



RESEARCH ARTICLE SUMMARY

EVOLUTION

Cycles of fusion and fission enabled rapid parallel adaptive radiations in African cichlids

Joana I. Meier*, Matthew D. McGee, David A. Marques, Salome Mwaiko, Mary Kische, Sylvester Wandera, Dirk Neumann, Hilary Mrosso, Lauren J. Chapman, Colin A. Chapman, Les Kaufman, Anthony Taabu-Munyaho, Catherine E. Wagner, Rémy Bruggmann, Laurent Excoffier, Ole Seehausen*

INTRODUCTION: Much of species diversity is thought to have arisen during adaptive radiations—the process whereby many species arise in short succession and diversify in their ecological niche use. It is not understood why, when given ecological opportunity, some lineages readily undergo adaptive radiations, whereas others do not. A lineage with exceptional propensity to radiate is that of the cichlid fishes of the Lake Victoria region. In this instance, each major lake harbors highly ecologically diverse cichlid assemblages, ranging from algivores to zooplanktivores to predators that feed on other members of the radiation. We had previously shown that all of these radiations evolved from a hybrid population between two lineages that merged about 150,000 years ago.

RATIONALE: In the Pleistocene dry period, >20,000 to ~16,000 years ago, Lake Victoria was completely dry, and any previous radiation would have died out. The deeper Western Rift Lakes Edward, Kivu, and Albert may still have hosted parts of their cichlid radiations. It thus remained

unclear whether the ecological guilds had colonized Lake Victoria from these deeper lakes or whether they evolved in a new adaptive radiation. In this work, we test whether the hundreds of ecologically diverse Lake Victoria cichlids in fact diverged from a common ancestor in less than 16,000 years and how they diversified so rapidly.

RESULTS: We generated a whole-genome dataset of 464 cichlids representing all major lakes in the region and several species of almost all the ecological groups in Lake Victoria. We find that the Lake Victoria cichlids evolved in the lake as an extremely rapid adaptive radiation. The process started from hybrid ancestry of at least three lineages that must have survived the dry period in swamps in the region. We find evidence that each of these parental lineages contributed ecologically relevant alleles that facilitated the rapid radiation in Lake Victoria. Hybridization between members of the emerging Lake Victoria Radiation additionally gave rise to yet more guilds

and species. Cycles of hybridization led to the fusion of lineages followed by diversification (lineage fission) thus occurred repeatedly throughout the evolutionary history. As shown previously, the hybridization event about 150,000 years ago facilitated the older radiations in the region, and in this work, we show that further cycles of fusion and fission allowed the lineage to retain large, phenotypically relevant genetic variation and thus to radiate extremely rapidly.

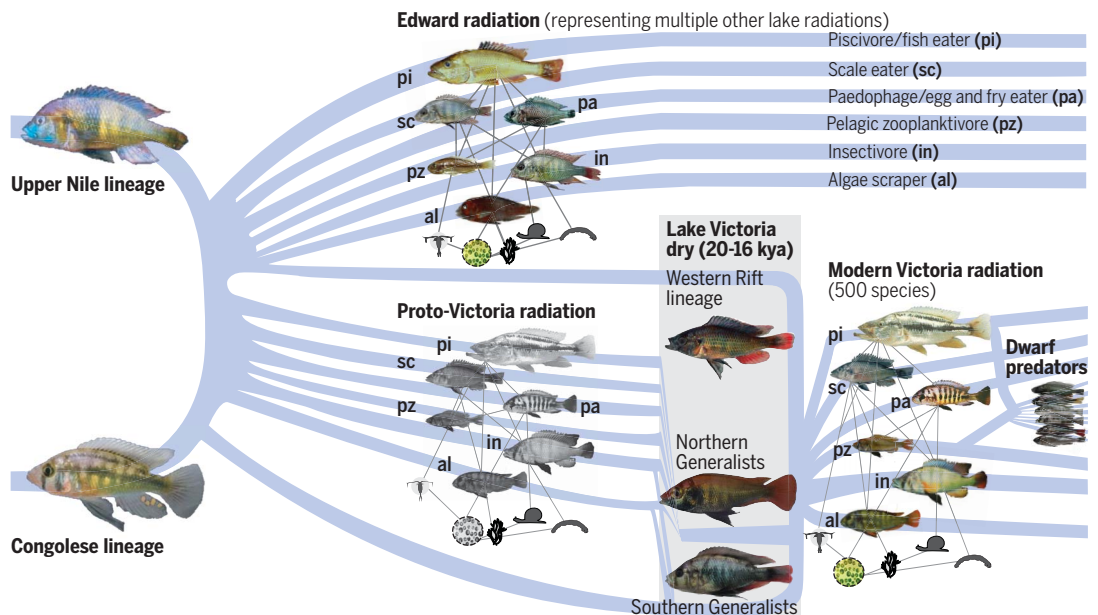
CONCLUSION: Multiple cycles of lineage fusion and fission likely explain the very high propensity of these cichlids to form parallel adaptive radiations across multiple trophic levels. It may be generally true that animal or plant lineages that have recently radiated are not only particularly prone to hybridize but are also prone to radiate again from the resulting hybrid populations, perpetuating and exacerbating the differences in diversification rates between lineages. The variation in radiation propensity is thus not a property of any one species but that of an evolving flock of species. This finding also suggests that we should grow beyond species-centric conservation strategies and aim to preserve entire species complexes to preserve their capacity to adapt and diversify. ■

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 Cite this article as J. I. Meier et al. *Science* 381, eade2833 (2023). DOI: 10.1126/science.ade2833

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<https://doi.org/10.1126/science.ade2833>

Multiple cycles of lineage fusion by hybridization and diversification led to increasingly rapid and extensive radiations of cichlid fishes, including the explosive evolution of 500 Lake Victoria species across four trophic levels in 16,000 years.

The blue lines reflect lineage fusion and fission events inferred in this work. The fish photos visualize some ecological groups that evolved in parallel in each lake, making up entire trophic networks.



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RESEARCH ARTICLE

EVOLUTION

Cycles of fusion and fission enabled rapid parallel adaptive radiations in African cichlids

Joana I. Meier^{1,2,3,4*}, Matthew D. McGee^{1,2,5}, David A. Marques^{1,2,6}, Salome Mwaiko^{1,2}, Mary Kische⁷, Sylvester Wandera^{8†}, Dirk Neumann⁹, Hilary Mrosso⁷, Lauren J. Chapman¹⁰, Colin A. Chapman^{11,12,13,14,15}, Les Kaufman¹⁶, Anthony Taabu-Munyaho⁸, Catherine E. Wagner¹⁷, Rémy Bruggmann¹⁸, Laurent Excoffier^{1,19}, Ole Seehausen^{1,2*}

Although some lineages of animals and plants have made impressive adaptive radiations when provided with ecological opportunity, the propensities to radiate vary profoundly among lineages for unknown reasons. In Africa's Lake Victoria region, one cichlid lineage radiated in every lake, with the largest radiation taking place in a lake less than 16,000 years old. We show that all of its ecological guilds evolved in situ. Cycles of lineage fusion through admixture and lineage fission through speciation characterize the history of the radiation. It was jump-started when several swamp-dwelling refugial populations, each of which were of older hybrid descent, met in the newly forming lake, where they fused into a single population, resuspending old admixture variation. Each population contributed a different set of ancient alleles from which a new adaptive radiation assembled in record time, involving additional fusion-fission cycles. We argue that repeated fusion-fission cycles in the history of a lineage make adaptive radiation fast and predictable.

Adaptive radiation, the rapid evolution of both species and ecological diversity within a lineage, has made substantial contributions to the diversity of life (1–3), but we are currently unable to predict which lineages form adaptive radiations and to what extent. Although ecological opportunity is a prerequisite (1, 4–6), whether or not an adaptive radiation will occur in the finite time available when the opportunity arises is difficult to predict (1). Of all lineages that colonized islands or lakes with unfilled ecological

niches, only a few have formed adaptive radiations (7), but some of these radiated repeatedly in different islands or lakes (1, 8, 9). Why this propensity to radiate differs so profoundly among lineages (7, 10) is an important but unresolved question.

A notable example of repeated, large-scale adaptive radiations is the haplochromine cichlid fishes in the Lake Victoria region of East Africa (11–13). In each major lake in this region,

the same lineage has evolved similar arrays of ecomorphological specialists that occupy almost all ecological niches available to fish, spanning three to four trophic levels from algivores to insectivores, zooplanktivores, and molluscivores up to fish predators, including egg and fry eaters, scale eaters, and top predators that prey on (sub)adults of other cichlid species and other fish (Fig. 1). They make up the bulk of the biomass in the ecosystem at any of these trophic levels, representing major elements in food webs largely assembled through adaptive radiation. The Lake Victoria region superflock (LVRS) includes at least 700 cichlid species that form rich sympatric assemblages in Lakes Victoria, Kyoga, and Kagera and in the Western Rift Lakes Edward, Kivu, and Albert as well as smaller species flocks in Lake Turkana and small crater lakes, such as Lake Saka (Fig. 2) (13–16). This is extraordinary for two reasons: (i) because none of these lakes is more than a few hundred thousand years old, and most are much younger, and (ii) because several other cichlid lineages, including other haplochromines, and at least 80 other fish lineages that colonized these same lakes hardly diversified at all (17–21).

Rapid diversification at the base of the LVRS may be explained by its hybrid origin (15). The LVRS lineage arose ~150,000 years ago through hybridization between two or three older lineages that had split from their common ancestor through geographical isolation 1.6 to 5.8 million years earlier (15). The resulting admixture variation likely facilitated radiations soon after the origins of this hybrid lineage (15). However, Lake Victoria had dried up since then,

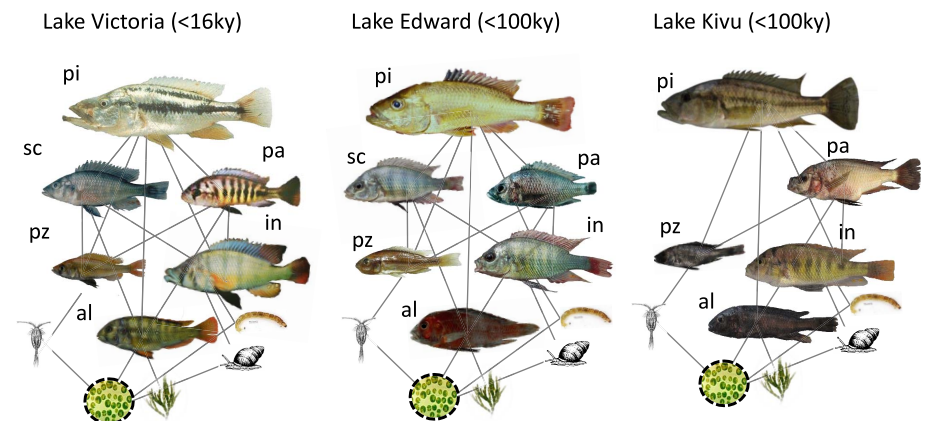


Fig. 1. Parallel radiations across multiple trophic levels in all major lakes in the Lake Victoria region.

