Evolutionary lability of a key innovation spurs rapid diversification

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Rates of lineage diversification vary considerably across the tree of life, often as a result of evolutionary innovations[1–5]. Although the ability to produce new traits can vary between clades and may drive ecological transitions[6–9], the impact of differences in the pace at which innovations evolve at macroevolutionary scales has been overlooked. Complex teeth are one innovation that contributed to the evolutionary success of major vertebrate lineages[10–12]. Here we show that evolutionary lability of tooth complexity, but not complexity itself, spurs rapid diversification across ray-finned fishes. Speciation rates are five times higher when transitions between simple and complex teeth occur rapidly. We find that African cichlids are unique among all fishes; they are dominated by lineages that transition between simple and complex teeth at unparalleled rates. This innovation interacted with the ecological versatility of complex teeth to spur rapid adaptive radiations in lakes Malawi, Victoria and Barombi Mbo. The marked effect on diversification stems from the tight association of tooth complexity with microhabitat and diet. Our results show that phylogenetic variation in how innovations evolve can have a stronger effect on patterns of diversification than the innovation itself. Investigating the impact of innovations from this new perspective will probably implicate more traits in causing heterogeneous diversification rates across the tree of life.

Variation in the processes of speciation and extinction has led to an uneven distribution of species across both geographic regions and the tree of life[1–4,13]. Evolutionary innovations are often cited when diversity varies considerably between clades, a classic example being the pharyngeal jaw of cichlid fishes[14]. These traits shape phenotypic, ecological or lineage diversification rates by facilitating access to new adaptive peaks, often by unlocking previously inaccessible resources[5,15–17]. However, clades can differ in their capacity to generate novelty[6–9,18]. Variation in how innovations evolve across clades has been overlooked as a feature, or as an innovation itself, that shapes macroevolutionary diversification patterns. This necessitates an altered approach to key innovation studies in which differences in evolutionary lability—the rate at which an innovation is gained and lost—could instead generate the observed differences in species diversity. This effect on diversification may be strong when the trait is tightly coupled with one or more axes of divergence and change in the state of the trait leads to ecological shifts[5]. Increased lability of ecological innovations may be a feature of many adaptive radiations because niche expansion is crucial during the speciation process[19]. However, identifying phylogenetic variation in lability requires replicated innovations across broad taxonomic scales to overcome the confounding effect of macroevolutionary singularity[18].

The teeth of jawed vertebrates show marked increases in complexity through the addition of tooth cusps over the past 200 million years[20]. Teeth with multiple cusps are a key innovation in the traditional sense. Their origination left a detectable effect on the tempo of mammalian and squamate evolution by expanding the range of achievable diets and increasing energy intake efficiency[10–12]. Complex teeth have also evolved in multiple orders of ray-finned fishes (Actinopterygii)[21], whose more than 35,000 extant species constitute half of vertebrate diversity. The success of some fish groups is frequently attributed to functional innovations, many related to the feeding apparatus, that stimulate new evolutionary trajectories[22,23]. Complex teeth, although found in lineages that occupy a range of habitats, are often associated with herbivory in productive shallow-water environments[24,25]. Transitions between simple and complex teeth are thus linked to change in diet and habitat, two important speciation axes in fishes[26]. These observations suggest that high lability of tooth complexity may be important for generating exceptional species diversity in adaptive radiations, during which diversification along these axes proceeds rapidly. Moreover, the replicated evolutionary origins and subsequent losses of complex teeth across fishes affords an opportunity to identify differences in lability across a broad phylogenetic scale. Here we reconstruct the evolution of complex teeth for more than 88% of extant ray-finned fishes to address how phylogenetic variation in the evolution of this vertebrate innovation has shaped the tempo of evolutionary diversification in fishes. We test explicit predictions that tooth complexity and its evolutionary lability are key innovations for African cichlids, a famous example of adaptive radiation. By interrogating the effects of each across phylogenetic scales, we show that exceptional diversification is explained by differences in lability rather than complexity itself.

