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p. 470







## ADAPTIVE RADIATIONS

# The genetics of niche-specific behavioral tendencies in an adaptive radiation of cichlid fishes

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Behavior is critical for animal survival and reproduction, and possibly for diversification and evolutionary radiation. However, the genetics behind adaptive variation in behavior are poorly understood. In this work, we examined a fundamental and widespread behavioral trait, exploratory behavior, in one of the largest adaptive radiations on Earth, the cichlid fishes of Lake Tanganyika. By integrating quantitative behavioral data from 57 cichlid species (702 wild-caught individuals) with high-resolution ecomorphological and genomic information, we show that exploratory behavior is linked to macrohabitat niche adaptations in Tanganyikan cichlids. Furthermore, we uncovered a correlation between the genotypes at a single-nucleotide polymorphism upstream of the AMPA glutamate-receptor regulatory gene *cacng5b* and variation in exploratory tendency. We validated this association using behavioral predictions with a neural network approach and CRISPR-Cas9 genome editing.

The behavioral repertoire in the animal kingdom is vast (1, 2). Many behaviors are directly linked to Darwinian fitness, such as those involved in predator avoidance, foraging, mating, and parental care (3–6). Behavior can also be crucial at the macroevolutionary scale, for example, in the context of reproductive isolation, speciation, interspecific competition, and extinction (7–9). Many of these factors, and especially adaptation and speciation (10), are key components of the evolutionary phenomenon of adaptive radiation, that is, the rapid evolution of an array of species through adaptive diversification into a variety of ecological niches (11, 12). For a long time, it has thus been speculated that behavior must play an important part in animal adaptive radiation (13–15). However, although the pivotal roles of ecology and of specific morphological traits (or trait complexes) are well established for many adaptive radiations (11, 16–18), only little is known about the contribution of behavior to niche adaptation in such outbursts of organismal diversity. This is most likely due to the challenges associated with quantifying and interpreting heritable behavioral variation across species. More specifically, a phenotypic and genotypic investigation of behavior in the context of adaptive radiation requires (i) an experimental paradigm, in which the same behavioral phenotype is quantified in the exact same way across many species, and (ii) an analytical framework

that enables the association of behavioral information with high-resolution ecological, morphological, and genetic data across all these species.

In this study, we investigated exploratory behavior and examined its genetic basis in one of the largest extant adaptive radiations in animals, the cichlid fishes of African Lake Tanganyika (16). Approximately 240 cichlid species have evolved in this lake from a common ancestor in just about 10 million years (16), featuring an unparalleled degree of morphological, ecological, and behavioral diversity (13, 19). We focused on exploratory tendency because this behavioral phenotype has previously been implicated in adaptation in general (20) and in dispersal strategies (21), habitat selection (22), and mate choice (23, 24) in particular, all of which are relevant in animal adaptive radiations (11). Furthermore, exploratory tendency is a ubiquitous trait for which standardized experimental procedures have been established (25).