Ecomorphs in the Victoria Radiation straddle four distinct trophic levels in the food web, ranging from algivores (al), to insectivores (in) and pelagic zooplanktivores (pz), scale eaters (sc) and paedophages (pa) eating eggs and fry of other cichlids, to top piscivores (pi). Very similar ecomorphs are also found in the other radiations in the Lake Victoria region, such as those in Lakes Edward and Kivu (scale eaters are not known from Kivu). Even though most ecomorphs are represented by several to many species in each radiation (e.g., more than 100 piscivores in Lake Victoria) and there are several distinct guilds at many trophic levels (e.g., epilithic algal browsers, epilithic algal grazers, epiphytic algal grazers, and phytoplanktivores), only one species is shown, representing one or two guilds per trophic level. [Photos of Victoria pi and sc by Frans Witte (HEST), al by Vianny Natugonza (NaFIRRI), Lake Edward pa by Nathan Vranken, and Lake Kivu cichlids by Guy Periat. All other photos by O.S.]

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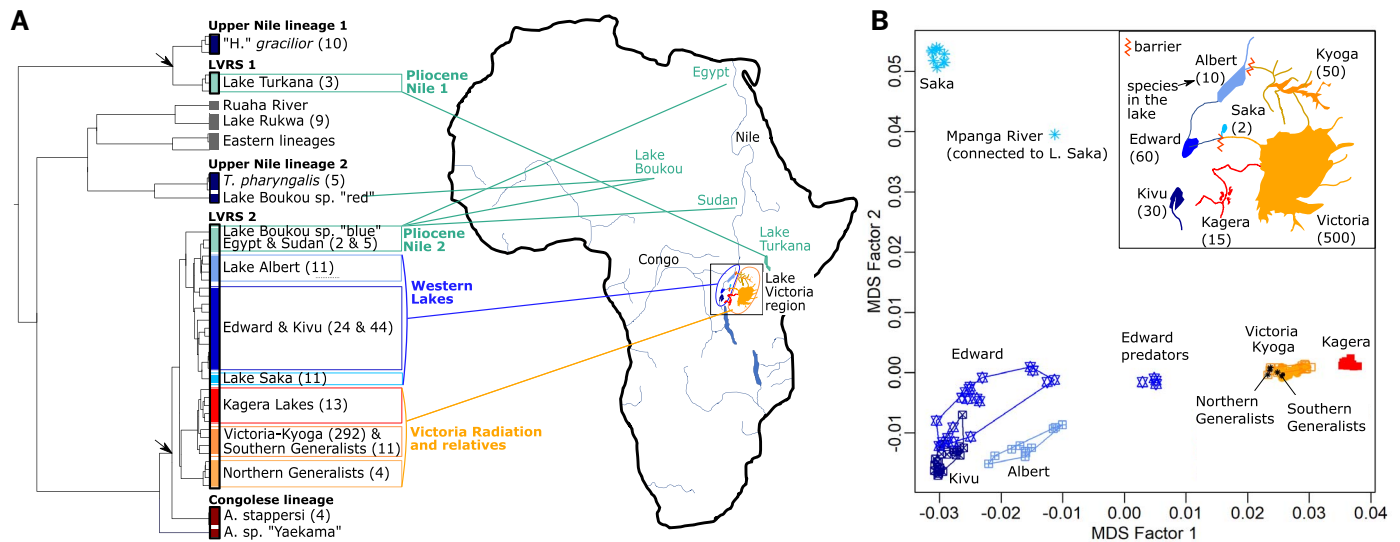


Fig. 2. Geogenomic structure of the LVRS. (A) (Left) The whole-mitochondrial genome tree shows that LVRS cichlids, although monophyletic in the nuclear tree (Fig. 3 and fig. S15), exhibit two mitochondrial lineages (LVRS1 and LVRS2). These lineages are sister to the two different parental lineages of the hybrid swarm from which the LVRS emerged, and both split from their sister lineages around the same time (arrows). Most calibration sets estimate these splits to a maximum of 350,000 years ago, which may be the time of the Congo-Nilotic hybrid swarm formation and thus the maximum age of the LVRS (table S1). Similarly, the much younger Victoria Radiation exhibits two divergent mitochondrial lineages that are almost as divergent from each other as they are from the Western Rift lake cichlids.

The tree was rooted on *A. alluaudi* (full trees with different calibrations on Dryad; dates are provided in table S1), and the group label colors correspond to those in Fig. 3. Species-rich lineages were down-sampled for a more balanced tree. The numbers of genomes per clade are shown in parentheses. (Right) Map of Africa with sampling locations; 127 genomes: The LVRS individuals mostly cluster by lake (Victoria and Kivu radiations down-sampled to 25 genomes, and Pliocene Nile cichlids excluded; MDS with all samples is provided in fig. S3). Lake Victoria and Kyoga cichlids are intermixed, forming a single radiation. (Inset) Map of the Lake Victoria region with the number of species known in each lake.

most recently from at least 19,000 to 16,000 years ago (22–24). It is unclear how any one lineage could retain this large admixture variation and the exceptional radiation propensity associated with it through this long desiccation phase. Theoretical studies have suggested that admixture can not only fuel the onset of one adaptive radiation but also maintain high adaptive radiation propensity for a long time if several descendent populations or species hybridize again (25). In this work, we test whether admixture played a role in the renewed adaptive radiation less than 16,000 years ago.

Despite its very young age, Lake Victoria hosts the largest and most ecomorphologically diverse cichlid fish assemblage within the region, with >500 endemic species in more than 20 ecological guilds (11, 26–28). We wanted to know whether, and how, this superdiverse Lake Victoria assemblage, spanning three to four trophic levels and more than 20 guilds, could have evolved in just 16,000 years. The high morphological similarity of corresponding ecomorphs from Lakes Victoria, Edward, Albert, and Kivu (Fig. 1) led earlier systematists to define genera across these lakes (13), which implied single origins of major ecomorphs followed by separate colonization of the different lakes. By contrast, some previous studies had claimed that the Lake Victoria radiation is monophyletic, but they lacked exhaustive taxon sampling or the phylogenetic resolution required

to rule out the idea that at least some of the Lake Victoria ecomorphs colonized the lake independently rather than having evolved inside the lake (14–16, 29). In this work, we test whether Lake Victoria cichlids evolved inside the lake in just 16,000 years and, if so, how they diversified so rapidly into many distinct guilds each including many species.

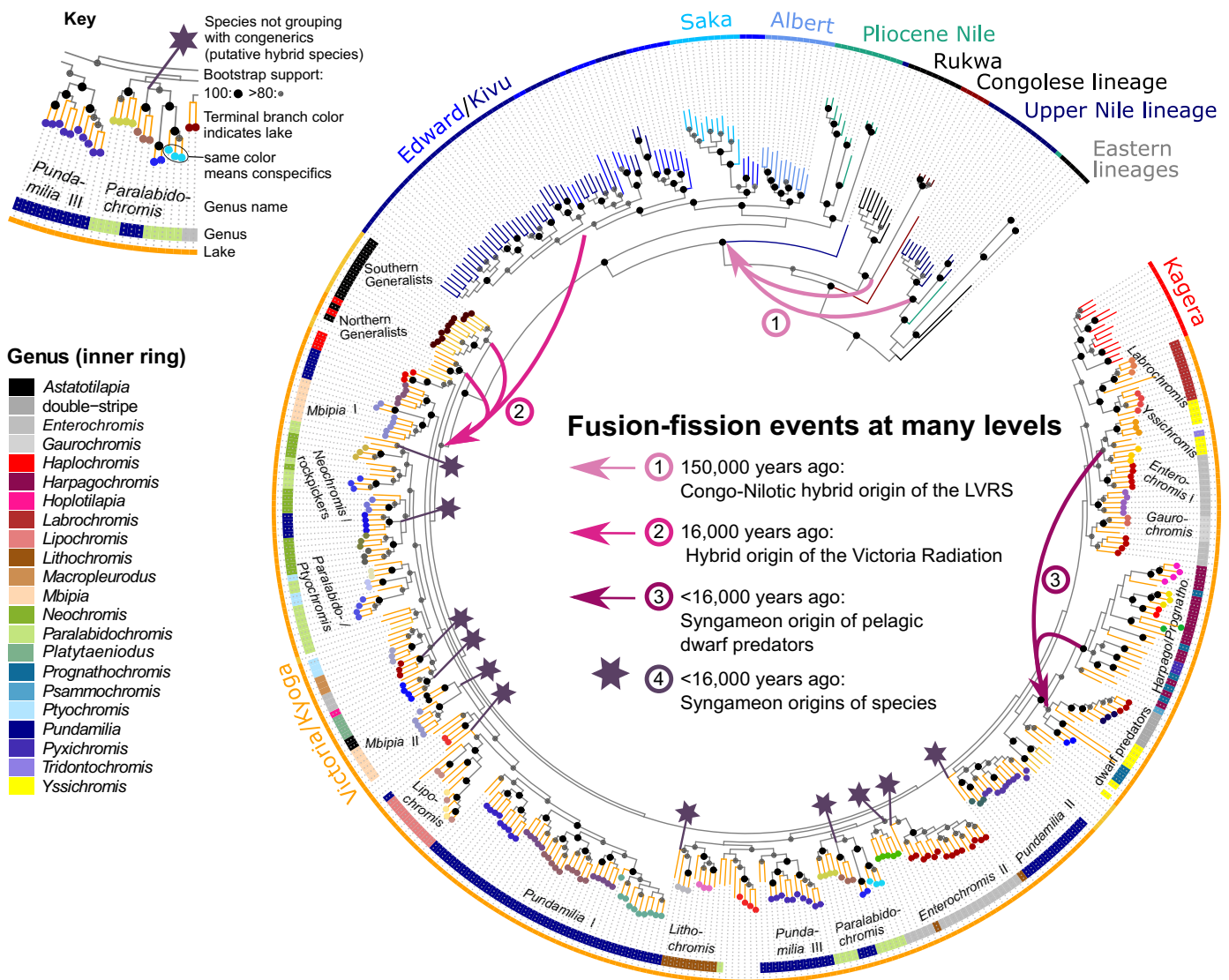
A monophyletic radiation composed of hundreds of species with high levels of sympatry

Our dataset encompasses 464 cichlid genomes. These include 288 genomes of 120 Victoria Radiation species representing all except one genus and ecomorph of Lake Victoria, 127 genomes of other LVRS cichlids representing nearly all ecomorphs in the other lakes in the region, and 49 outgroups (table S4 and fig. S1).