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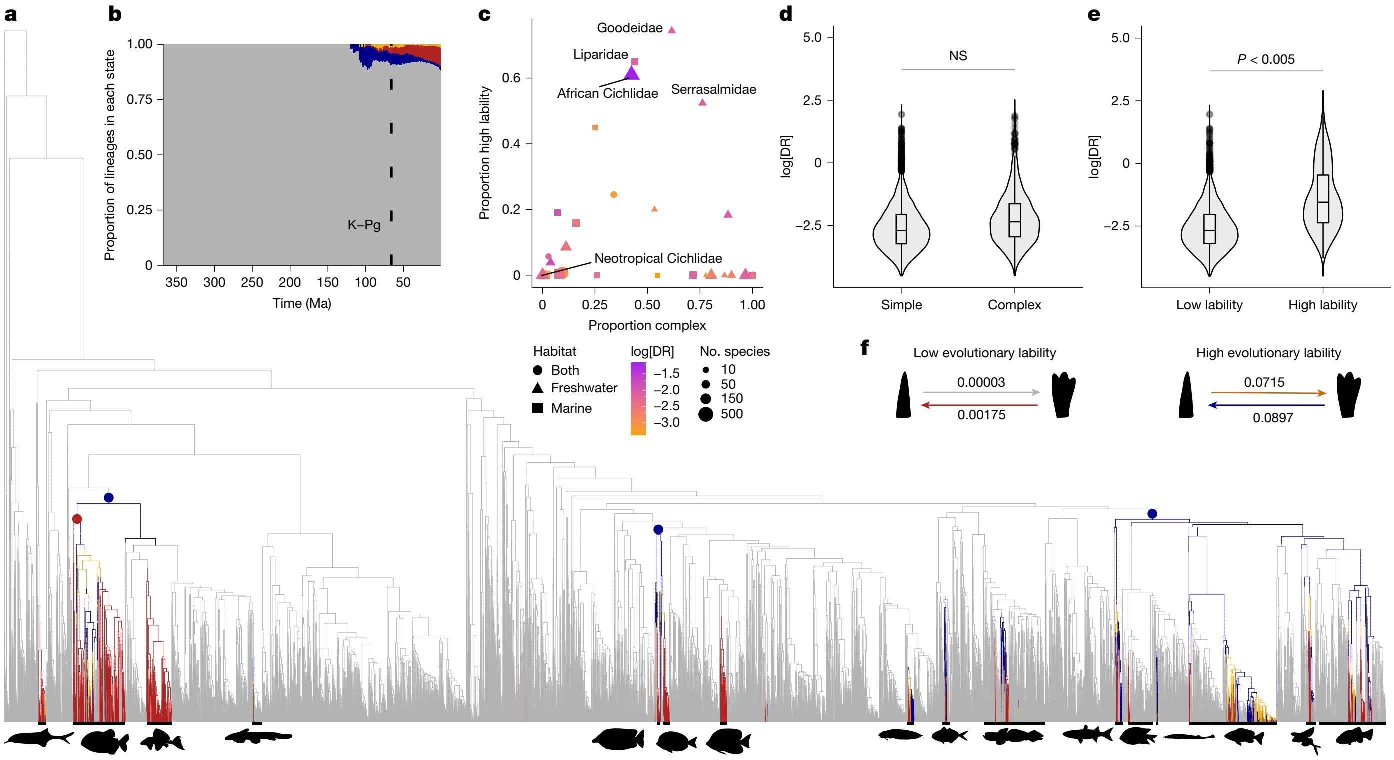

Fig. 1 | The evolutionary dynamics of tooth complexity across ray-finned fishes. a, MAP ancestral state reconstruction of complex teeth across ray-finned fishes (n = 11,508 species) using stochastic character mapping under a hidden-rates model with two rate categories. Branches are coloured by tooth complexity and lability (simple low lability, grey; simple high lability, dark blue; complex low lability, red; complex high lability, gold). Major rate increases about 100 Ma are marked with blue points, and the earliest transition to complex teeth is marked with a red point. Outlines represent highlighted clades (from left to right) Mormyridae, Characiformes, Loricariidae, Mochokidae, Siganidae, Acanthuridae, Pomacanthidae, Liparidae, Nomeidae and Stromateidae, Gobiidae, Mugilidae, Pomacentridae, Gobiesocidae, Cichlidae, Beloniformes and Cyprinodontiformes. **b**, Proportion of branches in each state of tooth complexity (simple and complex) and lability (low and high) in million-year intervals. The x axis represents time before present in million years, progressing from left (past) to right (present). The dashed line marks the K–Pg boundary about 66 Ma. Colours follow those in **a**. **c**, The proportion of lineages with complex teeth (x axis) and high lability (y axis) across families that have at least one lineage with complex teeth (n = 31 families). Point colour indicates the family mean speciation rate, shape represents habitat (freshwater, marine or both) and size indicates the number of species in the family. DR, diversification rate statistic. **d**,**e**, Distribution of log-transformed tip speciation rates between lineages with simple (n = 10,361 species) and complex (n = 1,147 species) teeth (P = 0.0602; **d**) and lineages with low (n = 11,075 species) and high (n = 433 species) lability (P = 0.0025; **e**). Box plots show the median (middle horizontal line), interquartile range (box), minimum–maximum values (vertical lines) and outliers (points). Two-tailed significance was assessed using non-parametric FiSSE tests. **f**, Transition rates, reported as the number of transitions per million years, between simple and complex teeth when lability is low compared to when lability is high. Arrows indicate transition direction; colours follow those in **a**.

Heterogeneous evolution of complex teeth

To study the evolution of tooth complexity across ray-finned fishes, we classified 30,915 extant species as having simple (single cusp) or complex (multiple cusps) teeth in their oral jaws (Supplementary Table 1), generating one of the largest datasets of a vertebrate morphological trait. Bayesian maximum a posteriori (MAP) ancestral state reconstruction and stochastic character mapping in RevBayes[27] reveals multiple evolutionary origins of tooth complexity across extant actinopterygians (Fig. 1a). Complex teeth have evolved at least 86 times, appearing first in the Early Cretaceous 110 million years ago (Ma), both in single lineages (for example, *Helotes sexlineatus*, the Eastern striped grunter) and at the base of large clades (for example, Characiformes; Fig. 1a and Supplementary Table 2). The proportion of lineages with complex teeth has gradually increased since the Cretaceous–Palaeogene (K–Pg) mass extinction (Fig. 1a,b). Despite this, complex teeth remain rare (11.7% of extant species) across fishes. Reversions to simple teeth are substantially more frequent (1.25–50 times higher transition rate) and numerous (n = 110 reversions). These often occur in large multicuspid clades (Fig. 1a,c) when lineages shift into specialized predatory niches (for example, *Hydrocynus*, the African tigerfish, in *Alestidae*). The frequent reversions parallel squamate dental evolution and contrast the more unidirectional pattern in mammals[11], and the numerous origins (n = 86) suggest that complex teeth have evolved from a simple state far more times in fishes than in squamates (24 independent origins[11]) and mammals (plesiomorphic[28]). Lineages with complex teeth dominate several diverse, primarily freshwater groups including Characiformes (Characidae and Serrasalmidae), Cyprinodontiformes (Cyprinodontidae and Goodeidae), Cichlidae and Loricariidae (Fig. 1a,c). They also appear in the enigmatic driftfishes (Nomeidae and Ariommatidae), lanternfishes (Myctophidae) and pencil catfishes (Trichomycteridae), albeit less frequently (Supplementary Table 1).

