

The ecological and genomic basis of explosive adaptive radiation

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Abstract:

Speciation rates vary tremendously among lineages, and our understanding of what fuels the rapid succession of speciation events within young adaptive radiations remains incomplete¹⁻¹¹. The cichlid fish family provides a notable example of such variation, with many slowly speciating lineages as well as several exceptionally large and rapid radiations¹². By reconstructing a large phylogeny of all described cichlid species, we show that explosive speciation is solely concentrated in several large young lake species flocks. Speciation rate increases are associated with absence of top predators but this is not a sufficient explanation for explosive speciation. Across lake radiations we observe a positive relationship between speciation rate and enrichment with large indel polymorphisms. Assembly of one hundred cichlid genomes within the most rapidly speciating cichlid radiation, found in Lake Victoria, reveals exceptional 'genomic potential' - hundreds of ancient haplotypes bearing indel polymorphisms, many associated with specific ecologies and shared with ecologically similar species from other older radiations elsewhere in Africa. Network analysis reveals fundamentally non-treelike evolution through recombining old haplotypes, with origins of ecological guilds concentrated early in the radiation. Our results suggest that the combination of ecological opportunity, sexual selection and exceptional genomic potential is the key to understanding explosive adaptive radiation.

This document is the accepted manuscript version of the following article:

McGee, M. D., Borstein, S. R., Meier, J. I., Marques, D. A., Mwaiko, S., Taabu, A., ... Seehausen, O. (2020). The ecological and genomic basis of explosive adaptive radiation. *Nature*, 586, 75-79. <https://doi.org/10.1038/s41586-020-2652-7>

Many of the geographical, ecological and genetic factors that play a role in speciation, are now well established, thanks to the maturation of theoretical and empirical speciation research over the past three decades¹⁻⁸. The origin of new species often starts in geographical isolation via gradual accumulation of reproductive incompatibilities and/or divergent adaptation, and ecological differentiation is often completed by ecological character displacement after return to sympatry⁵. Under some conditions individual speciation events can be sudden and rapid^{6,9}, but also these models fail to explain many rapid speciation events in short succession within one lineage and region. This exact phenomenon occurs within large adaptive radiations, as many new species emerge in very short succession and come together into rich assemblages of ecologically diverse species coexisting sympatrically within extremely short time spans, too short for incompatibilities to emerge and far too short for new heritable variation to accumulate between successive speciation events. This calls for explanations for which neither the classical allopatric models with subsequent character displacement nor ecological speciation models are sufficient^{2,6,9,10,11}.

We study the factors governing the dynamics of explosive diversification and accumulation of species diversity in the fish family Cichlidae, which contains over 1700 described, valid and extant species, over 5% of all extant teleost fishes. Roughly half of these species are lake endemics, often part of young and ecologically diverse species flocks that occupy many distinct adaptive zones¹². Other cichlids also display a wide range of ecological and morphological diversity, though they have diversified on much longer timescales.

Factors influencing speciation rate across all cichlids:

We estimate variation in speciation rates among cichlid fishes from a fully sampled phylogeny including all currently taxonomically valid cichlid species described prior to 2019 (n=1712, Fig. 1), by combining nuclear genes, mitochondrial genes, and meristic characters, and implementing topological constraints from previous phylogenomic studies of smaller subclades. We estimate speciation rates using the DR statistic^{13,14}. Our results verify that rates vary by four orders of magnitude across the family, and that sustained explosive speciation rates are indeed concentrated solely within several young lake radiations (Fig. 1a, 1b). These radiations, particularly that of Lake Victoria, possess some of the fastest sustained speciation rates ever observed in contemporary metazoans¹⁵. Note that these are not just very high rates at the macroevolutionary scale but the extremely narrow and recent time window within which hundreds of speciation events occurred in a single lineage are unparalleled also in microevolutionary studies of speciation.