## Exploratory tendency as component of niche adaptation

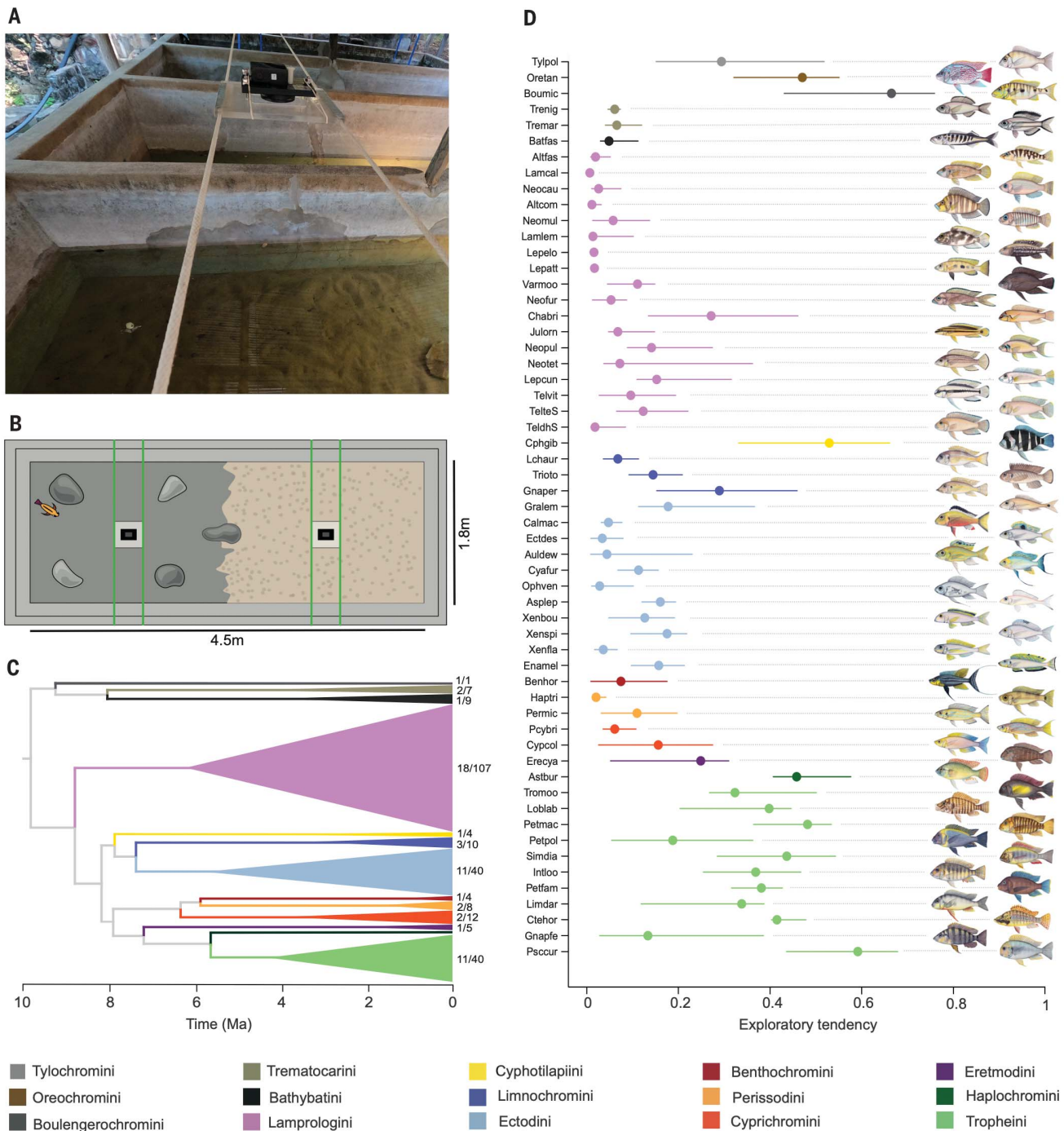
We first quantified exploratory behavior in 702 wild-caught adult cichlids from Lake Tanganyika (table S1) using a standardized open-field test under near-natural conditions in experimental ponds (430 cm by 156 cm by 109 cm) situated at the lake's shore (Fig. 1, A and B). Our sample typically included 12 adult individuals (both sexes combined) from 57 species (fig. S1A), covering the phylogenetic spectrum (Fig. 1C) as well as the ecological and morphological diversity (fig. S1B) of the lake's cichlid fauna. We found substantial differences between species in exploratory tendency (Fig. 1D and fig. S2), defined here as the relative proportion of the pond area visited by a test fish within a period of 15 min after its first movement in the novel environment [see (26)