To understand how the evolution of tooth complexity varies across Actinopterygii, we compared the fit of several Markov models of character evolution, including some that accommodate rate variation, using marginal likelihoods and Bayes factors. Our results show that the gain and loss of tooth complexity is a heterogeneous process across ray-finned fishes defined by significant variation in transition rates (Fig. 1a,c,f and Supplementary Tables 3–5; Bayes factor (BF) = 6.74). Most lineages over time, including 96.2% (n = 11,075 species) of extant actinopterygians in our analyses, are defined by low evolutionary lability (Fig. 1b). This is a process in which tooth complexity is gained at an exceptionally slow rate and is lost at a rate 50 times faster, resulting in a single origin and retention in most descendant lineages (Fig. 1c,f).

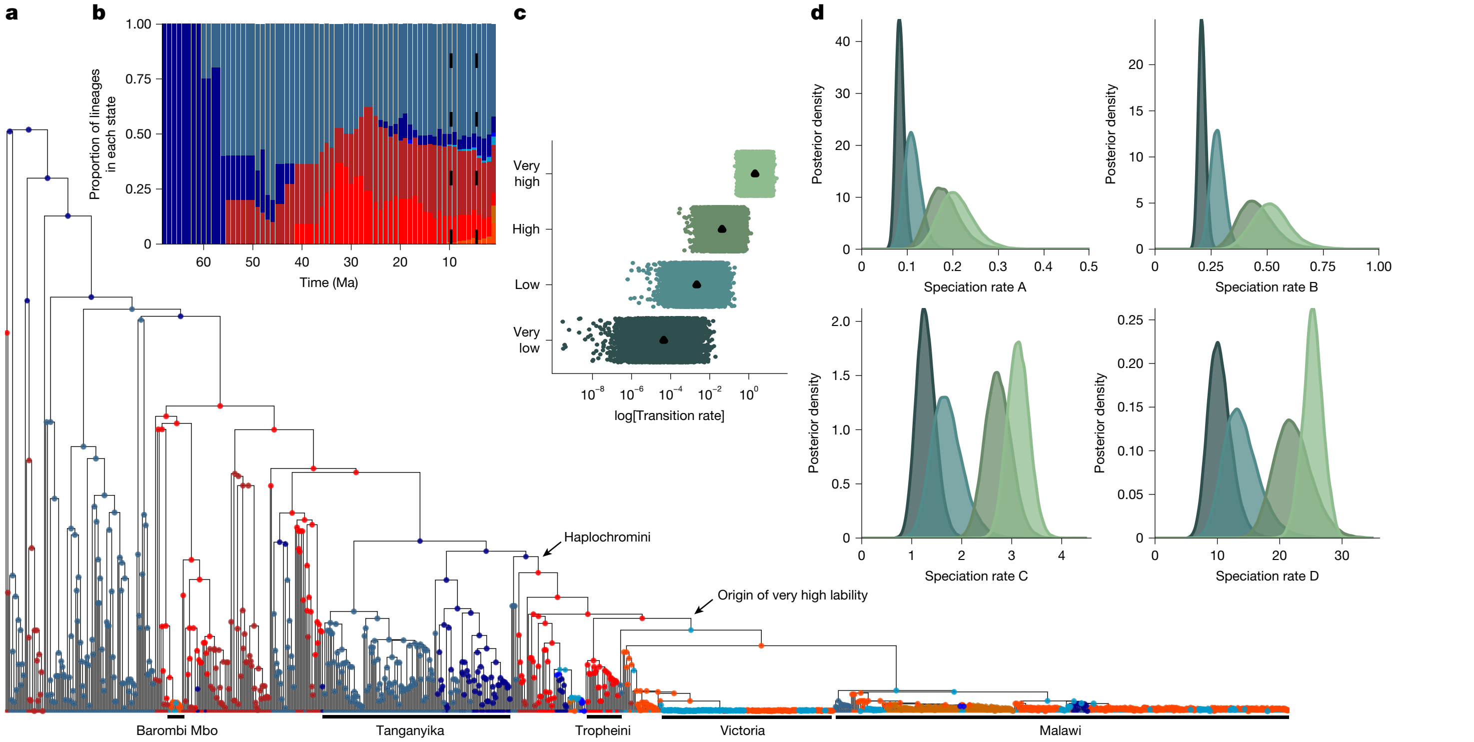

Fig. 2 | Rapid evolution of tooth complexity accelerates species diversification in African cichlids. a, MAP ancestral state reconstruction across cichlids from Africa, Madagascar and South Asia (n = 1,069 species) under an equal-rates model with four hidden rate categories. Lineages with simple teeth are coloured variations of blue, and lineages with complex teeth are coloured variations of red; brighter colours represent higher rates (that is, different levels of lability). **b**, Proportion of branches in each state of tooth complexity and lability in million-year intervals. The x axis represents time before the present in million years, progressing from left (past) to right (present). The dashed lines mark the ages of Lake Tanganyika (9.7 million years) and Lake Malawi (about 3.2 million years). All lineages endemic to Lake Victoria are found in the bar closest to the present. **c**, Posterior distribution of log-transformed transition rates between simple and complex teeth. The mean of each distribution is indicated with black triangles. Note the magnitude of variation between levels of evolutionary lability. **d**, Posterior distribution of speciation rates estimated under a MuHiSSE-4 model. Note the different scales of baseline speciation between the four hidden states. Colours follow the varying levels of lability in **c**.