Phylogenies based on whole-mitochondrial (Fig. 2A and fig. S15) or nuclear genomes (Fig. 3 and figs. S2 and S15) and multidimensional scaling (MDS) analyses (Fig. 2B and fig. S3) reveal that all LVRS cichlids from Lake Victoria and its satellite lakes form a single clade, including those from Lake Kyoga—a shallow extension of the Victoria Nile directly downstream of Lake Victoria. We conclude that these species belong to a single, very large, and very young adaptive radiation (referred to as the Victoria Radiation). Cichlids from the Kagera lakes upstream of Lake Victoria form a strongly supported clade nested within this Victoria

Radiation (visible in both mitochondrial and nuclear trees; red in Fig. 2 and Fig. 3), which implies yet another even-more-recent event of adaptive radiation (supplementary text).

The closest relatives of the Victoria Radiation are *Astatotilapia nubila* from swamps in the south of Lake Victoria, hereafter called Southern Generalists, and nubila-like generalists from Lake Kyoga, hereafter called Northern Generalists (Fig. 2 and Fig. 3). The sister clade to these combined in the nuclear whole-genome tree contains the radiations in the Western Rift lakes (Edward, Kivu, and Albert), the radiation in Rwenzori crater Lake Saka, and species from more northerly sites formerly connected to the Nile, including Lake Turkana, the Nile in Sudan and Egypt, Lake Boukou in the Sahara, and lakes in Egypt (called Pliocene Nile cichlids) (Fig. 2 and Fig. 3). Tests of admixture corroborate that all of these LVRS groups are derived from the same Congo-Nilotic admixture event (fig. S4, table S5, and supplementary text) (15). Although most LVRS cichlids are mitochondrially sister to the Congolese parental lineage, those of Lake Turkana are mitochondrially sister to the Upper Nile lineage (Pliocene Nile 1 in Fig. 2A), most likely because of differential fixation of mitochondrial haplotypes after the ancestral Congo-Nilotic admixture event (Fig. 2A and fig. S15). Our calibrated mitochondrial phylogeny suggests that the LVRS split from its Congo-Nilotic ancestors



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Fig. 3. Cycles of lineage fusion and fission throughout the evolutionary history of Lake Victoria region cichlids. Admixture plays a role throughout the evolution of the Victoria Radiation. It precedes the emergence of the entire LVRS (1), that of the Victoria Radiation (2), of new ecological guilds (3), and of many species (4) (see also Fig. 4). In the nuclear whole-genome tree, the Victoria Radiation forms a single clade including Kagera cichlids, with the Northern Generalists and Southern Generalists (*A. nubila*) as closest relatives. The Victoria Radiation is

characterized by ubiquitous reciprocal monophyly of sympatric species and is significantly structured by genus. Also shown is an IQtree reconstructed from 239,659 concatenated SNPs and 465 genomes (fully labeled in fig. S2), rooted on *A. alluaudi* (not shown). Terminal branch colors and outermost ring indicate lakes. For Victoria Radiation species with multiple sequenced individuals, the same color tip symbols indicate conspecific individuals. The hybrid clade of Lake Edward predators is not included in this analysis (see fig. S6).

~350,000 years ago, which is likely an overestimate resulting from the nonlinearity of the molecular clock <1 million years ago (Fig. 2A, table S1, and supplementary text).

We find evidence for occasional, secondary exchange between major lakes even after the beginning of the radiation in Lake Victoria: A predator species from Lake Edward received gene flow from Lake Victoria predators (Fig. 2B, figs. S5 and S6, and supplementary text). No cichlid collected outside of Lakes Victoria, Kagera, or Kyoga clustered within the Victoria Radiation clade, and none of the Victoria, Kagera, or Kyoga species grouped with West-

ern Rift lakes, Lake Saka, or Pliocene Nile cichlids (Fig. 2B and Fig. 3). Hence, the hyperdiverse Victoria-Kyoga assemblage represents a single radiation of >550 species across three to four trophic levels and 20 guilds, evolved in less than 16,000 years since the refilling of Lake Victoria. Nothing similar is known in the animal kingdom, so we investigated what might have made this possible.

A second hybrid swarm at the origin of the Victoria Radiation

Northern Generalists, the sister to the Victoria Radiation in the nuclear tree, show deep mito-

chondrial divergence with the Victoria Radiation (Fig. 2A and fig. S15). This divergence is nearly as deep as that between Victoria and the Western Rift lake cichlids, which indicates that these lineages began to diverge very soon after the LVRS origin. Even though in the nuclear phylogeny the Southern Generalists (*A. nubila*) are more distant from the radiation compared with the Northern Generalists, mitochondrially the Southern Generalists are not distinct from Victoria Radiation members. This cytonuclear discordance suggests renewed admixture at the base of the modern Victoria Radiation.

Alternatively, the two generalist groups could appear as sister clades to the Victoria Radiation in the nuclear tree because of either (i) geographical isolation or (ii) introgression from another lineage into the generalists. We can exclude alternative (i) because we have sampled the Southern Generalists <100 m from the shore of Lake Victoria in a small stream flowing into the northeastern Mwanza Gulf, where most of our Victoria Radiation cichlids have been sampled (table S4). The Northern Generalists have been sampled in Lake Kyoga at the exact same sites as the radiation members from Lake Kyoga. Alternative (ii) does not explain our data either. The Southern Generalists show a higher Congolese ancestry proportion and longer Congolese ancestry blocks compared with Western Rift lake cichlids (fig. S4), which would be in line with a second Congolese introgression event into the Southern Generalists. However, the higher Congolese ancestry is shared with all Victoria Radiation members, and the Congo-Nilotic local ancestry is highly correlated across the genome between Southern Generalists and the Victoria Radiation (fig. S4D). These findings support that the Congolese introgression was into their common ancestor and does not constitute recent Congolese introgression into the Southern Generalists after the latter split from the members of the radiation. In line with a renewed hybrid origin of the Victoria Radiation as supported by the admixture graph (Fig. 4), the Upper Nile ancestry proportion of the Victoria Radiation is intermediate between that of the Southern Generalists and the Western Rift lake cichlids (fig. S4A).

F-branch analyses reveal excess allele sharing of the Victoria Radiation with Western Rift lake cichlids (fig. S5). Fine-scale tests of admixture show that all Victoria Radiation members and the Northern Generalists show similar levels of strongly elevated allele sharing compared to all Western Rift lake cichlids (fig. S7), most strongly with cichlids from Lakes Edward and Kivu. Because all Victoria Radiation members, but not the Southern Generalists, share the same signature of gene flow from the Western Rift lake cichlid lineage, this gene flow must have occurred into the immediate ancestor of the entire Victoria Radiation after it split from the Southern Generalists. Such a scenario is also supported by the admixture graph model (Fig. 4A). Hence, we infer that when the modern lake filled, the modern radiation evolved inside the lake through renewed adaptive radiation from a hybrid swarm (Fig. 3) between two lineages of *A. nubilosa*-like swamp-dwelling generalists and cichlids derived from the Western Rift lineage that likely arrived through range expansion via the Katonga river swamp divide. The only LVRS cichlid inhabiting this swamp now is *A. kantonga*, phenotypically another *nubilosa*-like generalist (30). All three

lineages that seeded Lake Victoria are descendants of the older Congo–Upper Nile hybrid lineage. Given that the Southern and Northern Generalists show deeply divergent mitochondrial lineages not found outside the Lake Victoria basin, both may have survived the lake desiccation period in separate swamp refugia south and north of modern Lake Victoria.

Phylogenomic structure within the Victoria Radiation

To investigate how the radiation unfolded, we analyzed the phylogenomic relationships among Victoria Radiation members. Our 288 genomes (120 species) of the Victoria Radiation span all known genera and ecomorphs, except the extinct scale eater *Allochromis wellcomei*. To ensure that the genetic structure we study reflects adaptive radiation and not geographical variation and that phenotypically and genetically differentiated groups are biological species, we emphasized sympatry in our sampling design: We sampled as many species as possible in geographical sympatry in the south-east region of the lake (northern Mwanza and western-most Speke Gulf). The cichlid communities in these regions are species rich and well studied (11, 13, 31–34). Most of the species are widely distributed in the lake (11, 35). Notably, many of the species that form these rich communities rarely if ever occur in species-poor communities, which are confined to river inlets with turbid water and peripheral wetlands. Our 80 species from that region represent nearly the complete regional assemblage and 13 of the 14 ecomorphs. Additionally, we sequenced six species from the opposite extreme of Lake Victoria in the north and 15 species from Lake Kyoga, where again we sampled several species sympatrically. Hence, we simultaneously maximized sympatric sampling and sampling across the largest possible geographic distance in the system. For 52 of the 80 species from the southeast, we sequenced multiple individuals. With five exceptions, we find that these phenotypically delineated sympatric taxa form well-supported, reciprocally monophyletic clades in the nuclear phylogeny (Fig. 3, fig. S2, and supplementary text). We thus extend earlier results (36, 37) that Victoria Radiation species are reciprocally monophyletic groups maintained in sympatry and reliably diagnosed phenotypically by the combination of male nuptial coloration and morphology.

Based on nuclear genomes, species of the Victoria Radiation cluster by genus and ecomorph (Fig. 3 and fig. S8). Four of the ecomorphs and five genera form specific monophyletic clades. The other multispecies genera are composed of one or two well-supported clades and a few phylogenetically dispersed species (Fig. 3 and figs. S2 and S15). Genus explains nearly twice as much genetic variation (3.8%) as ecomorph (2.1%) in an analysis of molecular variance

(AMOVA) among the 114 species phenotypically assigned to an ecomorph and a genus (277 samples; table S2) (14).