for laboratory-based results in Malawi cichlid]. Variation in exploratory tendency was mainly explained by the factor “species” [linear model (LM): coefficient of determination ( $r^2$ ) = 0.541,  $P < 0.001$ ]. Body size as covariate “standard length” further improved the model ( $r^2$  = 0.602,  $P < 0.001$ ; fig. S3) and also explained some of the observed behavioral variance when tested as sole predictor in a model accounting for phylogenetic nonindependence using phylogenetic generalized least-square analyses (pGLS:  $r^2$  = 0.11,  $P < 0.01$ ,  $\lambda_{\text{pGLS}}$  = 0.912). Overall, the phylogenetic signal in the data was strong (Pagel's lambda: 0.96). Laboratory experiments with 16 of the 57 species [typically 10 lab-habituated individuals per species and using the same open-field test strategy yet in a smaller aquarium (1.5 m by 0.5 m) and, therefore, for a shorter time period (5 min);  $n$  = 132 wild-caught and  $n$  = 17 F<sub>1</sub> individuals; table S2] revealed that our measurements of exploratory tendencies were highly repeatable under laboratory conditions [repeatability ( $R$ ) = 0.78, standard error (SE) = 0.032,  $P < 0.001$ ; fig. S4A] and consistent with results obtained in the field (fig. S4B).

A key feature of adaptive radiation is that new species emerge rapidly from a common ancestor as a consequence of their adaptation to distinct ecological niches, resulting in a correlation between adaptive phenotypes and the environment (11). To examine if behavior is part of niche adaptation in the radiation of cichlid fishes in Lake Tanganyika, we tested for an association between exploratory tendency and two well-established environmental proxies for the lake's cichlid fauna: the stable carbon and nitrogen isotope compositions in muscle tissue, which inform about the macrohabitat niche along the benthic-pelagic axis ( $\delta^{13}\text{C}$  value) and the relative trophic level ( $\delta^{15}\text{N}$  value) of a species (16). Using pGLS, we uncovered a relationship between exploratory tendency and  $\delta^{13}\text{C}$  values (pGLS:  $r^2$  = 0.120,  $P < 0.01$ ,  $\lambda_{\text{pGLS}}$  = 0.989) but not  $\delta^{15}\text{N}$  values (pGLS:  $r^2 < 0.001$ ,  $P = 0.908$ ,  $\lambda_{\text{pGLS}}$  = 0.957). We further found that exploratory tendency is not correlated with the water depth at which a species occurs (pGLS:  $r^2$  = 0.02,  $P = 0.313$ ,  $\lambda_{\text{pGLS}}$  = 1.0) but with body shape and more precisely with principal component (PC) 1 of landmark-derived data (pGLS:  $r^2$  = 0.11,  $P < 0.05$ ,  $\lambda_{\text{pGLS}}$  = 0.919), which is known to capture the fishes' aspect ratio and primarily separate species along the benthic-pelagic axis (16). These results demonstrate that exploratory behavior is associated with macrohabitat adaptations in Tanganyikan cichlids and that more-benthic and deep-bodied species are more explorative compared with more-pelagic and slender-bodied ones (fig. S5). This in turn suggests that macrohabitat niche specialization involves both a morphological (body shape) and a behavioral (exploratory tendency) trait complex.

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**Fig. 1. Variation in exploratory tendencies in Tanganyikan cichlids.**

(A) Experimental ponds at the shore of Lake Tanganyika near Mpulungu, Zambia. Exploratory behavior was recorded with GoPro cameras mounted above the ponds. (B) Schematic top view and dimensions of the experimental ponds. The two main habitats of the lake (rock and sand) were recreated. Green lines illustrate the two camera mounting racks. (C) Time-calibrated species tree of Tanganyikan

cichlids [modified from (16)]. The Tanganyikan cichlids have been grouped into subclades, so called “tribes,” which comprise varying species numbers. The number of tested species out of the total number of species in each tribe are indicated. (D) Exploratory tendencies of all 57 cichlid species (medians with interquartile ranges) arranged in phylogenetic order [following (16)]. Tribes are color coded according to (16), and tribe names are provided at the bottom. For full species names, see table S1.