We identified an increase in the transition rate between simple and complex teeth—high evolutionary lability—originating during the Early Cretaceous (Fig. 1a,b) and defining just 3.8% (n = 433 species) of extant lineages. These taxa evolved complex teeth at a rate three orders of magnitude greater than when lability is low with a major reduction in the relative rate at which complexity is lost (Fig. 1f). These groups—primarily African Cichlidae, Liparidae, Mormyridae and Serrasalmidae—are notable in having a high proportion of lineages with complex teeth (Fig. 1c and Extended Data Fig. 1a,b), high speciation rates and high rates of phenotypic evolution[29–31].

We then explored the effects of tooth complexity and its evolutionary lability on speciation rates given that both innovations and phenotypic evolvability may shape speciation dynamics at large macroevolutionary scales[29,32]. We used a non-parametric test for state-dependent speciation to test for effects of tooth complexity and lability. For lability, we assigned each species to the MAP rate regime (low or high) estimated through our ancestral state reconstruction, regardless of tooth complexity. Although speciation rates for complex-toothed lineages are twice as high as those for simple-toothed lineages ($\lambda_{complex}$ = 0.239 (s.d. 0.556), λ_{simple} = 0.122 (s.d. 0.239)), tooth complexity alone does not have a significant effect on speciation rates (one-way phylogenetic analysis of variance (ANOVA), F = 170.58, Cohen's d = 0.27, P = 0.194; FiSSE two-tailed P = 0.06; Fig. 1d). Speciation rates for lineages with complex teeth are faster by 0.117 lineages per million years. The high tip-ratio bias[33], low power of FiSSE compared to formal state-dependent speciation and extinction (SSE) models, and numerous simple-toothed lineages with exceptional speciation rates (Extended Data Fig. 1) probably reduce our ability to detect significant rate asymmetry. However, we find that increased evolutionary lability, regardless of tooth complexity, increases speciation rates by five times compared to when lability is low (λ_{low} = 0.116 (s.d. 0.206), λ_{high} = 0.595 (s.d. 0.958); one-way phylogenetic ANOVA; F = 1267.05, Cohen's d = 0.69, P < 0.005; FiSSE two-tailed P < 0.005; Fig. 1e). Speciation rates for lineages that evolve complex teeth at higher rates with a lower relative rate of cusp loss are faster by 0.479 lineages per million years. Although there are many predominantly complex families (Fig. 1c), these results show that rapid switching between simple and complex teeth, but not complex teeth alone, has accelerated the diversification of some exceptional groups of ray-finned fishes.

Complexity evolves rapidly in cichlids

Among ray-finned fishes, cichlids have attracted intense interest from evolutionary biologists owing to their remarkable adaptive radiations. Many advances have been made in understanding their rapid accumulation of species diversity, implicating a combination of key innovations[14,34] and rapid ecological diversification driven by exceptional genomic potential[31,35–37]. Yet many proposed innovations are unable to explain varying rates of species diversification[38]. High lability of tooth complexity is concentrated within Cichlidae (>50% of all lineages with high lability; Extended Data Fig. 2c) but separates the continental radiations of Africa and the Neotropics (Fig. 1c). All Neotropical lineages have low lability and only one (*Herotilapia multispinosa*) has complex teeth. African cichlids are dominated by lineages that rapidly transition between simple and complex teeth with a high proportion of complex-toothed lineages, a feature unique among all ray-finned

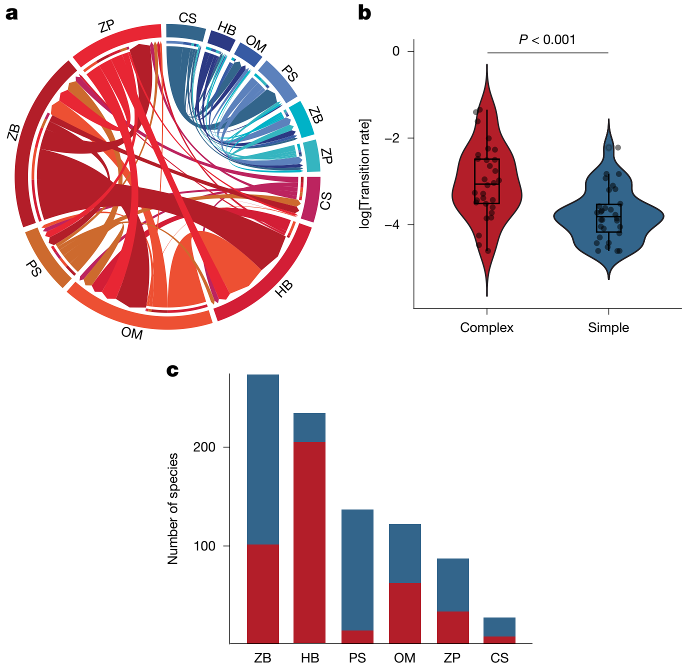

Fig. 3 | State-dependent diet diversification in cichlids. a, Directionality and magnitude of transitions between diet categories within simple (blue hues) and complex (red hues) lineages. The maximum width of inner connections is scaled by the mean estimated transition rate, and the width of outer bars is scaled by the total number of transitions to and from each category. Arrows indicate directionality. Labels correspond to diet (OM, omnivore; PS, piscivore; ZB, zoobenthivore; ZP, zooplanktivore; HB, herbivore; CS, carnivore specialist). **b**, Violin plot depicting a significant increase in mean log + 0.01-transformed diet transition rates when lineages have complex teeth ($P = 1.89 \times 10^{-4}$). Each point corresponds to the mean rate of the posterior distribution estimated for each transition ($n = 30$ simple; $n = 30$ complex). Box plots show the median (middle horizontal line), interquartile range (box) and minimum–maximum values (vertical lines). Statistical significance was calculated using one-way ANOVA. **c**, Number of simple (blue) and complex (red) lineages within each discrete diet category.

fishes (Fig. 1a,c). We further explored how complexity and increased evolutionary lability shape rates of species and ecological diversification within African cichlids.