To examine the extent to which extrinsic environmental variables or general lineage traits influence speciation rate variation across the cichlid phylogeny, we assembled a comprehensive set of predictor variables. Both Bayesian regression¹⁶ and a nonparametric test¹⁷ suggest that the presence of large visually oriented predatory fish¹⁸ and arid climate are major constraints to speciation rate in cichlids, while male-restricted ornamentation (indicative of evolution in response to sexual selection) and a wide gradient of water depth¹⁹ show weak positive effects (Fig. 1c). However, when we fit hidden state speciation and extinction (HiSSE) models²¹, none of the environmental and trait factors, whether alone or in concert, constitute a sufficient explanation for the uniquely high speciation rates observed in one of three lineages of

haplochromine cichlids of Lake Victoria (see Supplementary Information section 1.8). Further exploration with missing state speciation and extinction models²¹ suggested three regimes for speciation rate: a baseline rate, high speciation in Malawi, Xiloa, and the Lake Victoria Region Superflock, as well as a uniquely extreme speciation rate in Lake Victoria itself. This suggests that our environmental and trait variables, albeit influential, are insufficient to explain extreme cichlid diversification rates, and that some other process must be involved that is not fully captured by variables representing variation in ecological opportunity and sexual selection alone. What is this process?

To approach this question, we examined the genomic substrate of adaptive radiation across two ecologically divergent species from each lake adaptive radiation for which genomic data is available (n=8 different radiations). Typically, speciation genomics is performed through alignment of small reads to a reference genome, but regions containing indels, base pair insertions and/or deletions, will not always align properly. To avoid this issue, we assembled all genomes into de Bruijn graphs prior to reference alignment in order to accurately genotype indels²². We then counted the number of indels 5bp and larger fixed between the two species representing each radiation, filtering for linkage disequilibrium to account for the presence of multiple indels within large complex variants.

We find a positive association (Spearman correlation test, $p < 0.01$, Fig. 2a, Fig. S4) between speciation rate (estimated for each radiation from our large tree) and the number of divergently fixed indels relative to the time to most recent common ancestor (TMRCA). The fastest speciation rates by far are seen in Lake Victoria, and this radiation is enriched for very many indels divergently fixed between species even though TMRCA is extremely low (see Supplementary Information section 2.2). The lowest speciation rate, seen in a lineage of Tanganyikan lamprologines, was associated with many indels combined with old TMRCA. Radiations with intermediate speciation rates either had a low number of indels fixed between species and a recent TMRCA, as seen in Lake Ejagham, or a relatively high number of indels and a moderate TMRCA, as in the Malawi flocks. Our results suggest that the variation in speciation rate between these lineages in lakes is associated with whether a lineage has unusually many large indels for its age, and highlights the need to analyze indels as well as SNPs in studies of adaptive radiation and speciation.

We then examined why Lake Victoria cichlids might contain many more indels than expected for their relatively young age. We expanded our sampling of Victorian cichlids by producing assembly graphs of one hundred whole genomes of 100 different species representing every extant taxonomic genus, dietary guild and habitat specialization in the radiation. We identified indels 5bp and larger segregating within the Lake Victoria radiation at a minor allele frequency of 0.01 or greater (n=251,690 indels), then examined whether these indels were also present in one or more outgroup species, which included haplochromine cichlids from the independent radiation in nearby Lake Kivu, cichlids representing the two founding lineages of the entire Lake Victoria Region Superflock (20) that includes both Victoria and Kivu (Congolese *Astatotilapia* and Upper Nile *Thoracochromis*), as well as representatives of two much older haplochromine genera (*Serranochromis* and *Orthochromis*) over ten million years divergent from Lake Victoria that are endemic to Lake Mweru in the upper Congo and represent the extreme ends of the ecomorphological gradient in Lake Mweru²³.

A large number of the indels that segregate among Lake Victoria cichlids are also segregating across the outgroups (82,131 of 251,690; 43,442 fixed between outgroup taxa, 38,689 segregating within one or more outgroup taxa), suggesting that the Lake Victoria cichlid radiation contains many variants that existed up to ten million years before the modern radiation (Fig. 2b). Genome-wide association mapping between these indels and a series of ecological variables that capture the major ecological dimensions of cichlid adaptive radiation revealed many indels associated with diet and habitat and one associated with nuptial coloration, arranged in a highly polygenic architecture (Fig. 2b). Indel polymorphisms segregating in Lake Victoria but not across our outgroups were much less often associated with these traits (see Supplementary Information 2.4). We discuss one of the ancient ecology-associated regions in the following.

