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Speciation: Genomic Archipelagos in a Crater Lake

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The opening stages of speciation remain poorly understood, especially from a genomic perspective. The genomes of newly discovered crater-lake cichlid fish shed light on the early phases of diversification and suggest that selection acts on multiple genomic regions.

Despite decades of research into the topic, evolutionary biologists are still struggling to understand — let alone to predict — how, when, and under which circumstances one biological unit (species) splits into two (or more) such units. While it is well established that ecology, via divergent natural selection, can play a pivotal role in this process [1,2], we know relatively little about what happens to the genomes of diversifying lineages [3,4].

A new study by Malinsky *et al.* [5] makes use of an impressive set of more than one hundred whole-genome sequences to examine, from a genomic perspective, the early phases of divergence between two ecomorphs of cichlid fishes that have recently been discovered in a small crater lake in Tanzania. Volcanic crater lakes are fascinating natural laboratories for evolutionary biologists — especially for those with a keen interest in cichlids [5–9]. These lakes form when volcanic craters — so called 'calderas' or 'maars' — become filled with water, which is often the case in areas of high precipitation in the tropics or subtropics. Owing to their volcanic origin, crater lakes are geologically well datable, they are typically small in size, yet deep, and they lack in- and outflows, which impedes their colonization by aquatic organisms. If colonized, however, e.g. by a cichlid fish population, one can survey adaptation and, in some cases, divergence of that population in a closed setting and within a known time frame.

The investigation of Malinsky *et al.* [5] is situated in crater lake Massoko, which belongs to a series of maar lakes about 40 km north of Lake Malawi in the area of the East African Rift Valley (Figure 1A). Massoko is tiny (only about 700 m in diameter), up to 37 m deep, completely isolated from surrounding water bodies and around 50,000 years old [10]. Nevertheless, it contains two distinct ecomorphs belonging to the widely distributed cichlid genus *Astatotilapia*. These ecomorphs differ, as shown by Malinsky *et al.* [5], in male breeding coloration, mate preference, habitat preference, overall morphology, the

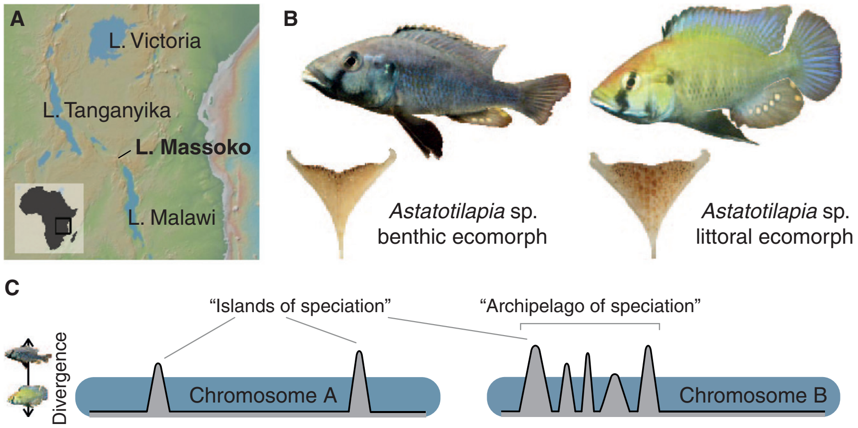

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Figure 1. The genomics of sympatric speciation in East African crater lake cichlids.
(A) Map of eastern Africa showing the three largest lakes in the area and the position of the crater Lake Massoko. (B) The two ecomorphs of *Astatotilapia* sp. in Lake Massoko. For each ecomorph, a male in breeding coloration is shown, as well as the lower pharyngeal jaw bone. The pharyngeal jaw apparatus constitutes a second set of jaws in the pharynx, which is functionally decoupled from the oral jaws, and used to process food (see [18,20] and Supplementary Movie in [20]). Images by Alexandra M. Tyers. (C) Schematic view of the signature of genomic divergence between the cichlid ecomorphs in Lake Massoko. Malinsky *et al*. [5] identified more than 50 ''islands of speciation'', which are characterized by high levels of divergence between the two ecomorphs. About half of these islands are organized in ''archipelagos'' on five linkage groups.

morphology of the trophic apparatus, and diet. A form with an elongated head and blue-colored males, feeding on (more) planktonic food, occurs in the deeper benthic zone of the lake, whereas a short-headed form with yellow males and a more littoral-based diet is primarily found in the shallow-water habitat (Figure 1B). Importantly, a phylogeny based on several thousand single nucleotide polymorphisms (SNPs) derived from restriction associated DNA (RAD) sequencing revealed common ancestry of the Lake Massoko cichlids, suggesting that they have evolved *in situ* in this isolated maar lake.