In MDS analyses of our genomic data, species from Lakes Victoria and Kyoga cluster together by genus and ecomorph, supporting that these two lake assemblages share a single adaptive radiation origin. For instance, all sequenced piscivores (11 individuals of five species from Lake Victoria and 10 species with one individual each from Lake Kyoga) cluster together (fig. S8), which indicates that morphologically specialized piscivores emerged only once in this radiation and subsequently

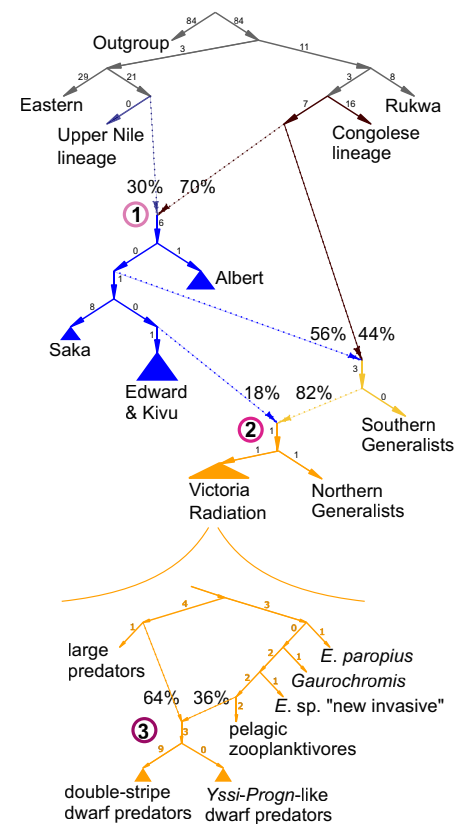


Fig. 4. Admixture graphs and f_4 quartet tree support four lineage fusion-fission cycles. An admixture graph model of the Lake Victoria region radiations (1) confirms the hybrid origin of the entire LVRS (15) and (2) suggests a hybrid origin of the Victoria Radiation. Dashed arrows indicate admixture edges with ancestry proportions as percentages. Solid arrows and corresponding numbers indicate drift. In addition, we find evidence for admixture within the Victoria Radiation having given rise to new ecological groups (3). An admixture graph model of the dwarf predators and their relatives suggests a shared hybrid origin of both dwarf predator groups. The two most divergent dwarf predator subclades are inferred to share a hybrid origin between large predators (*Harpagochromis* or *Prognathochromis* spp.) and *Yssichromis* zooplanktivores (see also fig. S13).

spread and diversified in and across both lakes. The divergence between piscivore species or that between egg and fry eaters (paedophages) sampled in the south of Lake Victoria and species of the same guilds sampled in the north of Lake Victoria or in Lake Kyoga is comparable to the divergence between sympatric species within either of these guilds sampled within either region (fig. S9). This indicates that gene flow in sympatry does not have a measurable effect on relatedness in our dataset.

Resuspension of old admixture variation facilitated rapid radiation across a food web

Many of the ecomorphs found in the Victoria Radiation also occur in the Western Rift lakes (Fig. 1). Given that the hybrid ancestry of the Victoria Radiation contains a Western Rift lineage genetic component (Fig. 3, Fig. 4A, and fig. S7), we hypothesized that alleles from Western Rift cichlids facilitated the explosive evolution of the ecomorphs in the Victoria Radiation. If so, we would predict that Victoria Radiation species share more alleles with Western Rift lake species of the corresponding ecomorph category than with ecomorphologically different Western Rift lake species. Although most genomic sites cluster the species clearly by lake irrespective of ecomorphology (Fig. 5A), the f_4 test compares the frequencies of two different alternative topologies in which species from different lakes cluster together (topologies 2 and 3 in Fig. 5A and table S6). In 64 of 120 comparisons, the f_4 test is positive, which indicates weak excess allele sharing of Lake Victoria cichlids with rift lake species of corresponding ecomorphs (Fig. 5B and table S6). Such allele sharing is strongest among members of the more anatomically specialized ecomorphs that are shared between lakes, most strongly so when piscivores or paedophages are included in the contrast and weakest or none among species of the morphologically generalized insectivores.

These findings are consistent with the evolution of morphologically specialized ecomorphs in Lake Victoria through selection on alleles derived from a Western Rift lineage that contributed to the hybrid swarm at the origin of the Victoria Radiation. To test whether, alternatively, parallel selection on alleles that were already segregating in the generalist ancestors of the Victoria Radiation could also explain this pattern, we assessed whether ecomorph-associated alleles are found in the Northern and Southern Generalists. We extracted single-nucleotide polymorphisms (SNPs) with an allele frequency difference of at least 0.9 between a specific ecomorph and all other cichlids of the Victoria Radiation (Fig. 5). For all of those sites, we checked whether the ecomorph-associated allele was present in the Southern Generalists, the Northern Generalists, or in the Western Rift lake cichlids. Only at a minority of sites (mean

16%, range 1.4 to 39%) was the ecomorph-associated allele absent in all three (Fig. 5D), which indicates that only a minority of radiation-relevant alleles might have evolved *de novo* in Lake Victoria. In four ecomorphs, all at the trophic level of algivores, the ecomorph-associated alleles were enriched for alleles being present only in either the Southern or the Northern Generalists (Fig. 5D). Conversely, three ecomorphs at the third trophic level and both top predator ecomorphs showed enrichment for ecomorph-associated alleles that were absent in Southern and Northern Generalists and were only found in Western Rift lake cichlids. This was especially strong for the piscivores (Fig. 5D). This suggests that the explosive radiation across the food web in Lake Victoria was likely only possible because of hybridization between the three founder lineages. Without the hybridization with the Western Rift lake cichlid lineage, the piscivory-associated alleles and, more generally, alleles associated with higher trophic levels would likely have been absent in the ancestors of the Victoria Radiation, but most of the algivory-associated alleles would be missing had the Victoria Radiation been seeded by cichlids from the Western Rift lineage alone (Fig. 5D). Despite their longer evolutionary history, algivores are ecomorphologically much less specialized in those lakes compared with those in Lake Victoria (13, 19).

Next, we tested whether the piscivore-associated alleles in Lake Victoria are also associated with piscivores in the Western Rift lake radiations. There are 21 piscivore-associated SNPs also sequenced in piscivores in Lakes Albert and Kivu. At 15 of these SNPs, the piscivore-associated allele is also found in Lake Kivu, and at four of those (26.7%), it is also associated with piscivores in Lake Kivu (fig. S10 and table S7). Similarly, at 14 of these SNPs, the piscivore-associated allele is present in Lake Albert, of which three are also enriched in piscivores of Lake Albert (21.4%). Many of the piscivore-associated alleles in the Victoria Radiation may therefore represent very old variants that have already been involved in the making of piscivorous cichlid ecomorphs in older radiations. Similarly, at 121 of 224 SNPs associated with paedophages in the Victoria Radiation and sequenced in both paedophages of Lakes Edward and Kivu, the paedophage-associated allele is also found in the Edward-Kivu radiation (54.0%; fig. S11). At 20 of those SNPs, the same allele is also overrepresented in the Edward-Kivu paedophages (16.5%). Exploring the other end of the food web, we find 30 SNPs associated with morphologically highly specialized epilithic algae browsers (*Neochromis* spp.) in the Victoria Radiation (fig. S12). Twenty-eight of those SNPs are located in a 38.4-kilo-base pair (kbp) region on chromosome 11 (tilapia chromosome 10). Our “*Neochromis*” individual

of Lake Albert is homozygous for the *Neochromis*-associated allele at three of those SNPs. Although the *Neochromis*-associated allele is absent in the Southern Generalists at all SNPs on chromosome 11, one of our Northern Generalist individuals (“*Astatotilapia*” sp. “cherry fin”) is homozygous for the *Neochromis*-associated allele across the 38.4-kbp region. This does not seem to be due to recent gene flow because this individual does not show genome-wide excess allele sharing with *Neochromis* compared with other Northern Generalists. At one of the two SNPs on other chromosomes, the *Neochromis*-associated allele is also associated with the unspecialized algae browsers in Lake Kivu and shared with the Southern Generalists (chromosome 12; fig. S12). The rapid emergence of the highly specialized algae browsers of Victoria thus might not have been possible with only Southern Generalist ancestry, but the combination with Northern Generalist ancestry through hybridization would have made it possible.

Our results are most consistent with at least two refugial lineages from a likely predesiccation Victoria Radiation and a Western Rift lineage that hybridized upon colonization of Lake Victoria after its refilling 16,000 years ago and provided critical genetic variation that facilitated the rapid radiation up (piscivores, paedophages, specialized insectivores) and down (various algivores, plant eaters, detritivores) the food web starting from nubila-like generalists (Fig. 6). It is likely that most alleles did not arise in these seeding lineages of the modern Victoria Radiation but represent preexisting variation from earlier radiations. Many alleles can be traced back to the Congolese or Upper Nile lineages that had previously merged into the ancestor of the entire LVRS (Fig. 5E). Although each refugial lineage alone had retained only a fraction of the original admixture variation, their merging into a single hybrid population in the new lake released much of that admixture variation again into segregation (Fig. 5F). Just like the onset of the entire LVRS <350,000 years ago (table S1), the onset of the Victoria Radiation <16,000 years ago is thus again characterized by the fusion of multiple lineages into a hybrid swarm, followed by splitting into many species, hereafter referred to as a lineage fusion-fission cycle (lineage fusion-fission level 2 in Fig. 3) (38).

Alternative scenarios for the origin of the Victoria Radiation are less well supported by our results (see table S3 for a comparison of six alternative scenarios). One alternative scenario might be that the Victoria Radiation was seeded by representatives of several different ecomorphs from Western Rift lakes and that ongoing low levels of gene flow in Lake Victoria explain their apparent nuclear monophyly. However, this scenario is inconsistent with the deeply divergent mitochondrial lineages in the Victoria Radiation and the Northern