**Genetic underpinnings of species-specific exploratory tendencies**

Exploratory tendency belongs to a suite of behavioral traits that are known for their relatively high heritability, comparable to that of life-history and physiological traits (27, 28). To

investigate the genetic underpinnings of variation in exploratory tendencies in Tanganyikan cichlids, we performed an association study. To this end, we generated a new variant call set from available genomic data (16) and calculated alternative allele frequencies from genotype

likelihoods for each species ( $n = 57$ ) and single-nucleotide polymorphisms (SNPs) ( $n = 40.3$  million). To assess the strength of the association between median exploratory tendency and allele frequencies at each SNP, we applied two complementary approaches: a

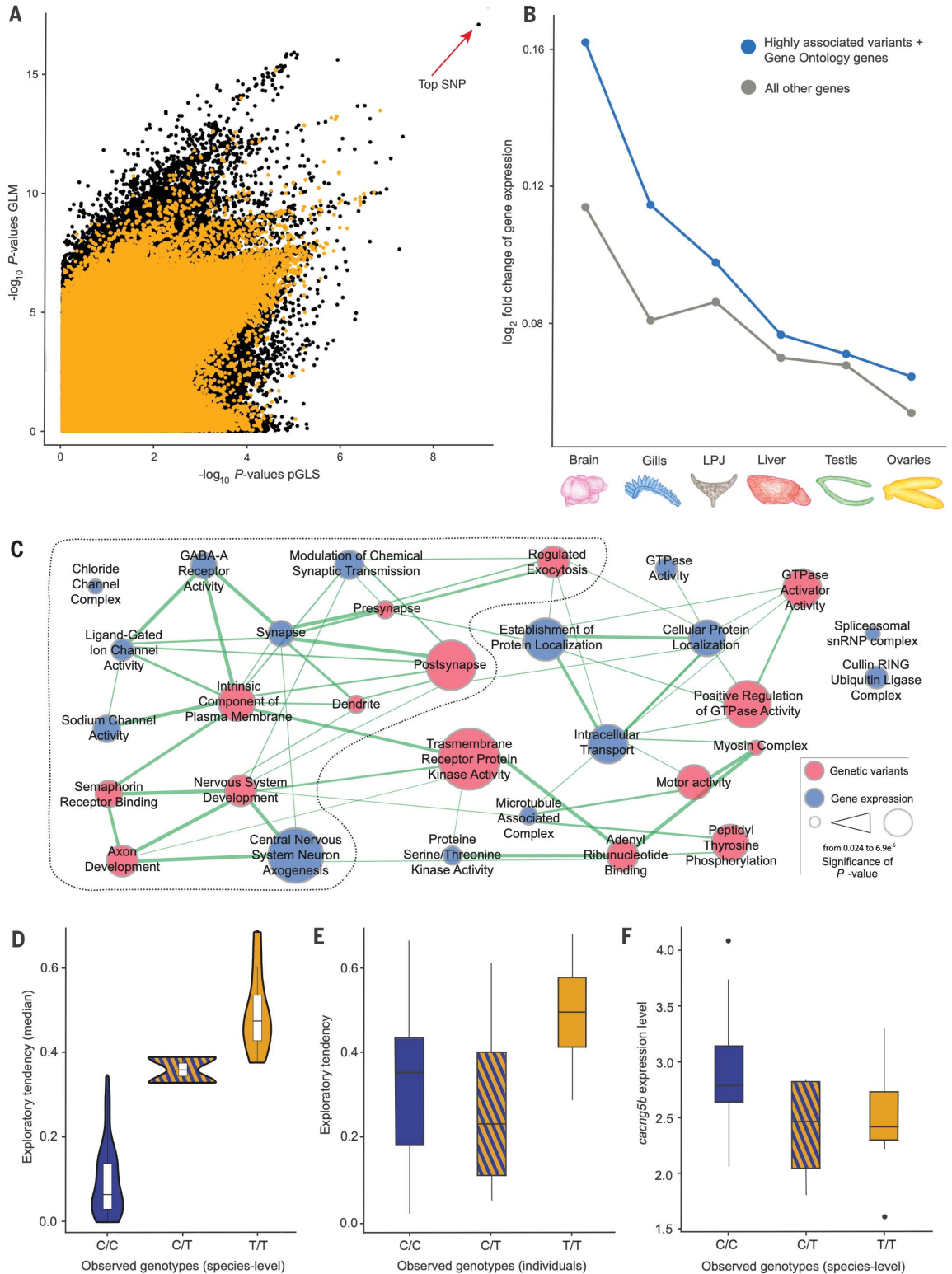
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## Fig. 2. The genetic underpinnings of exploratory tendency in Tanganyikan cichlids. (A) *P* value distributions from GLM and pGLS approaches measuring the strength of association between genetic variants and exploratory tendency. Empirical data are depicted in black, overlaid with simulated results in orange.