On chromosome 9 we observe a region that is fixed across all morphologically specialized fish-eating Lake Victoria cichlid species we sequenced (14 species), but is also seen in morphologically similar fish-eating specialists phylogenetically distant from the radiation. Several piscivory-associated indels in this region on chromosome 9 (Fig. 2c) occur in an intron of a gene coding for an uncharacterized regulatory protein in the ubiquitin family that occurs adjacent to the mesenchymal stem cell gene *THEM6*. Fixation of this haplotype is shared between Lake Victoria piscivores, the Lake Kivu predator *Prognathochromis vittatus* and predatory cichlids in the evolutionary distant genus *Serranochromis* in southern Africa (Fig. 2d). A comparison of internal branch lengths of gene trees both flanking and within this region suggests this is due to introgression rather than incomplete lineage sorting (see Supplementary Information).

The evolutionary divergence in our large cichlid phylogeny suggests a most recent common ancestor between *Serranochromis* and the Lake Victoria Superflock roughly ten million years ago (Fig 2e), by far exceeding the divergence between lineages that gave rise to the hybrid swarm founding the Lake Victoria region superflock (20). Currently the genus *Serranochromis* and the lineages ancestral to the Lake Victoria Superflock have very limited geographical range overlap (Fig. 2f), with one rare species, *S. janus*, known to occur in the nearby Malagarasi drainage²⁴ where it could have plausibly interacted with the founding lineages of the Lake Victoria Region Superflock, given that the region contains at least one extant representative of the Congolese founding lineage, *Astatotilapia stappersii*.

The presence of ancient indel polymorphisms, the hybrid origin²⁰ and the explosive speciation rate of the Lake Victoria cichlid radiation all pose substantial challenges for reconstruction of its evolutionary history, as evolution through reshuffling and recombination of ancient variants violates assumptions of a treelike evolutionary history, and incomplete lineage sorting is rampant. To overcome these challenges, we reconstruct networks from sharing of identity by descent (IBD) blocks^{25,26} instead of using phylogenetic methods for the Lake Victoria radiation. IBD block sharing networks permit us to uncover how ecology and sexual selection interacted to allow for rapid speciation and the colonization of many different adaptive zones and also permit us to reconstruct the relative timing of the emergence of the major ecological guilds.

We utilize the temporal information contained within IBD segment size²⁵ to examine the imprint of ecology and sexual selection on species differentiation at different stages of diversification in the Lake Victoria cichlid radiation. The sharing of small IBD segments

represents older snapshots of the evolutionary relationships²⁷, whereas the sharing of larger segments indicates more recent relationships. In all but the smallest IBD segment size class, which represents the earliest stages of the radiation, we find that both diet and macrohabitat have positive effects on species clustering in the network structure of the radiation such that more closely related species share the same macrohabitat and belong to the same trophic guild significantly more often than less closely related species.

We also found a smaller negative effect of male nuptial coloration on species clustering in the networks reflecting more recent ancestry (Fig. 3b), indicating that species with recently shared ancestry are divergent in male nuptial coloration more often than expected and that genetically more distantly related species more often share similar nuptial coloration (phylogenetic overdispersion of nuptial coloration in contrast to phylogenetic clustering of diet and habitat). These results suggest that young species, i.e. shortly after speciation, are likely to exhibit different nuptial coloration, but similar ecologies, and is consistent with population-level work on the mechanisms of speciation in the Victoria radiation²⁸. Our IBD results are complemented by an analysis of D-statistics across the radiation which also reveals widespread nontreelike evolution as well as divergence driven by ecology and sexual selection (Extended Data Fig. 1).

Understanding the genomic architecture of adaptive radiation:

Previous work proposed that cichlid adaptive radiations proceed in stages, where macrohabitat divergence precedes dietary divergence²⁹, but this hypothesis is not supported for the Lake Victoria species flock. Instead, our results suggest simultaneous divergence in diet and macrohabitat, divergence that depended critically on exceptional 'genomic potential' in the form of extraordinarily high density of ancient indel polymorphisms, many directly linked to ecological divergence. Without this genetic variation consisting of many ancient haplotypes that affect ecology and mating and that could be recombined in many different ways to create the highly polygenic genomic architecture of this radiation, the number of new species that could have evolved and persist in sympatry in the 15,000 years since the filling of the lake would likely have been much more limited. Adaptive radiation across the food web would have been much slower, and very possibly never have occurred in the limited time, had these transitions been dependent on waiting times for new mutations.