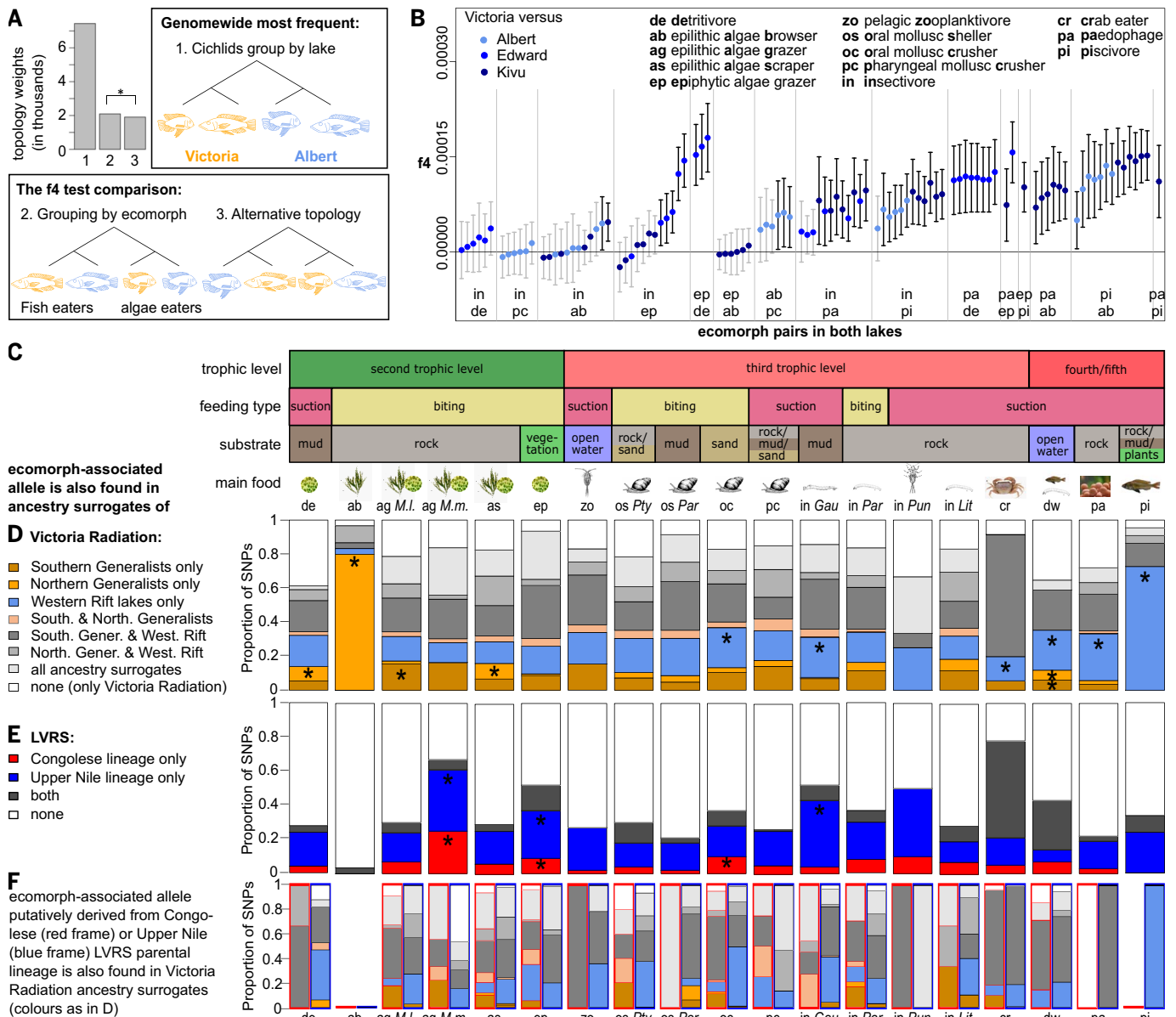


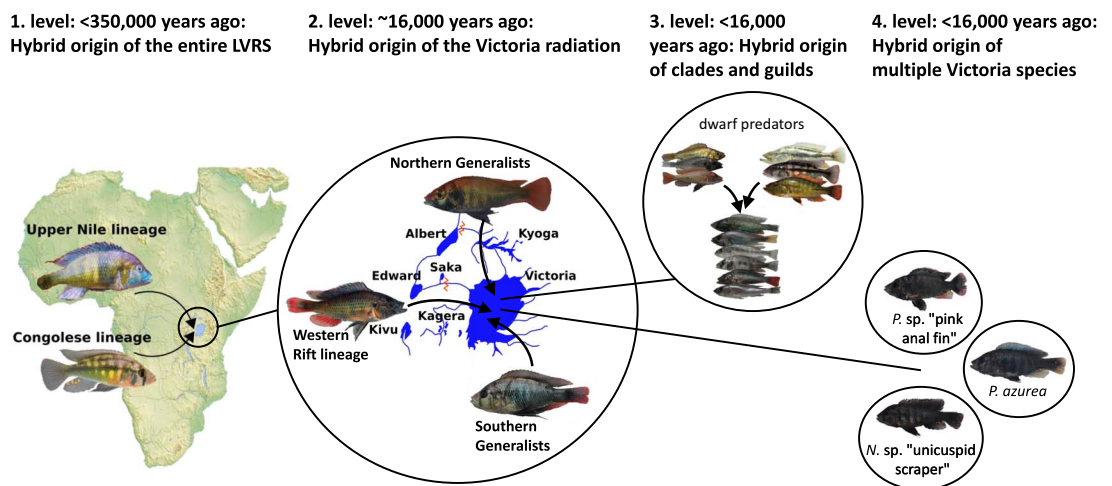
Fig. 5. Explosive trophic radiation in Lake Victoria through reuse of refueled admixture variation. (A) Victoria Radiation ecomorphs show slight excess of allele sharing with cichlids of the same ecomorph in Western Rift lakes. Among the three possible topologies with two pairs of corresponding ecomorphs from different lakes, in most 50-kb windows, the ecomorphs group by lake (topology 1). However, of the two other topologies, the topology grouping species by ecomorph (topology 2) is slightly more frequent than the alternative topology (topology 3) (t test; $*P = 3.8 \times 10^{-7}$). (B) Many Victoria Radiation members show slight excess allele sharing with species in the corresponding ecomorphs of the Western Rift lakes. The f_4 test compares the number of SNPs supporting topology 2 or 3 [see (A)]. In many comparisons, the f_4 test is positive, consistent with assembly of ecomorphs in Lake Victoria by sorting of admixture variation from the rift lake lineage. Error bars show three standard deviations from the mean (black if above zero). The ecomorph pairs are indicated at the bottom and are sorted by increasing ecomorphological specialization. For nonmonophyletic ecomorphs, each clade is tested separately (table S6). (C) Ecological multidimensionality of the ecomorphs. (D) Most ecomorph-associated alleles are found in at least one ancestral lineage surrogate (Southern Generalists, Northern Generalists, Western Rift lakes) and have thus likely not evolved newly in the Victoria Radiation. The proportion of SNPs in different putative ancestry

categories is shown in different colors. Some ecomorphs show a high proportion of ecomorph-associated alleles that are only found in one of the ancestral lineage surrogates. For the three categories of ecomorph-associated alleles shared with only one of the ancestor surrogates, we tested whether the category is overrepresented (asterisks indicate that the observed value exceeds the top 5% of resampled SNPs). For ecomorphs that are not monophyletic, each monophyletic group was tested separately. *M.I.*, *Mbipia lutea*; *M.m.*, *M. mbipi*; *Par*, *Paralabidochromis*; *Pty*, *Ptyochromis*; *Gau*, *Gaurochromis*; *Lit*, *Litochromis*. (E) Following the same approach as in (C), we found that a large proportion of the ecomorph-associated alleles is also present in our LVRS ancestry surrogates of the Congolese and Upper Nile parental lineages, indicating that these ecomorph-associated alleles stem from the original hybrid swarm that gave rise to the entire LVRS. (F) The ecomorph-associated alleles found among the LVRS parental lineages specifically in the Congolese (red frame, left) or the Upper Nile lineage (blue frame, right) are shown with proportions of SNPs in each ancestry category of Victoria Radiation ancestry surrogates. The Congo-Nilotic alleles that were combined in the LVRS ancestor through admixture were more recently combined again in the resuspended admixture variation at the base of the Victoria Radiation, facilitating the rapid emergence of immense ecological and phenotypic diversity within just 16,000 years.

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Fig. 6. Lineage fusion-fission dynamics in the history of the Lake Victoria Radiation.

Genomic analyses support four levels of lineage fusion-fission events in the evolutionary history of the Victoria Radiation: The entire LVRS is derived from hybrid origin between Congolese and Upper Nile lineage cichlids—i.e., all radiations in the Western Rift lakes and Lakes Victoria, Kyoga, Kagera, and Saka and some cichlids further downstream of the Nile (level 1). Hybrid origin of the Victoria Radiation after the lake refilled 16,000 years ago (level 2). Hybridization among Victoria Radiation members gave rise to new ecological groups (level 3) and hybrid species with novel trait combinations (level 4). [Photos by Adrian Indermaur (Congolese lineage), Erwin Schraml (Western Rift lineage), M.D.M. (Northern Generalists), Frans Witte/Hest and M.D.M. (large predators), and O.S. (all others).]



Generalists that are not shared with the Western Rift lake cichlids nor with any other cichlid radiations. It is more likely that these mitochondrial lineages stem from generalists that survived the Pleistocene dry period in swamps within the Lake Victoria basin, as indeed is the case still today. Such refugial populations of generalists may represent populations that emerged from the fusion of several specialized ecomorphs of a predesiccation Victoria Radiation and may thus carry many ecologically relevant alleles that had already been tested by natural selection in the past. The excess allele sharing of the Victoria Radiation with Western Rift lake cichlids suggests that some migrants from the Western Rift have contributed to the ancestry of the Victoria Radiation, but highly consistent Western Rift ancestry proportions across Victoria ecomorphs (fig. S7) is most consistent with a Western Rift lineage contribution before or right at the onset of the radiation and is inconsistent with Western Rift ecomorphs having colonized and persisted in Lake Victoria independently.

Syngameon conditions facilitated further evolutionary novelty

We find that like many other recent radiations (39), Lake Victoria cichlids form a so-called syngameon—a complex of species interconnected by hybridization that is sufficiently rare for species to remain distinct in sympatry (fig. S17). Our data also support the syngameon hypothesis for adaptive radiations (40), which predicts that recurrent hybridization between nonsister species of a radiation facilitates further diversification. We will illustrate this in one example. A fineSTRUCTURE analysis revealed a strong signal of admixture at the clade level in pelagic dwarf predators (fig. S13 and lineage fusion-fission level 3 in Fig. 3), an ecomorph that is specific to the Victoria Radiation—i.e., not shared with the Western

Rift radiations. Dwarf predators are sister to the large piscivores in the nuclear phylogeny (Fig. 3) but resemble pelagic zooplanktivores in body shape, size, and habitat occupation. We sequenced nine species, and all show the same signature of hybrid ancestry between piscivores and pelagic zooplanktivores (Fig. 4 and fig. S13). An admixture graph analysis with the dwarf predator clade split into the two most divergent subclades (*Yssichromis-Prognathochromis*-like and double-stripe group) suggests that both groups share the same admixed ancestry with 64% piscivore ancestry and 36% zooplanktivore ancestry (Fig. 4). Different species of dwarf predators represent novel unique mosaics of traits from the parental lineages: Some resemble morphologically zooplanktivorous *Yssichromis* but either have longer jaws or very elongate bodies; others resemble piscivorous *Prognathochromis* but are tiny; yet others have been described as intermediate between these genera [*Haplochromis argens* (41) or taxonomically ambiguous [double-stripe group (42)]. All live in open water, but some species live inshore over sand or rocks, whereas others live far offshore. This large morphological and ecological variation is in line with differential sorting of the parental alleles facilitating this so-called radiation in a radiation of small pelagic predators (lineage fusion-fission level 3; Fig. 3).

There are also indications that hybridization between nonsister taxa has spurred the origin and subsequent radiation of additional ecological guilds (supplementary text), such as the rock-picker clade species that eat chironomid midge larvae living in epilithic algae beds. Most rock-picker species cluster with epilithic algae browsers (*Neochromis*) in the concatenated tree but with morphologically specialized benthic invertebrate eaters (*Paralabidochromis*) in the quartet tree (figs. S14 and S16), and they combine morphological traits of both genera (43).

At the species level, we find many additional signatures of admixture among nonsister species (lineage fusion-fission level 4; Fig. 3, Fig. 6, and fig. S17). In particular, many species that cluster away from their morphologically determined genus in our concatenation tree (Fig. 3) show excess allele sharing with members of the major clade of that genus (supplementary text) and often cluster with it in the quartet analysis (fig. S14). Many of these admixed species contribute to very dense niche packing: Taxa with signatures of intergeneric admixture often fill ecomorphological space between their respective parent genera (supplementary text). Finally, we find evidence for recurrent gene flow from the swamp-dwelling Southern Generalist *A. nubila* into the Victoria Radiation (fig. S17 and supplementary text).