(B) Fold change in gene expression across different organs comparing genes that contain highly associated variants and feature a functional Gene Ontology term ( $n = 240$ ) and all other genes ( $n = 21,823$ ). See also fig. S8. LPJ, lower pharyngeal jaw bone.

(C) Enrichment map showing the top five terms from each Gene Ontology category for both the gene set containing highly associated variants and the genes that are most differentially expressed along the phenotypic axis. The level of overlap between terms is indicated by the thickness of the edge between them, and the size of each node is proportional to the *P*-value significance. The dashed line surrounds terms related to the functioning and/or development of the central nervous system.

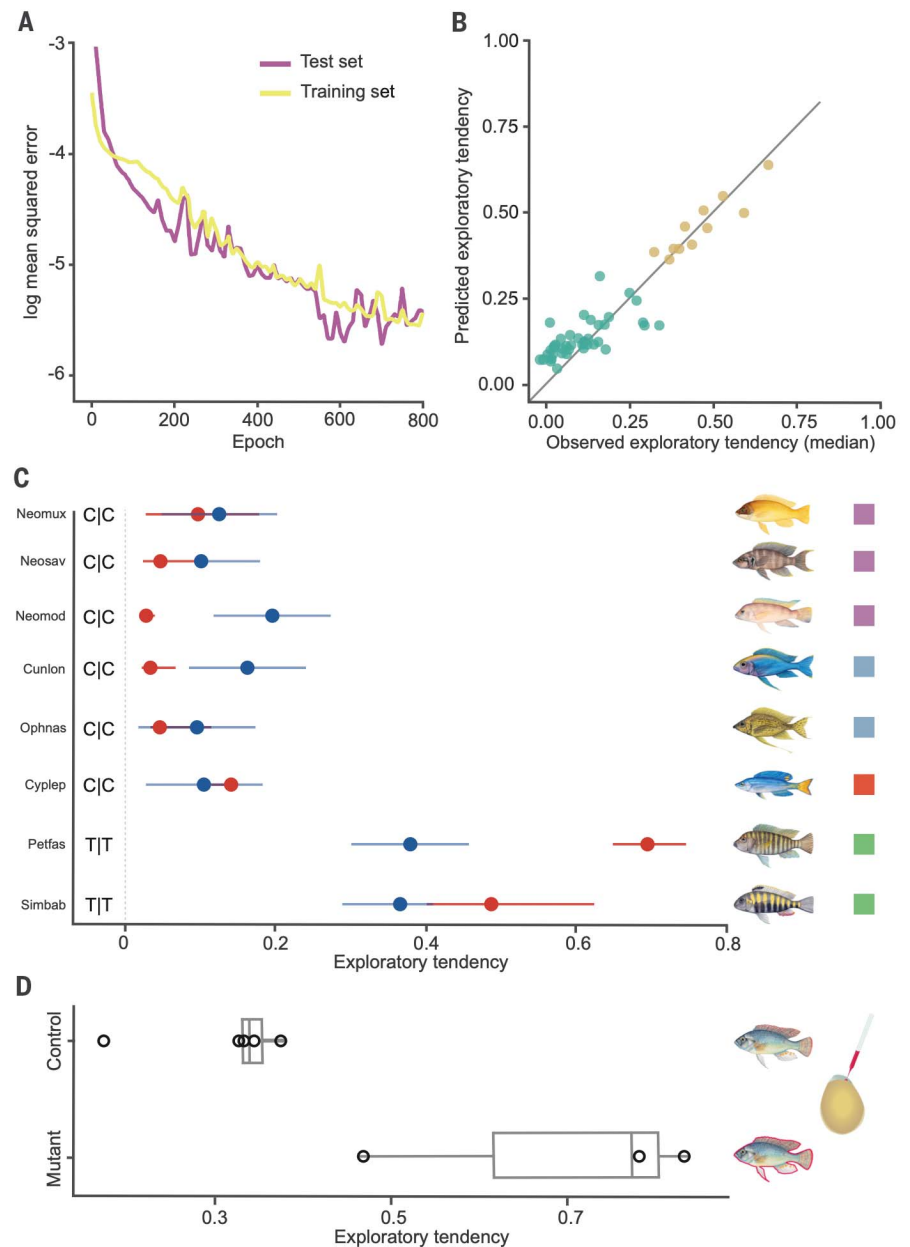
(D) Species homozygous with a "C" at the top SNP show low median exploratory tendencies, species homozygous with a "T" show high median exploratory tendencies, and polymorphic species (i.e., at least one of the two individuals is polymorphic) are intermediate. Box plots represent the median and interquartile ranges, and violin limits represent the range. (E) Exploratory tendencies in 41 additionally genotyped individuals belonging to four polymorphic species (see also fig. S12). (F) Species homozygous with a "C" have a higher gene expression of *cacng5b* [ $\log_2(\text{TPM} + 1)$ ] (TPM is transcript per million) than species homozygous with a "T," whereas polymorphic species are intermediate ( $n = 43$ ; LM and pGLS:  $r^2 = 0.152$ ,  $P < 0.05$ ). The center lines of the box plots in (E) and (F) represent the median, the box limits represent the lower and upper quartiles, and whiskers span data points within 1.5 $\times$  interquartile range from the box.