We generated an expanded dataset of tooth complexity classifications covering 92.7% of described cichlid species and representing all genera from Africa, Madagascar and South Asia ($n = 1{,}069$ species; Supplementary Table 6). We then fitted an expanded set of hidden Markov models over a recent complete phylogeny of Cichlidae[31] to further study how tooth complexity evolves within African cichlids. We find that tooth complexity evolves in African cichlids at unparalleled rates under a process that contrasts with that of all other actinopterygians. Complex teeth evolve and are lost at equal rates (BF = 15.46), unlike the global process in which complexity is far more likely to be lost than gained (Fig. 1a,f and Supplementary Table 7). These rates vary by ten orders of magnitude across the cichlid tree (Fig. 2a,c and Extended Data Fig. 3), and an exceptionally high rate is unique to rapidly diversifying lineages (Fig. 2a), including many haplochromines endemic to lakes Malawi and Victoria, as well as oreochromines endemic to Lake Barombi Mbo. This notable increase in lability is recent, originating within the Haplochromini about 9 Ma (Fig. 2a,b).

Lability and complexity are innovations

Innovations may accelerate lineage diversification by increasing speciation, decreasing extinction or both[5]. To formally test whether tooth complexity increases rates of lineage diversification within African cichlids, we compared the fit of SSE models in RevBayes[27]. We fitted these models over four subtrees to account for the extreme speciation rate variation within African cichlids[31] and compared models within each subtree using marginal likelihoods and Bayes factors. We find that tooth complexity alone cannot explain patterns of lineage diversification; character-independent models were strongly supported across all subtrees (Supplementary Table 8), suggesting that speciation and extinction rates do not depend on whether lineages have simple or complex teeth.

Change in tooth complexity is primarily associated with shifts in habitat and diet in cichlids[39]. Therefore, we tested whether increased lability of tooth complexity shapes speciation and extinction rates. We assigned each species to the MAP transition rate class estimated from our ancestral state reconstruction to represent four discrete levels of lability (very low, low, high and very high). We then compared the fit of four-state hidden-state speciation and extinction models and character-independent models fitted across the full tree ($n = 1{,}069$ species). We find decisive support (BF = 175.91) for a state-dependent model in which high lability consistently increases speciation rates across different background rate regimes (Fig. 2d and Supplementary Table 9). Speciation rates are 1.3–2.5 times higher when lability is increased across all four hidden states (MuHiSSE-4; Fig. 2d, Extended Data Figs. 4 and 5 and Supplementary Table 10). This effect on diversification is largely consistent across different relative extinction scenarios (Extended Data Figs. 6 and 7), as well as under a simpler model (MuHiSSE-2; Extended Data Figs. 8 and 9 and Supplementary Table 11). These hidden states primarily separate riverine and Lake Tanganyika lineages from those in lakes Malawi, Victoria and Barombi Mbo, which have a higher background diversification rate (Extended Data Figs. 4 and 8). Differences in evolutionary lability explain speciation rate variation within lake radiations, between riverine lineages and across habitats.

Although we find that tooth complexity alone does not significantly affect rates of lineage diversification within African cichlids, we tested whether complexity shapes the rate of ecological diversification, a major axis of divergence in adaptive radiations[19]. Using primary literature, we placed 875 species into 6 discrete diet categories (Supplementary Table 6). We used a reversible-jump Markov chain Monte Carlo method in RevBayes to estimate dietary transition rates when lineages have simple and complex teeth. Although all diets include species with both simple and complex teeth (Fig. 3c), mean transition rates between diets are 3.28 times higher when lineages have complex teeth (one-way ANOVA; d.f. = 59, $F = 15.9$, Cohen's $d = 1.03$, $P < 0.001$; Fig. 3a,b). This significant increase in the rate of ecological diversification is facilitated by elevated transitions through herbivory and omnivory (Fig. 3a). Complex teeth are thought to be an adaptation to herbivory, and indeed we find evidence for correlated evolution between these traits (Pagel's model; likelihood ratio = 136.237, $P < 0.0001$; Supplementary Table 12). These results support the hypothesis of complex teeth being a crucial tool for transitions towards this axis of ecological specialization within fishes. In addition, the diverse arrangements of multiple cusps may support a greater diversity of tooth functions[40]. The versatility provided by complex teeth to fill a range of ecological niches (Fig. 3a–c) probably gave lineages with complex teeth an advantage in rapidly changing rift lake environments[41,42].