Cycles of lineage fusion and fission spur explosive adaptive radiation

Theory predicts that cycles of lineage fusion and fission can facilitate retention, resuspension, and reuse of old genetic variants over very long periods of time (25, 38, 44, 45). If an ecologically relevant haplotype is lost in one species because of drift or selection, it may still be present in other species experiencing independent drift and different selection. As long as the species retain the opportunity to hybridize and produce fertile hybrids, once-lost haplotype variation can be resuspended into segregating variation through admixture (25). In much the same way that metapopulation dynamics facilitate the retention of genetic variation in spatially structured metapopulations (46–48), our data support evidence for meta-species-flock dynamics [syngameon dynamics (39, 40)] to maintain and restore genetic variation crucial for adaptive radiation.

In the geologically unstable environments of the Lake Victoria region, lineage fusion-fission dynamics likely facilitated the rapid recovery of

species richness, ecological diversity, and food web structure through adaptive radiation after periods of extinction and collapse (Fig. 6) (2). It has been hypothesized previously that Pliocene-Pleistocene climatic fluctuations leading to geographic range splitting and reconnection may have facilitated speciation [a so-called speciation pump (49–52)]. In most taxa that have been studied in this context, bursts of diversification coincide with periods of isolation—e.g., by divergence between glacial refugia (53), sky islands (54), rainforest refugia during dry periods [(49), but see (55)], or oceanic islands during low sea levels (56, 57). In contrast to many of these studies, we show that orders-of-magnitude more diversification is associated with periods of coming together, fueled by genetic admixture and ecological opportunity. Admixture upon secondary contact may have facilitated further diversification in some of those other systems too, but this remains unstudied in most cases [but see (54)]. The role of hybridization in such range dynamics may thus be underestimated.

In archipelagos of multiple islands, colonization of new islands and admixture between species from radiations on older islands would facilitate the recurrent evolution of similar species on the newer islands [e.g., Darwin's finches (58), Hawaiian *Cyrtandra* plants (59), or Hawaiian silverswords (60, 61)]. Although in these systems there is evidence for admixture variation having facilitated diversification, it remains to be studied whether there were also cycles of lineage fusion and fission involved as we describe them here.

We propose that cycles of lineage fusion and fission are key to explaining why the cichlids of the LVRS predictably undergo adaptive radiations rapidly in every lake. More generally, we propose that once one radiation has occurred, be it slowly in a phase of lasting habitat stability or rapidly after hybridization, subsequent radiations will be facilitated by the richness of ecologically relevant genetic variants now present in the different species as long as the radiation members retain the ability to reshuffle and recombine those variants through hybridization. Lineages that have relatively recently undergone an adaptive radiation are thus particularly prone not only to undergo fusion (62) but also to radiate again from out of the fused population (63), exacerbating the differences in diversification rates between groups of taxa. To this end, the variation in radiation propensity or evolvability is not a property of any one species but that of an evolving flock of species.

Our results have implications for the conservation of the endemic cichlids of the African Great Lakes and likely also for other species radiations. The entire LVRS species flock is highly threatened by the combined effects of anthropogenic eutrophication, habitat mod-

ification, species introductions, and climate change. Current conservation efforts are strongly oriented toward the preservation of individual species rather than the species flock as a whole; yet, the secret to conserving the future potential for the evolution of new species and new radiations lies in conserving the species flock community as a whole. A serious rethinking of conservation interventions and strategies is in order, particularly with regard to the value of natural hybrid populations that are often dismissed as detrimental or evolutionary dead ends in single-species perspectives—a view that, according to our results, could jeopardize the key property of this species flock to diversify repeatedly through rounds of hybridization (lineage fusion) and speciation (lineage fission).

Materials and methods

Taxonomic sampling

We sampled haplochromine cichlids in the Lake Victoria region from all major lakes with evidence of adaptive radiations and from several lakes and wetlands that used to be or are still connected to the Nile drainage system. We sampled multiple species of each major radiation to represent the full ecological diversity of haplochromine cichlids in each of the lakes. Several lakes in the region could potentially have contributed colonists to the colonization of Lake Victoria after its Pleistocene desiccation and could hence have contributed to the seeding of the rapid radiation that followed. The deeper rift lakes, Kivu or Edward, likely did not completely desiccate during the Pleistocene dry spell (64–66) and thus may still harbor older lineages, possibly dating back to the first radiation after the original Congo-Nilotic hybridization event (15). The Kagera lakes region upstream and to the west of Lake Victoria, in the uplands between Tanzania and Rwanda, might have harbored open water bodies during the dry spell because it is located at higher elevation [1300 m above sea level (67)] and received more rainfall. Some samples were obtained from collaborators, but most samples were collected by the authors using gill nets, seine nets, trawl nets, or hook and line. Fish were euthanized with an overdose of MS-222. All sampling was done under the relevant collection permits and in compliance with national and international guidelines for ethical treatment of animals. Identification of most samples was done by OS (table S4).

Whole-genome sequencing

We extracted DNA from fin clips with a standard phenol-chloroform method (68) and generated PCR-free Illumina libraries following Meier *et al.* (69). We sequenced the libraries to a mean depth of 21.7x (range: 9 to 49x) with 150-bp paired-end reads generated on HiSeq

3500 (Illumina Inc.) at the NGS platform of the University of Bern.

We mapped the reads to the *Pundamilia nyererei* reference genome version 2 (70) with Bowtie2 v 2.3.3 (71) using the local alignment mode (-local) with default options allowing for one mismatch in seed alignment (-N 1). Genotypes and variants were called with GATK v. 3.5 (72). First we used Haplotype Caller to generate for each individual a gvcf file with all sites (-ERC BP_Resolution) where the base quality was at least 20 (-stand_call_conf 20.0) and emit variants with call quality of at least 30 (-stand_emit_conf 30.0). Next, we combined all gvcf files with GATK GenotypeGVCFs to a single vcf file, calling only variable sites (default option).

The resulting vcf file was filtered with vcfutils v. 1.16 (73) to remove genotypes with less than six reads or a genotype quality below 20. Indels (insertions and deletions) and sites with more than 50% missing data were removed. Sites showing evidence of paralogous regions collapsed in the reference genome were removed by computing the mean sequencing depth across all individuals for each site with vcfutils. We then computed the mean and interquartile ranges across all sites. Sites that exceeded the mean plus 1.5 times interquartile range were removed. In addition, we masked sites with more than one 35-kmer self-mapping in the reference genome using the SNPable tool with stringency 0.5 (74), as well as regions identified as repetitive by a default run of RepeatMasker v. 4.0.6 (75).

Phylogenetics

To infer a nuclear genome phylogeny, we used the vcf file of all individuals and thinned it to a minimum distance of one site per 1 kb with vcfutils v. 1.16 (-thin 1000) (73). The thinning was performed to allow faster running of IQtree but also to obtain a genome-wide summary that is less affected by single genomic regions with strongly different histories (e.g., introgressed inversions or regions under strong selection). Sites on the mitochondrial genome were removed. We converted the resulting vcf file to a phylip file with a custom script (<https://github.com/joanam/scripts/blob/master/vcf2phylip.py>). Next, we used IQtree v. 2.1.1 (76) to infer the best site model with ascertainment bias correction (option -m GTR+ASC) and to reconstruct a maximum likelihood phylogeny with 1000 ultrafast bootstraps (77). We ladderized the tree with the R package ape v. 5.5 (78). Next, we plotted this nuclear phylogeny as circular tree using the R package ggtree v 3.14 (79). We visualized color-coded genus and lake information in circles around the tree using “geom_fruit” and species with tip circle colors using “geom_tippoint” of ggtree.

For the mitochondrial phylogeny, we used full mitochondrial genomes including monomorphic

sites. This required generating a vcf file with GenotypeGVCFs from GATK v. 3.8.1 (72) with the-ERC_BP_Resolution option for all mitochondrial genome sites (-L chrM). We set genotypes with less than five reads as missing and removed sites with more than 50% missing data. We then converted the mitochondrial vcf to phylip and ran IQtree as detailed above for the nuclear phylogeny but by using the GTR model. We then compared the mitochondrial and the nuclear trees by plotting them side by side as a co-phyloplot. For this, the trees were read into R and prepared for optimal comparison with the R package ape v. 5.5 (78). The most divergent outgroups (*Astatoreochromis alluaudi*, *Pseudocrenilabrus*, *Thoracochromis brauschii*) were removed with the function “drop.tip,” and the trees were rooted with “root” and the option “edgelabels=T.” Next, the trees were ladderized with “ladderize,” and the tip labels were replaced by species names. Using the R package phytools v. 0.7-70 (80), we combined the two trees with the function “cophylo,” whereby the mitochondrial tree was rotated to optimize matching with the nuclear tree. The trees were then plotted facing each other with the function “plot.cophylo” and the positions of each sample in the two trees were linked with a curved line in a color reflecting the lake. Symbols indicating bootstrap support were added with “nodelabels.cophylo.”

To obtain a dated mitochondrial phylogeny, we ran BEAST v. 2.6.7 (81) on a subset of five individuals per radiation to get a reasonably balanced tree. We added Lake Malawi samples for tree calibration downloaded from the NCBI Short Read Archive and mapped them to the *P. nyererei* genome as detailed above. We converted the vcf file to phylip with a custom Python script (<https://github.com/joanam/scripts/blob/master/vcf2phylip.py>) and converted it to fasta with custom awk code (awk “NR>1{print ‘>\${1}\n’\$2}” \$file.phylip > \$file.fasta). Next, we ran partitionfinder (82) to infer the best partition scheme of all mitochondrial genes, whereby the first, second, and third codon positions of all exons were given separately. This resulted in 27 partitions, each modeled separately in BEAST. The mitochondrial data were read into Beauti to specify a calibrated Yule tree prior, a relaxed clock model, and normal priors on the crown of the Malawi radiation and of the Malawi-Victoria split using five calibration sets following Meier *et al.* (83), as given in table S1. The Markov chain Monte Carlo (MCMC) chain length was set to 10 million with a pre-burnin of 100,000, and trees were logged every 20,000 steps. As suggested by the first BEAST run, the subtree slide size was set to 0.733 for the calibrated Yule model. We used TreeAnnotator v. 2.6.7 of the BEAST2 package to compute confidence intervals for the radiation nodes with a posterior probability limit of 0.8. We checked whether all ESS values were above 200 and

whether two independent runs had converged with Tracer v 1.7.1 (84). The calibrated trees were visualized in FigTree v1.4.4 (<https://github.com/rambaut/figtree/releases/tag/v1.4.4>).