Our results drive home the need to utilize both large-scale comparative methods and fine-scale speciation genomics together in order to understand the drivers of speciation. Phylogenetic comparative methods are necessary to rigorously identify different evolutionary regimes, particularly regimes with the high rates typical of some but not all adaptive radiations. Similarly, comparative genomics of many representatively chosen species within these radiations and their outgroups are required in order to discover and understand the non-treelike dynamics and genomically heterogeneous ancestry that can characterize and fuel these rapidly evolving regimes. Our insights into the factors underlying cichlid diversification in general, and the special circumstances that permitted the exceptional rates of explosive adaptive radiation in Lake Victoria, make us hopeful that nesting genomically informed speciation research with macroevolutionary analyses of diversification will soon allow a comprehensive understanding of why some clades produce spectacular radiations while others do not³⁰.

Author contributions:

MM and SB designed the phylogenetic analyses with assistance from OS and BO. Trait data were gathered by SB and OS with assistance from MM. GIS data was gathered by MM. Genomic data was gathered by SM, JM and MM. MM and OS designed the genomic analyses with assistance from JM and advice from DM, LE and RB. MM performed Uganda fieldwork with assistance from AT and coordination by OS. OS and SM performed Tanzania fieldwork with assistance from MK. MM and OS wrote the manuscript with assistance from SB, DM, and JM, with comments from and final version approval by all authors.

Acknowledgements:

We thank Rich Bireley and the Sacramento Aquarium Society, Peter George and the New England Cichlid Association, Marco Welss and the IGV, Rick Borstein of the Greater Chicago Cichlid Association, and the American Cichlid Association for advice and access to specimens for photography in Figure 1. We thank Kim Pedersen and Jakob øgaard for Uganda fieldwork assistance along with NaFiRRI staff, including John Balirwa, as well as cooperation from Kyoga region village elders. We thank TAFIRI for hosting OS team members during fieldwork. We thank Katie Wagner, Jacco van Rijssel, Florian Moser, Oliver Selz, and Les Kaufman for discussions. This research was funded by Swiss National Science Foundation grant #31003A_163338 to OS, LE and RB, an American Cichlid Association Guy Jordan Fellowship to SB, and Australian Research Council DE180101558 to MM.

Data availability:

Genomic data is available at NCBI BioProject ID: PRJNA626405. Data files and scripts are available via Dryad DOI: <https://doi.org/10.5061/dryad.fn2z34tr0>

Fig. 1: Cichlid speciation rates and their predictors on macroevolutionary timescales.

(a) A time-calibrated phylogeny of cichlids ($n=1712$), colored by speciation rate, with the two fastest evolving clades, Lake Victoria and Lake Malawi, highlighted on the tree. Photos show morphologies of cichlids representing the vast phenotypic and ecological variation in this family. (b) Distribution of speciation rates, measured using the DR statistic for all cichlid species. The highest speciation rates are found in Lake Victoria, Lake Malawi and the Lake Victoria Region Superflock (LVRS) comprised of Lakes Edward, Albert, Kivu and species flocks in minor lakes of the region, followed by Lake Tanganyika, most cichlids, and then Madagascar cichlids. (c) Effect size distributions of various extrinsic abiotic and extrinsic and intrinsic biotic predictors of speciation rate across all described cichlids ($n=1712$). Boxplots indicate the 50% credible interval, violin plots indicate 95% credible intervals.

Fig. 2: Large indels associated with speciation and adaptation across cichlid radiations.