Evolutionary rates often show time dependency that may signal interesting biological phenomena[29,43]. The strong effect that lability has on diversification rates uncovered in our analyses indicates a speciational mode of character change in extant fishes. We suggest that this uniquely high lability of tooth complexity and complexity itself are key innovations for African cichlids, which have interacted to spur rapid diversification along multiple ecological axes of divergence. A rapid change in tooth complexity can drive divergence along depth gradients because complex teeth are tightly associated with herbivory in littoral habitat, where algal productivity is high. The dietary versatility (Fig. 3a) of complex teeth accelerates ecological diversification, and rapid reversion to simple teeth can allow further ecological specialization, such as piscivory[44]. Habitat and ecology are known axes of speciation in cichlids[26,38] and divergence in tooth complexity also characterizes sympatric ecotypes at early stages of speciation[45]. Haplochromine species, which have colonized lakes Malawi and Victoria and represent replicate examples of explosive adaptive radiation, have both increased lability of tooth complexity (Fig. 2a) and a propensity to radiate in lakes[38]. Rapid transitions between simple and complex teeth may facilitate simultaneous divergence in diet and along habitat gradients in rift lakes. Together, these innovations allowed species in lakes Malawi, Victoria and Barombi Mbo to take advantage of expanding ecological opportunities as the lakes filled, spurring rapid adaptive radiation. Continued increases in tooth complexity within Actinopterygii and across the vertebrate tree may be necessary to maintain diversification rates as niches continue to fill and there is an inevitable push to feed at a lower trophic level[11,46,47].

Flexible development underlies lability

Although rare across living fishes, producing complex teeth requires only a few changes within a highly conserved developmental program[21,48]. Clades that rapidly lose and gain complex teeth may take advantage of this by maintaining a flexible system of tooth development, leading to rapid evolutionary transitions between simple and complex teeth. Many haplochromine cichlids in lakes Malawi and Victoria undergo ontogenetic transformations in tooth complexity through consecutive tooth replacements, in which complex teeth in juveniles can be gradually replaced with simple teeth in adult fish[39]. This ontogenetic shift in tooth complexity suggests that all haplochromine lineages have the inherent developmental capacity to produce complex teeth, irrespective of adult ecology. Differential tuning of developmental pathways over ontogeny underlies trophic innovations in haplochromine cichlids[49]. Change in the timing of events during tooth development[50], therefore, could be a mechanism for uniquely rapid transitions between simple and complex teeth in this exceptional group.

Conclusions

The evolution of tooth complexity shapes rates of lineage diversification across the largest group of vertebrates, not by an effect of complexity itself but by a strong effect of increased evolutionary lability. We further show that both tooth complexity and lability are key innovations for African cichlids that interact to catalyse species and ecological diversification in rift lake radiations and explain some of the highest speciation rates seen in vertebrates. Our results offer a counterpoint to the traditional view of evolutionary innovations as traits that rarely evolve and directly increase rates of lineage diversification[5]. Differences in how innovations evolve across clades can have an even greater effect on diversification when the trait is tightly coupled to an axis of divergence, such as diet or habitat. This new concept of evolutionary innovation—increased lability of a discrete trait, or an ‘evolutionary seesaw’—reflects clade-specific differences in evolvability that could explain macroevolutionary variation in speciation rates[29]. Defining traits as key innovations from this new perspective is supported when the trait is linked to known speciation axes, and developmental mechanisms may underlie the differences in lability[32]. Identifying these differences in lability requires broad comparative studies and multiple origins of the trait, two criteria often missing from traditional key innovation studies. Considering evolutionary innovations in this manner will probably implicate many previously overlooked traits as important drivers of the widespread variation in species diversification rates across the tree of life.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-025-08612-z.

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Methods

Tooth complexity classification

We generated a dataset of tooth complexity classifications for 30,915 extant species of ray-finned fishes[51], which represents all families, from the existing literature (Supplementary Table 1). We considered species to have complex teeth if primary teeth with more than one cusp were present on the maxilla, premaxilla or dentary of adult fish. Although complex teeth may vary in the total number of cusps (2–12), this binary classification reflects a major evolutionary transition with functional implications, following the traditional view of a key innovation. The data include all orders of Actinopterygii and missing data are not biased towards any particular group. We generated an expanded dataset for cichlid lineages from Africa, South Asia and Madagascar (n = 1,069) representing 92.7% of taxonomically valid species described before 2019 (ref. 31 and Supplementary Table 6). All categorizations are based on adult fish. We quantified the proportion of lineages with complex teeth and proportion of lineages with high lability for each family that had at least one complex lineage and at least ten species in the tree built with genetic sequence data (n = 31 families). These criteria excluded Anablepidae (five species in tree), Scoloplacidae (one species in tree), Astroblepidae (zero species in tree), Ephippidae (eight species in tree), Scatophagidae (three species in tree), Nomeidae (nine species in tree) and Ariommatidae (three species in tree). We calculated these proportions for Neotropical and African cichlids, two monophyletic groups, separately to highlight the marked difference between these two continental radiations (Extended Data Fig. 1b).

Phylogenies

We used the Fish Tree of Life[1] as the backbone phylogenetic hypothesis for our analyses across ray-finned fishes. As phylogenies built using birth–death polytomy resolvers and similar methods break down natural phylogenetic patterns and should not be used for analyses of trait evolution[52], we pruned our data to match a time-calibrated tree built using only genetic sequence data (n = 11,508 species) for all comparative analyses; we recognize that the total number of transitions is probably underestimated because of this. For our analyses within cichlids, we used the time-calibrated phylogeny of ref. 31, which includes all taxonomically valid species before 2019 pruned to include the 1,069 species for which we had data on tooth complexity.