Because concatenated nuclear phylogenies cannot account for incomplete lineage sorting or gene flow, we additionally performed a quartet analysis to infer a species tree that is slightly less affected by incomplete lineage sorting. With a dataset thinned to 1 SNP per 500 bp (vcftools-thin 500), we inferred the number of ABBA and BABA patterns for all species triples within the Victoria Radiation and for comparisons with the other lake radiations using Dsuite v. 0.4 (85). We specified *Astatotilapia burtoni* as outgroup. Using our Dsuite output, we calculated quartet support as the proportion of SNPs, summed to 100%, that supported each of three possible topologies for each combination of three taxa plus our outgroup using a custom R script. We then used our weighted quartets as input to wQFM (86), which calculates a species tree topology based on weighted quartets. To compare the quartet species tree with the concatenated nuclear phylogeny, we created co-phyloplots with the R packages ape and phytools, as described above.

Analyzing genomic variation in the LVRS

To study genomic variation among LVRS samples, we generated MDS plots for the entire LVRS and specific radiation subsets. We converted the 1-kb thinned vcf file to a gds file with the R package SNPRelate v. 1.26 (87). Next, we computed the genetic distance matrix with the function “snpgdsIBS” from and used “cmdscale” from the stats v. 4.1.1. R package to perform MDS. The MDS results were then plotted with convex hulls visualizing the MDS space occupied by each ecomorph or genus. For this, we used the “chull” function of the grDevices package v. 4.4.1 to obtain the coordinates of the convex hulls and plotted them onto the MDS plot with the “polygon” function of the graphics package v. 4.4.1.

To test the effect of sample size on the position of the Victoria Radiation relative to the Southern and Northern Generalists in the MDS, we reran the MDS analysis with 1000 different sets of four randomly sampled individuals each of the Victoria Radiation, the Northern Generalists, the Southern Generalists, and the Lake Kivu radiation. For each group, we inferred the convex hulls with the “chull” R function as above and checked whether the convex hull of the Victoria Radiation overlapped with that of the two Generalist groups using the “st_intersection” function of the “sf” R package v. 1.0.3 (88).

To test how much genomic variance within the endemic radiation of Lake Victoria was explained by genus or ecology, respectively, we ran a nested Analysis of Molecular Variance (AMOVA). We selected all Victoria Radiation

species with known ecomorph and genus assignment and at least three individuals sampled. We used one million bi-allelic SNPs randomly sampled from a vcf file filtered for a mean sequencing depth between 20 and 40 with vcftools v. 1.16 (73). The “poppr” R package (89) was used to run AMOVAs with species nested in genus or in ecomorph. To assess significance, we ran 999 permutations of the sample matrix as a null distribution to compute empirical *P* values.

Tests of admixture

We tested admixture at different levels: (i) at the onset of the LVRS, (ii) at the origin of the Victoria Radiation, and (iii) among Victoria Radiation members.

Testing for admixture at the onset of the LVRS

First, we tested whether our data corroborate the Congo-Nilotic hybrid origin of the entire LVRS of cichlids (15) and whether the many additional taxa sampled in this work all show the same admixture proportions. We computed D statistics with ADMIXTOOLS v. 4.1 (90) to test for excess allele sharing of each LVRS taxon (P1) with the Upper Nile lineage representatives (P2) as sister group to the LVRS taxa, and *A. burtoni* as the outgroup (all tests are given in table S5). To infer ancestry block sizes, we computed f_d statistics and counts of ABBA, BABA, and BBAA sites (91) with these four taxa in sliding windows of 10 kb. Windows with less than five ABBA, BBAA, and BABA sites were discarded. To determine whether the Upper Nile introgression found in all LVRS groups is due to a single shared ancestral admixture event or due to independent admixture events into different groups, we computed the proportion of BABA sites (allele shared with Upper Nile) among BABA + BBAA sites (allele shared with the Congolese lineage) across 10-kb windows for each LVRS group. We then tested for a correlation of the BABA/(BABA + BBAA) proportion of different LVRS groups across 10-kb windows with a linear model with the “lm” function of the “stats” v. 3.6.2. R package. A single admixture event with some degree of genome stabilization (fixation of ancestry blocks) before splitting into different groups should lead to high correlation, whereby the same windows would show high or low Upper Nile ancestry proportion in different LVRS groups. Next, we tested whether any of the LVRS groups showed more recent Upper Nile or Congolese lineage introgression, which should lead to larger ancestry blocks derived from that lineage. Following Meier *et al.* (15), we classified windows with BABA/(BABA + BBAA) > 0.7 as Upper Nile origin, and windows with BABA/(BABA + BBAA) < 0.3 as Congolese ancestry windows. Ancestry tracts were defined as consecutive sliding windows of the same category ignoring

single sliding windows without data. A peak of long Upper Nile or Congolese ancestry tracts indicates recent introgression from that lineage.

To estimate the Congo-Nilotic admixture proportions of the LVRS, we reconstructed admixture graphs with the “qpgraph” function of the ADMIXTOOLS 2.0.0 R package (92). Admixture graphs are models of the demographic history with drift and admixture edges connecting the populations. Model comparison and parameter inference is performed with f3-statistics, whereby the best model is the one leading to least deviation in allele sharing (f-statistics) between the observed data and the expected f3-statistics given the model. We used the fully automated graph exploration provided in ADMIXTOOLS where the user only specifies the number of admixture edges and ADMIXTOOLS infers the phylogenetic relationships between all populations, which populations are admixed, and which lineages are the relatives of the parental populations. We used block bootstrapping for model comparison, whereby each graph is evaluated multiple times on a random subset of SNP blocks.

Testing for admixture at the origin of the Victoria Radiation and admixture from other lineages outside the Victoria Radiation into specific Victoria Radiation groups

Next, we tested for another fusion-fission event at the base of the modern Victoria Radiation. To test whether, in addition to its main ancestry (from refugial populations within the Victoria catchment), the Victoria Radiation received admixture from the Western Rift lakes or Lake Saka, we computed D statistics as described above. We used different Victoria Radiation cichlid groups (monophyletic groups of the same ecomorph) or the Northern Generalists as P1, Southern Generalists (*A. nubila* from swamps south of Lake Victoria) as P2, different Western Rift lake cichlids as P3, and *A. alluaudi* as the outgroup. If only specific groups (e.g., piscivores of Lake Victoria) had received gene flow from Western Rift lake cichlids (e.g., piscivores of another lake), we would expect elevated D statistics for this group. By contrast, similarly high D statistics across all groups would indicate introgression into the shared ancestor—i.e., the lineage that seeded the Victoria Radiation.

To assess signatures of introgression between the Victoria Radiation and more distantly related groups, we computed fbranch statistics with Dsuite (85). We used a tree reconstructed with IQtree v 2.1.3 whereby each lineage or radiation is represented by the individual with least missing data and *A. burtoni* is specified as the outgroup. For computing Dstats we used a vcf file of all individuals but reduced to bi-allelic SNPs thinned for one SNP per 1 kb with vcftools. We ran “Dsuite Dtrios” to

compute f4 statistics and “Dsuite Fbranch” to compute the fbranch statistic with z scores (“-Z True”). We set all fbranch scores with $z < 3$ (nonsignificant) to zero with a custom script (<https://github.com/joanam/scripts/blob/master/removeNonsignDsuite.r>) so as to only focus on the admixture events with strong evidence of admixture. We visualized the fbranch scores as a matrix with darker red color indicating higher fbranch statistics.

In the admixture graph reconstruction described above, the Victoria Radiation and its closest relatives (Southern and Northern Generalists) were modeled as separate groups allowing to infer admixture at the base of the Victoria Radiation in the same admixture graph that also accounts for the ancestral Congo-Nilotic admixture origin of the entire LVRS.

In addition, we used fineSTRUCTURE v. 4.1.0 (93) to test for recent introgression between any individuals of the Victoria Radiation and any individuals from the other lake radiations. First, we phased the dataset with Beagle v. 4.1 (94) using the recombination map from Feulner *et al.* (70). Next, we ran fineSTRUCTURE with default parameters, again using the recombination map and specifying each individual as its own population. FineSTRUCTURE revealed strong excess allele sharing between Lake Edward and Lake Victoria piscivores. To assess whether the direction of introgression was from Victoria piscivores into Edward piscivores or vice versa, we used DFOIL v. 2017-011-25 (95). DFOIL requires five populations and can only handle a single individual per population. We thus ran the pipeline multiple times with all possible combinations of three Southern Generalist (*A. nubila*) individuals (P1), two Victoria piscivores (P2), three Edward piscivores (P3), three Kivu piscivores (P4), and two *A. burtoni* as outgroup. For each combination, we extracted the individuals from the 1-kbp pruned vcf file and converted it to fasta as explained above for BEAST. Next, we used fasta2dfoil.py of the DFOIL pipeline to get the counts of specific allele sharing patterns and ran DFOIL with these counts with the dfoilalt option to ignore singleton patterns (e.g., ABAAA). We then plotted the distributions of DFO, DIL, DFI, and DOL patterns, which represent different tests of excess allele sharing and together predict the direction of introgression (95). Lastly, we reconstructed an admixture graph with a single admixture edge as described above with Lake Edward groups, Lake Kivu groups and Victoria Radiation groups modeled as separate groups to infer the ancestry proportions of Lake Edward piscivores.

To test whether all Lake Edward piscivores are affected by introgression or only *H. squamipinnis*, we took advantage of a sample of another Lake Edward piscivore species, *Harpagochromis kimondo*, which we had previously excluded from all analyses as this sample has very low

sequencing coverage (4.8x). We called all sites and genotypes with GATK GenotypeGVCF with this sample and all LVRS members from Lakes Edward and Kivu and *A. stappersi* as outgroup. We then filtered the vcf file for a minimum genotype depth of 3x, maximum missing data proportion per site of 50%, applied the three masks as detailed above, and thinned the data to 1 site per kilo-base pair. This file was then converted to phylip format with our custom vcf2phylip.py script and ran iqtree2 as above. In addition, we ran Fbranch as detailed above.

Admixture within the Victoria Radiation

Lastly, we tested whether admixture events among Victoria Radiation members may have spurred further diversification within Lake Victoria. We ran a fineSTRUCTURE analysis as described above with all Victoria Radiation cichlids to test for recent introgression among different groups. In addition, we ran an fbranch analysis with Dsuite as described above but with each species in the Victoria Radiation separately. We used a tree reconstructed with IQtree whereby each species is represented by the individual with least missing data and *A. burtoni* is specified as the outgroup. We used the vcf file of 1-kb thinned SNPs with all individuals to compute f4 statistics in “Dsuite Dtrios.” Next, we ran “Dsuite Fbranch” to compute the fbranch statistic and visualized the significant fbranch scores as a matrix with darker red color indicating higher fbranch statistics.