generalized linear model (GLM) and a pGLS. Because the GLM does not control for phylogenetic relationships and the pGLS does not consider the possibility of allele sharing between species owing to incomplete lineage sorting and/or gene flow (29), we chose our  $P$ -value thresholds by comparing the empirical results against chance associations retrieved from data simulated under neutrality (Fig. 2A). Coalescent simulations, with one recombination event per chromosome per generation and taking into consideration the evolutionary history of the Tanganyikan cichlid assemblage, revealed that single topology tracts are very short (fig. S6). This implies that linkage disequilibrium is broken down between most SNPs in our dataset and, therefore, that SNPs provide independent signals. By taking the intersection of significantly associated SNPs from both approaches, GLM and pGLS, we identified 1199 highly associated variants, with a moderate overrepresentation of coding mutations (fig. S7). That these variants passed the imposed thresholds suggests that their association to variation in exploratory tendency is due to natural selection acting on them at some point in the evolutionary history of the Tanganyikan cichlid radiation.

We identified 784 genes that contained one or more of these highly associated variants, with most of the genes containing a single variant (exceptions are listed in table S3). We then tested if highly associated variants alter the expression of genes in their proximity ( $\pm 5$  kb from their transcription start or end coordinates). An examination of adult gene expression profiles available for 43 (table S1) of the focal species (30) revealed that genes that contain highly associated variants and for which a functional Gene Ontology term was available ( $n = 240$ ) show greater fold change and greater difference in fold change compared with all other genes ( $n = 21,823$ ) and that this effect was strongest in brain transcriptomes (Fig. 2B and fig. S8), consistent with the fact that these variants are linked to a behavioral phenotype. Next, using GLM and pGLS  $P$  values and fold-change levels as criteria, we identified the most differentially expressed genes in relation to exploratory tendency in the brain transcriptomes. To examine if the thus identified 1245 genes as well as the genes that contain highly associated variants are, on the whole, biased toward particular gene categories, we performed Gene Ontology enrichment analyses, in which we corrected for gene set overlap due to the Gene Ontology graph structure and accounted for biases due to variations in gene length. Approximately half of the significant enrichment terms for both the differentially expressed genes and genes containing one or more highly associated variant were related to the function and/or development of the central nervous system (see Fig. 2C for a network illustration of the top five



**Fig. 3. Phenotypic effects of the top locus.** (A) Mean squared differences between neural network predictions and ground truth for the selected neural network as a function of training epoch for the training and test dataset. (B) Predicted exploratory tendency scores compared with the observed (empirical) behavior. The two classes of genotype value are color coded in green (“C”) and yellow (“non-C”). Test and training sets are shown together. (C) Predicted exploratory scores (blue) largely match the empirical values (red) (medians with interquartile ranges; color coding is the same as in Fig. 1A; for full species names, see table S1). (D) CRISPR-Cas9 mutant *A. burtoni* fish ( $n = 3$ ) show a much higher exploratory tendency than control fish ( $n = 5$ ). All individuals were siblings. The box plot shows medians with interquartile ranges.

terms from each category and fig. S9 for a full report).