Character evolution models

We used continuous-time Markov models implemented in RevBayes v1.2.1 to study the evolution of tooth complexity across ray-finned fishes and within cichlids. For our dataset across ray-finned fishes (n = 11,508 species), we fitted equal-rates (ER) and unequal-rates (ARD) models. As the evolution of a trait can vary across large phylogenies[53,54], we fitted additional ER and ARD models each with two hidden rate categories (HR2-ER and HR2-ARD). These hidden states are rate classes that allow transition rates to vary between classes but impose the constraints of the ER and ARD models within each class. We set a prior of 200 transitions across the tree. We also fitted a model that allowed the process (that is, ER or ARD) to vary across the tree, and rates to vary between the processes (H2-variable). For this, we set a prior of 200 transitions under ARD, 400 transitions under ER, and 10 transitions between these processes. We used a power posterior analysis and stepping-stone sampler to estimate marginal likelihoods for each model. The simulation used 10 stones sampling 1,000 states from each step with a 5,000-generation burn-in. For our expanded cichlid dataset (n = 1,069 species), we fitted ER, ARD, HR2-ER and HR2-ARD models, as well as ER and ARD models with four hidden rate categories (HR4-ER and HR4-ARD). We used a prior of 100 transitions between simple and complex teeth. We again used a power posterior analysis and stepping-stone sampler to estimate marginal likelihoods for each model. The simulation used 100 stones, sampling 1,000 states from each step with a burn-in of 10,000 generations. When comparing all character evolution models, we used a flat Dirichlet prior distribution for the root state frequencies. We compared model fit using Bayes factors, for which $\ln[\mathrm{BF}(M_0, M_1)] = \ln[P(X|M_0)] - \ln[P(X|M_1)]$ and $\ln[P(X|M_0)]$ is the log-transformed marginal likelihood of M_0, $\ln[P(X|M_1)]$ is the log-transformed marginal likelihood of M_1, and $\ln[\mathrm{BF}(M_0, M_1)]$ is the log-transformed Bayes factor. To estimate ancestral states and transition rates for the best-fit model (HR2-ARD) across ray-finned fishes, we ran two independent Markov chain Monte Carlo (MCMC) replicates for 50,000 generations with 10% burn-in, with root state frequencies set to an equal probability of simple across both hidden rate categories[21]. We verified that both chains converged on the same posterior distribution with Kolmogorov–Smirnov tests in the R package convenience[55], with a precision (α) level of 0.01, and retained a single run for analyses (Extended Data Fig. 2k–p). For cichlids (HR4-ER), we ran 2 independent MCMC replicates for 50,000 generations with 10% burn-in and set root state frequencies to an equal probability of simple or complex across the two lower hidden rate categories owing to complete uncertainty of the root state under a flat Dirichlet distribution. We verified convergence with Kolmogorov–Smirnov tests (α = 0.01) and retained a single run for analyses (Extended Data Fig. 3e–j). We note that the MCMC sampler in RevBayes requires fewer generations to reach convergence because each generation is more computationally intensive. We used ancestralStateTree to compute the MAP ancestral state estimation and characterMapTree to generate the MAP character history through stochastic character mapping[56]. We visualized these MAP reconstructions using the R package RevGadgets v1.2.1[57].

State-dependent diversification

We used the non-parametric test FiSSE[58] to test for state-dependent diversification across our ray-finned fish dataset (n = 11,508 species) because the computational burden of other models (that is, HiSSE) in a Bayesian framework is prohibitive at this scale. The R functions used to run FiSSE are available at https://github.com/macroevolution/fisse/tree/master/run_fisse. FiSSE analyses used a tolerance of 0.1 and a parsimony rate type because our ancestral state reconstruction suggests that the use of an Mk model (equivalent to an ER model) is not supported (Fig. 1f and Supplementary Table 3). Two-tailed P values are reported. We estimated speciation rates using the DR statistic[59]. This metric is considered an estimate of 'recent' speciation because it puts more weight on recent splitting events compared to splitting events deeper in the tree. Accordingly, the DR statistic may be robust to issues of non-identifiability[60]. To supplement our FiSSE analyses, we conducted phylogenetic ANOVA analyses on log-transformed DR values in the R package phytools v2.0.4[61]. Group sample sizes were 10,361 simple and 1,147 complex species, and 11,075 low and 433 high species for FiSSE and ANOVA tests for effects of tooth complexity and lability, respectively. We used Cohen's d to estimate effect sizes, for which d is the difference in group means divided by the pooled standard deviation. For our expanded cichlid dataset, we fitted a suite of formal Bayesian SSE models in RevBayes v1.2.1. Character evolution models indicated that the evolution of tooth complexity is a heterogeneous process across African cichlids (Fig. 2a and Supplementary Table 7), which violates an assumption of SSE models[62]. SSE models fitted over the full phylogeny did not converge, probably for this reason. To accommodate this, and better account for the extreme diversification rate heterogeneity within Cichlidae[31], we created four subtrees. Our subtrees represented Lake Tanganyika (n = 200 of 240 estimated species[35]; sampling fraction 0.83), Lake Malawi (n = 374 of 399 described species[31]; sampling fraction 0.94), Lake Victoria region superflock (LVRS; n = 169 of a conservative 300 estimated species; sampling fraction 0.56) and lineages in rivers and smaller lakes (n = 317 of 318 described species[31]; sampling fraction 0.99). We excluded lineages endemic to Lake Barombi Mbo from this analysis. For each subtree, we fitted the same set of seven SSE models, which included BiSSE[62], character-independent models[63] with two, three and four rates (CID-2, CID-3 and CID-4) and HiSSE models[63] with two, three and four hidden states (HiSSE-2, HiSSE-3 and HiSSE-4) in RevBayes. For all models, we used a normal distribution as the prior distribution of the log speciation and extinction rates, with mean ln(no. taxa/2) divided by the age of the tree. The prior expected number of character transitions was unique to each subtree; Lake Tanganyika (10 transitions), Lake Malawi (200 transitions), Lake Victoria (50 transitions) and rivers (20 transitions). We used power posterior analysis and stepping-stone sampling to calculate marginal likelihoods of all ($n = 28$) models, with 50 stones sampling 1,000 states from each step and 5,000-generation burn-in. We compared models within each subtree using Bayes factors. Models did not properly mix or reach convergence over the LVRS subtree, possibly owing to the young age and high number of species in Lake Victoria itself. For these reasons, we do not interpret state-dependent patterns for the LVRS subtree.