(a) Positive association between speciation rate (phylogenetic mean of the log-10 transformed DR statistic; see Supplementary Information section 2.2 for additional speciation rate metrics) and LD-filtered 5bp+ indels relative to TMRCA. Blue line indicates the regression line from a linear regression; grey shading indicates 95% confidence intervals for the mean. (b) Venn diagram of indels ($n=38,689$) segregating in the Lake Victoria radiation that also segregate either within Lake Kivu, LVRS founding lineages, and/or Lake Mweru. Outer ring indicates the genomic positions of ancient large indels significantly associated with diet, habitat or nuptial

coloration (n=214). (c) Phylogeny of the region on chromosome 9 that is deeply divergent between piscivores and others in the Victoria radiation, with each allele having its closest relatives not within the Lake Victoria radiation but in morphologically and ecologically corresponding cichlids from Lake Kivu and Lake Mweru. The right-hand phylogeny contains the same species from our cichlid megaphylogeny in Figure 1. (d) Multiple sequence alignment (20kb) of the ancient chromosome 9 haplotype associated with piscivory, showing multiple large indels (highlighted in yellow) segregating across East Africa but sorted into and fixed in a clade containing all Lake Victoria piscivores. Species are, from top to bottom, *Paralabidochromis flavus* (Victoria), *Paralabidochromis paucidens* (Kivu), *Orthochromis* sp. 'red cheek' (Mweru), *Harpagochromis cavifrons* (Victoria), *Prognathochromis vittatus* (Kivu), and *Serranochromis* sp. 'checkerboard' (Mweru). (e) Map (Google, TerraMetrics 2020) showing the locations of Lakes Victoria, Kivu, and Mweru, as well as Lake Tanganyika and the northern tip of Lake Malawi, with a 250km scale bar for reference.

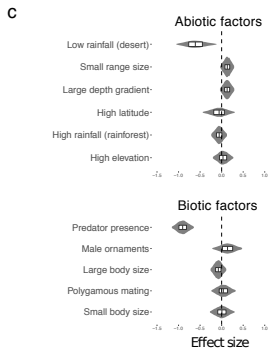
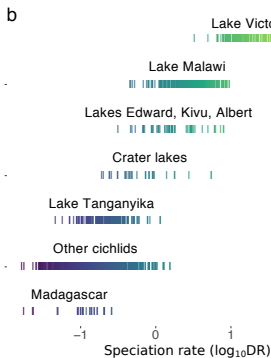
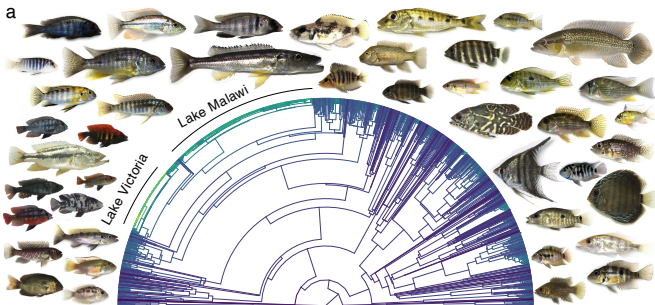
Fig 3. Networks of identity-by-descent blocks reveal the evolutionary history of the Lake Victoria cichlid radiation.

