judging from the large number of blue and red/yellow sibling species. If females prefer conspicuous males individual variation in sensitivity for colours (in females) and in pigmentation (males) will lead to such a frequent occurrence of colour dichotomy (see also ref. 9).

Evidence for the importance of sexual selection for the maintenance of reproductive isolation comes from behavioural experiments in monochromatic light which masks colour differences⁸. Under these light conditions a breakdown of preferences for conspecific mates occurs. Sadly, important additional evidence comes from a recent loss of cichlid species in Lake Victoria. The increased turbidity of the water due to human activities is causing a breakdown of reproductive barriers. Females can no longer distinguish males of sibling species from their own when visibility is poor and hybridize with males from other species^{6,7}. Hybrids are fully fertile and therefore the species diversity of parts of Lake Victoria has seriously declined with increasing turbidity of the water. There is a great danger of further decline because of the continuing pollution. Hopefully the new knowledge on the importance of mate recognition for maintaining species diversity will lead to effective measures that will curb pollution.

The hypothesis of Seehausen et al.⁶ can explain allopatric speciation where after allopatric divergence incipient species later overlap in distribution. But their hypothesis also allows for fully sympatric speciation in which the two incipient species initially occur together and are not kept apart by geographic barriers, but solely by mate choice of the females as for example in the models of Lande¹⁰, Turner and Burrows¹¹ and Payne and Krakauer¹². Spatial heterogeneity does play a role in the sympatric speciation scenario as well, because depth differences are correlated with differences in colour perception which is relevant for mate preferences and speciation can only take off when novel 'compatible' male and female types (i.e. red males with females that prefer red males) temporarily stay together. Allopatric speciation of cichlid species will certainly have played a role in Lake Victoria since it is huge and displays many different habitats. However, the abundance of sympatrically occurring colour morphs as well as the common absence of mating barriers other than behavioural ones suggests that sympatric speciation has played an important role.

Stabilising species diversity through adaptive radiation

The hypothesis of Seehausen et al.⁶ on the importance of sexual selection for the generation of speciation events and for the maintenance of species barriers nicely adds to a much older hypothesis on the speciosity of cichlid fishes. This much discussed

hypothesis was first proposed in 1973 by Liem¹³ and bears on the importance of the versatile pharyngeal jaw apparatus in the evolution of cichlid fishes.

A high number of speciation events and mating barriers produced by sexual selection are not enough to maintain species diversity. Species diversity is determined by the balance of the numbers of species that originate and go extinct. When after speciation events the new species are indistinguishable ecologically, species will be lost in a process akin to random drift¹⁴. However, the species will never be exactly similar ecologically, in which case the extinction process will be considerably more rapid, except when the differences lead to niche differentiation^{15,16}. This niche differentiation has taken place in cichlids on a large scale, leading to a spectacular adaptive radiation. Adaptive radiation can only take place when species are splitting up repeatedly and mate recognition systems or other mechanisms are keeping the adaptively diverging populations apart¹⁷. Conversely, the many newly emerged species can only continue to coexist when adaptive radiation takes place. Thus, the origination of large numbers of species and a rapid adaptive radiation necessarily go together.

The ecological and morphological basis for the radiation

The striking diversity of feeding niches that characterizes cichlids of Lake Victoria^{13,18,4} suggests that the adaptive radiation primarily occurred by rapid specialization for different feeding niches. This implication is strengthened by the observation that sibling species are always characterized by small differences in feeding behaviour²² (Bouton pers. comm.).

Recent support for Liem's¹⁸ hypothesis comes from a comparison of the pharyngeal jaw apparatus in cichlid fishes with that of the presumed generalized percoid ancestors^{19,20}. This comparison supports a hypothesis of Vermeij²¹ that speciose taxa are characterized by more independent elements than taxa that are less speciose. A large number of independent elements increases the number of potential solutions for a particular biomechanical problem. Therefore, bodyplans with more independent elements can be more easily modified and diversified than body plans with fewer independent elements. During the evolution of the cichlid pharyngeal jaw apparatus two decouplings have occurred¹⁹. These decouplings have increased the number of independent elements and, thus, the number of degrees of freedom of the cichlid pharyngeal jaw apparatus compared to that of generalized percoids.

There are two reasons why the flexible and versatile pharyngeal jaw apparatus of cichlids promotes evolutionary diversification. First, it provides behavioural plasticity and second, it provides evolvability. To start with the first, although cichlids usually act as specialists, occupying many different feeding niches, the flexible pharyngeal jaw apparatus combined with the capacity for learning enables them to eat very different prey items. Therefore starvation is not a likely cause of extinction¹⁸. This is probably relevant right from the start of the speciation process, because when limiting similarity forces parts of a polymorphic population towards extinction, this type of phenotypic plasticity can grant them a reprieve by allowing rapid phenotypic niche shifts. The flexibility of the pharyngeal jaw apparatus probably also is conducive to allopatric speciation: When a population becomes geographically isolated in an different habitat, behavioural plasticity will help them to survive.

The second reason for the importance of the versatile pharyngeal jaw apparatus for evolutionary diversification is that but small behavioural and morphological changes allow cichlids to specialize on different food items^{13,19}. Moreover, the phenotypic plasticity (including behavioural changes) already let changes in the right direction occur. These phenotypic adaptations can subsequently be assimilated genetically. This makes them great evolvers.

Rounding up: a general scenario for adaptive radiation

It is vital that insights from different disciplines are combined when analysing sympatric and parapatric speciation processes, because such speciation events can only have an influence on species diversity when both reproductive barriers come into existence between different morphs and disruptive selection occurs so that extinction because of limiting similarity is avoided¹⁶. In the case of the haplochromine cichlids of Lake Victoria the following scenario can now be proposed by combining insights: sexual selection for strikingly coloured males is the driving force behind the generation and reproductive isolation of colour morphs. Disruptive selection on feeding and other specializations promotes the divergence of these incipient species and the resulting niche shifts promote their coexistence. Rapid diversification is possible because of a pharyngeal jaw apparatus with a large number of independent elements which can easily be modified. This flexible pharyngeal jaw apparatus also allows behavioural flexibility which together with a capacity for learning makes cichlids unusually resilient against extinction. There are thus two selection processes acting together, a process of species splitting due to sexual selection and a process of adaptive radiation due to disruptive selection. The last is necessary for coexistence.

Integration of the theory of sexual selection and speciation with the theory of adaptive radiation exemplified by our cichlid story, leads to a widening of the concept of Vermeij²¹. Bodyplans of organisms with many independent elements not only allow diversification, but are more likely to allow rapid diversification when subjected to disruptive selection¹⁷. In addition it is possible, at least in the case of cichlids, that such body plans allow wider behavioural plasticity. In this context we note that the bony fishes are both very speciose compared to other vertebrate classes and characterized by a particularly large number of loosely connected bony elements in their heads.

Coda

We now have a convincing scenario of the happy coincidence of mechanisms that led to the most explosive speciation and adaptive radiation in vertebrate evolution known to us. Hopefully the increased turbidity of Lake Victoria which is not only causing hybridization of species, but presumably also preventing further speciation events, will soon be brought to an end so that these speciation processes can go on and the cichlid fauna can continue its intriguing path.

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