Among the 1199 highly associated variants, one SNP stood out in both the GLM and the pGLS approaches (Fig. 2A and fig. S10). The genotypes at this “top SNP” (C|C, C|T, and T|T; the C|T category included species with at least one of the individuals being polymorphic)

showed a nearly perfect correlation with low, medium, and high exploratory tendencies across the 56 ingroup species used for this analysis (LM:  $r^2 = 0.749$ ,  $P < 0.001$ ; pGLS:  $r^2 = 0.499$ ,  $P < 0.001$ ,  $\lambda_{\text{pGLS}} = 0.10$ ; Spearman correlation:  $r^2 = 0.711$ ,  $P < 0.001$ ; Fig. 2D and fig. S11). We genotyped an additional 41 individuals from four species polymorphic for the top SNP (all

belonging to the same tribe, Tropheini) and found a weaker yet substantial and significant association of the top SNP with exploratory tendency [analysis of variance (ANOVA):  $F = 4.789$ ,  $P < 0.05$ ; Spearman correlation:  $r^2 = 0.345$ ,  $P < 0.05$ ; Fig. 2E and fig. S12]. The genotypes at the top SNP thus explain differences in exploratory tendency observed at the macro-evolutionary scale as well as differences among individuals within polymorphic species.

The top SNP is located 526 base pairs upstream—with respect to the Nile tilapia genome (*Oreochromis niloticus*; RefSeq: GCF\_001858045.1)—of the transcription start site of *cacng5b* (calcium voltage-gated channel auxiliary subunit 5b), a gene that encodes a type II transmembrane AMPA receptor regulatory (TARP) protein. TARP proteins control the density and distribution of the glutamate-activated AMPA receptors in vertebrates and, therefore, have been implicated in synaptic plasticity (31–33). We confirmed *cacng5b* expression in the brains of all 72 Tanganyikan cichlid species transcriptionally profiled by El Taher *et al.* (30), including 43 of our focal species, whereas its expression levels were much lower in other tissues, as were those of most other genes of the *cacng* gene family (fig. S13). We then used the brain transcriptomes (30) to compare *cacng5b* expression levels across three groups of species according to their genotypes (C|C, C|T, and T|T) and found a significant correlation between genotype and levels of gene expression ( $n = 43$ ; LM and pGLS:  $r^2 = 0.152$ ,  $P < 0.05$ ,  $\lambda_{pGLS} = 0.0$ ; Spearman correlation:  $r^2 = 0.333$ ,  $P < 0.05$ ), with C|C species showing the highest levels of gene expression and T|T species the lowest (Fig. 2F and fig. S14). In zebrafish, *cacng5b* is expressed in the ventral habenula (34), a part of the brain known to modulate fear response and motor behavior (35). Using targeted quantitative real-time polymerase chain reaction (qPCR), we confirmed that also in cichlids, *cacng5b* expression is higher in the habenula compared with other parts of the brain (table S4).

The coding region of *cacng5* is conserved across vertebrates, being among the more slowly evolving members of the *cacng* gene family (fig. S15 and table S5). The region that harbors the top SNP shows conservation across East African cichlids and between these and *Tylochromis polylepis* that diverged ~47 million years ago (36), but it was not conserved between African and neotropical cichlids that diverged ~62 million years ago (36) nor with other even-more-distantly related teleosts (fig. S16). Phylogeny-guided reconstructions that include outgroup species reveal “T” as the ancestral state and possibly two independent transitions to “C” over the course of the cichlid radiation in Lake Tanganyika (fig. S17), suggesting that the basin’s early colonizers belonged to an explorative and probably benthic cichlid species.