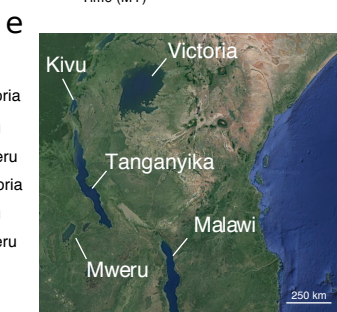
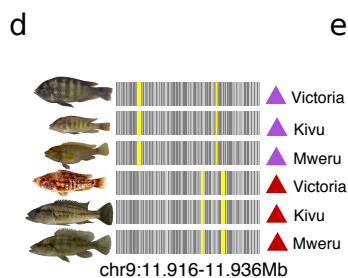
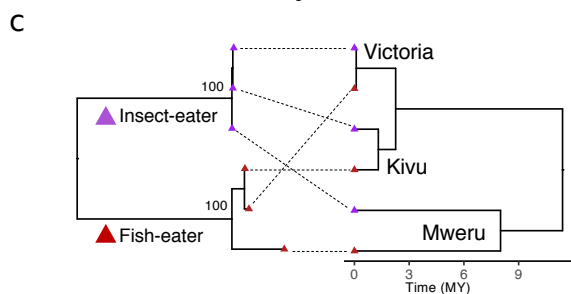
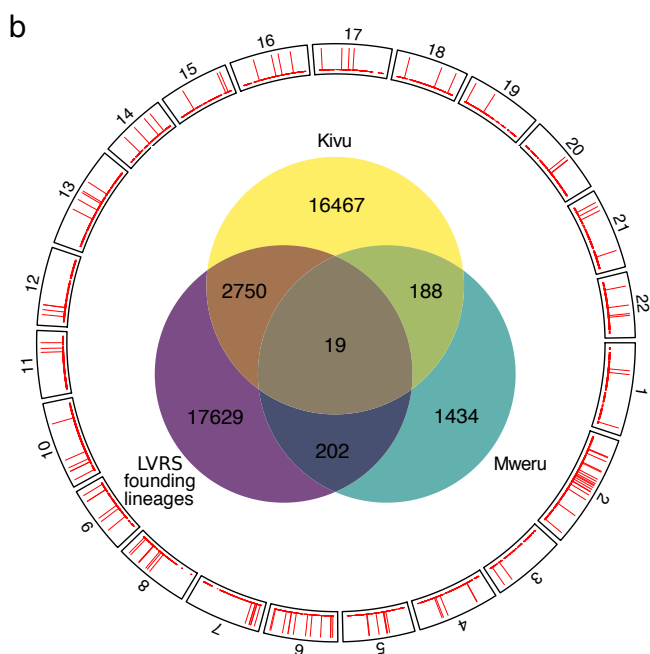
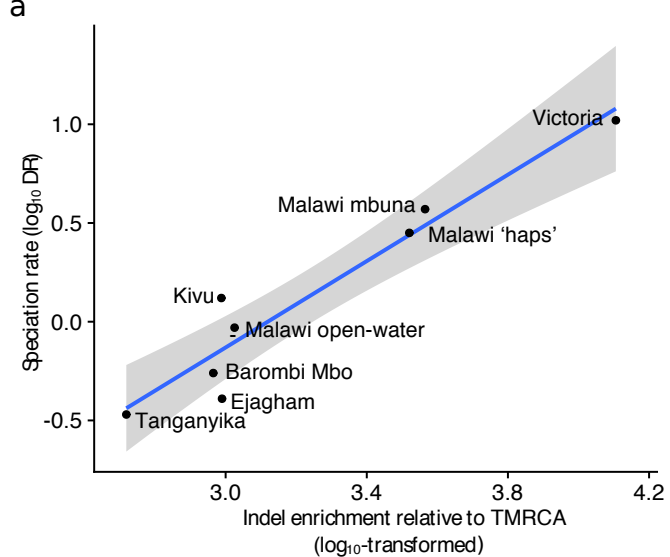
(a) Identity by descent (IBD) network of the Lake Victoria radiation. Nodes are the 100 Lake Victoria cichlid species and links represent the number (thickness of links) of IBD segments (n=37179) shared between species. Species with similar diets and habitats exhibit more IBD sharing. (b) Ecological predictors of the presence of IBD segments of a given size, taking into account the non-independence of pairwise comparisons (n=4,186) between genomes. We use three different block size categories representing different relative time points during the unfolding of the radiation corresponding to (i) coalescence of all species in a common ancestor, (ii) the beginning and (iii) continuation of adaptive radiation into different ecological specialists with module structure driven by diet and habitat. Effect sizes (odds ratio = $e^{\text{effect size}}$) indicate whether IBD sharing between genomes is more likely between species with the same diet, habitat, or male nuptial coloration than between species with different diet, habitat, or male nuptial coloration. Boxplots indicate the 50% credible interval, violin plots indicate the full credible interval.

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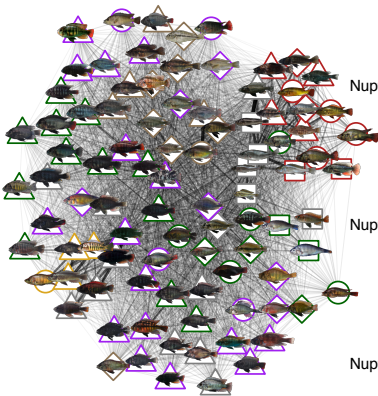


a

Habitat



Diet



b