One strong signature of excess allele sharing was seen between a group of small pelagic predators (“pelagic dwarf predators”) and pelagic zooplanktivores. To test whether all dwarf predator species share the same admixed ancestry, we computed the introgression statistic f_{DM} in 50-kbp window to compare how correlated the ancestry proportions are between the two most divergent groups of dwarf predators (double-stripe dwarf predators and *Yssichromis-Prognathochromis*-like dwarf predators). We computed f_{DM} with the ABBABABAwindows.py script (97) using large piscivores as P1, either dwarf predator group as P2, pelagic zooplanktivores as P3, and *A. alluaudi* as the outgroup. We then tested for a correlation across windows between f_{DM} values of the two tests with different dwarf predator groups with a linear model with the “lm” function of the “stats” v. 3.6.2. R package. Lastly, we reconstructed admixture graphs as described above with the two dwarf predator groups modeled separately and including the large piscivores, the pelagic zooplanktivores, and close relatives, in addition to *A. alluaudi* specified as the outgroup. To test for two independent admixture events, we reconstructed admixture graphs with one and with two admixture edges. We then tested which of the two admixture graphs is

better supported by running 100 block-bootstrap replicates on the two best graphs and comparing the likelihood score distributions with “fits = qpgraph_resample_multi(f2_blocks, list(bestAdmix1Graph\$edges, bestAdmix2Graph\$edges), nboot = 100)” and “compareFits<-compare_fits(fits[[1]]\$score_test, fits[[2]]\$score_test).”

Ecomorph-associated alleles

To address the question to which extent the reciprocally monophyletic cichlid radiations of different lakes use the same alleles for the parallel evolution of similar ecomorphs, we tested for excess allele sharing among ecomorphologically similar cichlids from different radiations. We computed F_4 statistics with ADMIXTOOLS v. 4.1 (90) for pairs of ecomorphs from the Victoria Radiation and the corresponding ecomorph pairs from different Western Rift lake radiations (table S6). Species of the same ecomorph in Lake Victoria were tested as a single group if they were monophyletic. For polyphyletic ecomorphs, each monophyletic group was tested independently. To compare the proportion of the genome supporting either of the three possible topologies with two pairs of corresponding ecomorphs (Fig. 5A), we inferred for each 50-kb window, which of the topology is most supported using TWISST 1.1 (96).

Next, we tested whether admixture from Western Rift cichlids was consequential for the rapid evolution of the morphologically specialized ecomorphs in the Victoria Radiation. We consider Southern Generalists and the Northern Generalists as surrogates for the generalist ancestors that would have colonized the newly formed Lake Victoria. In addition, we combine all Western Rift lake cichlids to test whether introgression from Western Rift lakes could have introduced the ecomorph-associated allele to the ancestral lineage of the Victoria Radiation. If the ecomorph-associated alleles are found in the Northern and Southern Generalists, a single generalist lineage might have sufficed to introduce the ecomorph-associated allele into the Victoria Radiation ancestor. By contrast, if an ecomorph-associated allele is absent in both generalist ancestor surrogates but is found in Western Rift lake cichlids, the introgression event from a cichlid lineage related to Western Rift lake cichlids might have introduced the allele that were likely contributed to the evolution of the ecomorph. We extracted SNPs with a minimum allele frequency difference of 0.9 between specific ecomorphs and all other cichlids of the Victoria Radiation with vcftools v. 1.16 (73). For these sites, we then computed the allele frequencies for all cichlids of the Western Rift lakes including Lake Saka cichlids and for our 11 Southern Generalists samples and the four Northern Generalists samples. We polarized the alleles as derived for the ecomorph-associated allele and assessed whether that allele is found in the

Western Rift lake cichlids, in Northern Generalists, and/or in the Southern Generalist *A. mubila*. To test whether ecomorph-associated alleles are more often shared with a specific ancestor surrogate than expected, we extracted 100 sets of SNPs matching the ecomorph-associated SNPs in number and allele frequency range. We considered putative “ancestry categories” as enriched if the observed proportion of SNPs only found in a specific ancestor surrogate was higher than the top 5% of the control SNPs sets.

Next, we checked whether the ecomorph-associated alleles were found in the Congolese and Upper Nile lineages uniquely, in both, or in neither. For this, we used the same approach as described for the Victoria Radiation ancestor surrogates. Lastly, we assessed how many of the ecomorph-associated alleles that can be assigned to either the Congolese or Upper Nile lineage are also found in the Northern and Southern Generalist lineage or the Western Rift lineage. This would reveal whether the admixture between the several seeding lineages at the base of the Victoria Radiation resuspended adaptive polymorphisms that had already been brought together once through admixture ~150,000 years earlier but had subsequently been lost in the individual refugial populations that seeded Lake Victoria.

For the most distinct ecomorphs with ecomorphologically corresponding species in other lakes, epilithic algae browsers, piscivores, and paedophages, we additionally visualized the distribution of the SNPs across the genome and assessed whether within the Western Rift lakes, the frequency of the ecomorph-associated allele is also higher in the corresponding ecomorph than in other cichlids of the same radiations. For each radiation, we computed the allele frequency difference between individuals of the corresponding ecomorph and ecologically different individuals. We tested whether this difference is greater than expected using a control dataset of SNPs with the same range of allele frequencies in the Victoria Radiation. For each Western Rift lake radiation, we computed the allele frequency difference between individuals belonging to the corresponding ecomorph and all other individuals in this control dataset. We considered a SNP to be ecomorph-associated in a radiation if its allele frequency difference was greater than the 95th quantile of the allele frequency differences in the control dataset.

D_{XY} between sympatric and allopatric species

To test whether opportunity for gene flow makes sympatric species appear more closely related, we took advantage of the fact that we have sequenced multiple piscivore species each from the Mwanza and Speke Gulf in the south of Lake Victoria, from the Napoleon Gulf on the opposite end of Lake Victoria in the far north, and from Lake Kyoga (distance from Mwanza

Gulf to Lake Kyoga sites, 490 km). We had also sequenced paedophages from the south of Lake Victoria and from Lake Kyoga that allowed for further contrasts of sympatric and allopatric species. We generated vcf files of the individual with the highest sequencing depth of each piscivore and paedophage species with GATK’s “GenotypeGVCFs” as above but using the option “-allSites” to retain monomorphic sites. We filtered the file with vcftools for maximum 50% missing data and minimum genotype depth of five reads and applied the same repeat masks as above with vcftools. We computed D_{XY} values among sympatric and allopatric paedophage species and sympatric and allopatric piscivore species with PIXY 1.2.7 (97) in a single window per chromosome. Lastly, we computed the average D_{XY} in R as the sum of all differences divided by the sum of all counts as recommended in the PIXY manual.

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ACKNOWLEDGMENTS

We dedicate this paper to our colleague, collaborator, and friend Sylvester Bwaku Wandera, known to most of us as SB. SB was chief fish taxonomist at Uganda's National Fisheries Resources Research Institute in Jinja for as long as most of us can remember. He studied cichlids and other fish in many lakes of the region and discovered many species. SB sadly passed away weeks before this paper was published. We thank C. Drögemüller, T. Leeb, P. Nicholson, and the NGS platform of the University of Bern, Switzerland, for sequencing services and support, and we thank N. Zemp, A. Minder, and the entire GDC at ETH Zürich, Switzerland, for bioinformatics support. Many thanks to the Tanzania Fisheries Research Institute (TAFIRI) for hosting O.S. and his team during fieldwork from 1989 to now; to the National Fisheries Resources Research Institute (NaFIRR) of Uganda for repeatedly hosting M.D.M. and O.S. during fieldwork; and to Makerere University Biological Field Station at Kibale for hosting O.S., L.J.C., and C.A.C. during work on Lakes Edward and Saka. Many thanks to M. Kayeba, M. Haluna, and the late R. Enoke, A. Marwa, and A. Peters for decades-long technical support and friendship during the fieldwork of O.S. and his students in Mwanza. Many thanks to O. Selz, F. Moser, J. van Rijssel, and I. Magalhaes for fieldwork at Lake Victoria; to E. Schraml for samples from Egypt; to O. Lucanus for samples from Lake Boukou; and to A. Nightingale for samples from Lake Turkana. We thank A. E. Sharafeldeen (Sudan Institute of Natural Sciences), Z. N. E. Mahmoud, M. S. Mohamedain, and M. Gedo for repeated help to facilitate travel, collecting, and export permits, and we thank A. A. S. Abdalla, M. A. Abdallah (Fisheries Research Centre Kosti), and T. Moritz (Deutsches Meeresmuseum, Stralsund) for support and cooperation in Sudan. Many thanks also to the members of the Seehausen laboratory and the Ewag

department for the many excellent discussions. **Funding:** This research was funded by Swiss National Science Foundation grant 31003A_163338 to O.S., R.B., and L.E. and the NSF grant DEB-1556963 to C.E.W. J.I.M. is supported by a St. John's College research fellowship, a Branco Weiss Fellowship at the University of Cambridge, and a Royal Society University Research Fellowship at the Wellcome Sanger Institute. **Author contributions:** J.I.M. and O.S. designed the study with support from D.A.M. and C.E.W. O.S. gathered and identified most of the cichlid samples. O.S., M.K., H.M., S.M., M.D.M., S.W., A.T.-M., J.I.M., and D.N. performed the fieldwork with support from L.J.C., C.A.C., and L.K. J.I.M., S.M., M.D.M., and D.A.M. performed the laboratory work. J.I.M. analyzed the data with support from O.S. and D.A.M. J.I.M. and O.S. wrote the manuscript with contributions from D.A.M. and all other authors. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** The raw read data have been uploaded to the Short Read Archive (SRA) under Bioproject PRJNA928336. All sample accession codes are given in table S4. Custom code and pipelines used in this study, as well as phylogenies, are available on GitHub at <https://github.com/joanam/VictoriaRegionSuperflock>. **License information:** Copyright © 2023 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.ade2833

Supplementary Text

Figs. S1 to S18

Tables S1 to S8

References (98–111)

MDAR Reproducibility Checklist

Submitted 11 August 2022; accepted 21 August 2023

10.1126/science.ade2833



Cycles of fusion and fission enabled rapid parallel adaptive radiations in African cichlids

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Science **381** (6665), eade2833. DOI: 10.1126/science.ade2833

Editor's summary

Adaptive radiation produces a great deal of diversity during the process of evolution, but not all lineages radiate, and in fact, most don't. For decades, researchers have been interested in why radiations occur and many studies have looked at this using the striking radiation of African rift lake cichlids. Meier *et al.* studied the radiations within Lake Victoria and confirmed that the radiation in this lake, covering many trophic guilds, occurred only 16,000 years ago. Furthermore, they found that the radiation was able to occur so rapidly because of a repeating process of hybridization and specialization. —Sacha Vignieri

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