### Validating the phenotypic effect of the top locus

To validate that variation at the top locus has an effect on the behavioral phenotype, we first adopted the strategy of data-driven phenotypic predictions for a set of other cichlid species that, initially, had not been empirically examined with regard to their exploratory tendency. We started with a simple binary threshold based on the top SNP genotype, predicting a low exploratory tendency for “C species” and a high exploratory tendency for “T species.” We set the exploratory tendency threshold at 0.35, which is the midpoint between the non-overlapping distributions of phenotypic values in species fixed for the two alleles (Fig. 2D). Next, to predict specific phenotypic values, we designed a purely data-driven feed-forward neural network (37) and trained it with three input variables for a set of 56 species: the top SNP information, the stable carbon isotope signature, and PC1 of body shape. The top SNP genotype was an important contributor to the predictions, showing very high covariance with the predicted values ( $r = 0.85$ ). After the training phase and sanity tests (Fig. 3, A and B), we used the neural network to predict the behavioral phenotype of eight additional cichlid species occurring at our field site and belonging to four different tribes (see Fig. 3C). We then returned to Lake Tanganyika to put our predictions to the test using the same experimental ponds and assay as before (Fig. 1, A and B). Overall, we found strong agreement between the newly obtained empirical data and the predictions (Fig. 3C). Specifically, the genotype alone correctly predicted high or low exploratory tendencies with a binary threshold for all eight species, a result that has a probability of lower than 0.01 of occurring by chance (fig. S18). The predictions from the neural network approach had an average error of 0.113, which was better than 87% of cases when test species were chosen at random (fig. S19).

Complementary evidence for the functional role of the top locus was obtained by *in vivo* sequence editing using a CRISPR-Cas guide. For this experiment, single guide RNA (sgRNA) and Cas9 RNA were co-injected into one-cell-stage embryos of *Astatotilapia burtoni* (38), which introduced small (between 2 and 5 bp long) deletions immediately after the top SNP (2 to 5 bp downstream). These insertions likely disrupt a potential promoter function toward the downstream *cacng5b* gene, whose coding region remained unaffected by the experimental manipulations (table S6). Given the inverse relationship between genotype-specific exploration tendencies (Fig. 2E) and *cacng5b* expression levels (Fig. 2F), we predicted that any such disruption should increase exploratory tendency in mutant fish. We obtained three adult mutant fish that, together with five adult control fish (injected but not mutant), were tested

for their exploratory tendency. Mutant fish showed a much higher exploratory tendency compared with the control individuals (Fig. 3D), demonstrating a causal link between this narrow genomic region and exploratory tendency.

### Conclusions and outlook

We examined phenotypic variation in a fundamental behavioral trait—exploratory behavior—across the adaptive radiation of cichlid fishes from Lake Tanganyika, tested for its association with ecology and morphology, and investigated its genetic underpinnings. We found that exploratory tendencies vary among closely related cichlid species and that these species-specific differences are highly consistent. Exploratory tendencies correlated with macrohabitat adaptations, providing rare evidence that a behavioral phenotype is involved in niche adaptation in a large-scale adaptive radiation. We found that 1199 genetic variants are highly associated with exploratory tendency, which, in principle, is consistent with a polygenic nature of this trait. At the same time, we identified one SNP that shows a near perfect association with whether a species is explorative or not and confirmed this link through behavioral predictions and genome editing. This top SNP is located in the putative promoter region of *cacng5b*, a gene that encodes a protein that regulates AMPA glutamate receptors. That the human ortholog of this gene has been implicated in psychiatric disorders (39), which show a strong relationship with abnormalities on basic dimensions of personality (40, 41), and that human personality dimensions show similar phenotypic properties to a set of so-called (nonhuman) animal personality traits, including exploratory behavior (42–44), raises the intriguing possibility of a shared genetic network underlying personality traits across vertebrates.

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#### SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.adj9228](https://doi.org/10.1126/science.adj9228)

Materials and Methods

Figs. S1 to S19

Tables S1 to S6

References (50–85)

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