To investigate the genomic signature of divergence in Lake Massoko's cichlids in more detail, Malinsky *et al.* [5] inspected whole-genome sequences of 146 individuals representing the two Massoko ecomorphs, as well as small specimens from within that lake that could not be unambiguously assigned to any of the two ecomorphs, plus additional *Astatotilapia* specimens from outside Lake Massoko. A phylogeny on the basis of these genomes confirmed the monophyly of the Lake Massoko cichlids and identified a fish from nearby Mbaka River as their closest relative, suggesting an initial colonization of Lake Massoko by Mbaka River fish. Coalescence analyses further support this scenario and suggest that the split between the two ecomorphs in Lake Massoko occurred only within the past 500–1,000 years. The authors then applied three measures to study the patterns of genomic differentiation between the two ecomorphs along the genome, relative divergence (F_{ST}), absolute sequence divergence (d_{XY}) and the difference in nucleotide diversity (π). While there was not a single fixed difference between the ecomorphs, the authors could identify close to one hundred regions in the genome that are highly diverged. Fifty-five of those highly diverged regions (HDRs) featured high d_{XY} values, while showing normal values of π, making them strong candidates for genomic regions causally implicated with speciation. These 'islands of speciation' were not randomly distributed across the genome, though. Instead, 27 of these clustered on only five chromosomes, forming some sort of 'genomic archipelagos of speciation' (Figure 1C).

The work by Malinsky *et al.* [5] provides an unprecedented view into the genomic changes associated with the early phases of adaptive divergence between a pair of cichlid ecomorphs. This is made possible because of their strategy of applying whole-genome sequencing to a large number of individuals, which enabled full resolution genome scans, and of integrating this precise genomic information with data on ecology, morphology and behavior. The study thus exemplifies the power — and feasibility — of using whole genomes to survey adaptation and organismal diversification at the population level [11,12]. Lower resolution genome scans, designed to capture only a fraction of the genome so that the distances between individual markers are comparably large, would almost certainly have failed to recover most of these HDRs (in case of the Massoko cichlids, HDRs can be as small as 4.4 kB [5]). Lower resolution genome scans, e.g. involving RAD sequencing, should thus be seen as a temporary phenomenon that, at least in the field of population and speciation genomics, will soon be replaced by whole-genome sequencing – especially, as sequencing is becoming more and more automated.

The findings of Malinsky *et al.* [5] findings are in line with previous studies investigating the genetic architecture of adaption (and diversification), which revealed that, just as seen in the Massoko cichlids [5], multiple loci on several chromosomes are involved in divergent evolution [11,13–15]. A burning question emerging from these studies relates to the actual function and phenotypic effect of these genomic regions — individually and jointly. Malinsky *et al.* [5] exerted the common approach [11,16] of subjecting the regions in question to a gene-ontology enrichment analysis, hinting at a significant enrichment for the gene-ontology terms morphogenesis, cytoskeleton, protein translation, hormone signaling and sensory systems (the latter includes a rhodopsin gene that occurs in two variants with different allele frequencies in the ecomorphs). It is fairly easy to envisage how each of these gene-ontology categories may relate to a particular trait or phenotype previously implicated with cichlid diversification [17,18]. However, only functional experiments will inform about the phenotypes associated with these HDRs and their relative contributions to adaptation and divergence. Now that these regions have been identified, such functional tests should be performed.

One aspect that has not been explored in detail by Malinsky *et al.* [5] is that of sympatric speciation, although the system has all the ingredients to become yet another textbook example of speciation in the absence of geographical barriers and involving cichlids in a crater lake [6–9]. The geographical and taxonomic context makes the case of the Lake Massoko cichlids particularly exciting. While the previously known examples of sympatric speciation in cichlids come from crater lakes in Cameroon and Nicaragua and involve lineages that are phylogenetically rather distant to the cichlid faunas in the East African Great Lakes, the ecomorphs discovered in Lake Massoko belong to the haplochromines and, hence, to the by far most species-rich cichlid clade that is famous for its adaptive radiations in Lake Victoria and Lake Malawi [19]. It is questionable, however, whether the study of small cichlid radiations in crater lakes — even if founded by haplochromines — will tell us much about what happened with the cichlids in Lake Victoria, Lake Malawi and Lake Tanganyika. To answer this question, it will probably be necessary to examine an entire massive cichlid adaptive radiation in similar detail as has been done for the Lake Massoko cichlids.

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Visual Neuroscience: The Puzzle of Perceptual Stability

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Our world appears stable, although our eyes constantly shift its image across the retina. What brain mechanisms allow for this perceptual stability? A recent study has brought us a step closer to answering this millennial question.

While reading this dispatch, your eyes constantly jump across the text at high speed by means of fast eye-movements, so-called saccades. Moving a camera at that speed would result in a blurred mesh that would not allow detection of any single character. Yet the perception of our world is anything but blurred: instead, the foveae of our eyes guarantee high resolution snapshots not only of this paragraph, but also of the world around us. While the past hundred years have seen an increasing