To test whether differences in evolutionary lability affect rates of lineage diversification, we first assigned all species to the MAP transition rate class estimated from our ancestral state reconstruction. The level of evolutionary lability was thus a binary trait for ray-finned fishes (low or high) and a four-state trait for cichlids (very low, low, high or very high). We again used FiSSE and phylogenetic ANOVA to compare speciation rates, estimated using the DR statistic, for different levels of lability across ray-finned fishes. For cichlids, we compared four-state HiSSE models with two (MuHiSSE-2), three (MuHiSSE-3) and four (MuHiSSE-4) hidden states as well as CID-2, CID-3 and CID-4 models fitted over the full tree ($n = 1,069$ tips), using power posterior analysis and stepping-stone sampling (10 stones, 1,000 samples from each step, 5,000-generation burn-in) to estimate marginal likelihoods; we compared the models using Bayes factors. Bayesian hidden-state models inherently test the null hypothesis of character-independent diversification; if this hypothesis is supported, the posterior distribution of diversification rates within a hidden state would overlap. We interpret this, along with formal model comparison, as combined evidence to support or refute the hypothesis of character-dependent diversification. Models had a prior of ten transitions in the level of lability. We used MCMC to sample the posterior distribution of speciation and extinction rates for the MuHiSSE-2 and MuHiSSE-4 model to account for instability in the marginal likelihood estimates of more complex models (Supplementary Table 9). We ran two independent chains of 50,000 generations with 10% (MuHiSSE-2) and 20% (MuHiSSE-4) burn-in and verified convergence of the runs with Kolmogorov–Smirnov tests ($\alpha = 0.01$; Extended Data Fig. 5). We combined the runs and verified convergence of the combined runs using checkConvergence in the R package convenience ($\alpha = 0.01$).

Distinguishing between high rates

Ancestral state reconstructions assume that diversification rates are uncorrelated to the character state; high transition rates may therefore be a product of high diversification rates. To address this, we first fitted a HiSSE model using the R package castor[64] to estimate transition rates between simple and complex teeth while accounting for differences in speciation and extinction between lineages (100 trials, 100 bootstrap samplings, sampling fraction = 0.328). Convergence failed after multiple optimization attempts, probably owing to the high tip bias towards species with simple teeth and rarity of lineages with high lability, which decreases the power and reliability of SSE models[33,62,65]. We report the estimated transition rates (Supplementary Table 5) to illustrate that qualitative patterns are similar to the HR2-ARD model. For all analyses in the main text, we use the transition rates estimated under the HR2-ARD model. Second, we conducted FiSSE tests over simulated character histories. We simulated 100 character histories of a 2-state character with 2 hidden states (HR2-ARD) across the Actinopterygian tree ($n = 11,508$ species) using a fixed transition matrix using the rTraitDisc function in the R package ape[66]. We populated the matrix with the mean rates estimated from the observed data under the HR2-ARD model, rescaled the matrix by a factor of 100, and set equilibrium frequencies equal across all states. For each simulation, we pulled out tip states and conducted FiSSE tests. We find that under the simulated data, tip speciation rates are similar between low and high lability (Extended Data Fig. 2d,e). Median λ values for low and high lability are similar ($\lambda_{low} = 0.134$, $\lambda_{high} = 0.120$). The distribution of two-tailed P values for FiSSE tests under the simulated data falls outside the significance level of 0.05 (96/100 tests; Extended Data Fig. 2f).

Extinction rate assumptions

To test whether our results were robust to assumptions on the extinction rate, we followed the methods of ref. 67 to place lower bounds on the prior distribution of extinction rates for both the MuHiSSE-2 and MuHiSSE-4 models. Extinction rates (μ) were defined as a linear function, with $\mu = A \times \lambda + \delta$, in which $A = 0.7$, 0.8, 0.9, 1 or 1.1, and δ is a random variable that allows extinction to be greater than $A \times \lambda$. A represents a lower bound on the extinction fraction (μ/λ), so $A = 0.7$ delineates that extinction rates must be at least 70% of speciation rates. For each A, we estimated speciation and extinction rates under the MuHiSSE-2 and MuHiSSE-4 model using MCMC; each chain was run for 100,000 generations. The posterior distributions of speciation and net diversification rates for all values of A (0.7, 0.8, 0.9, 1.0 and 1.1) and when μ and λ are freely estimated are shown in Extended Data Fig. 9 (MuHiSSE-2) and Extended Data Figs. 6 and 7 (MuHiSSE-4). We find that when $A = 0.7$, 0.8 or 0.9, the effect of lability on net diversification rates is consistent with the patterns under the free MuHiSSE-2 and MuHiSSE-4 model (Extended Data Figs. 7 and 9a), but the magnitude of the estimated rates is reduced. When $A = 1.0$, we find that the posterior distributions of rates largely overlap within all hidden rate categories. When $A = 1.1$, we find the reverse effect, in which increased lability appears to decrease net diversification rates. This reversed effect is probably due to the constraint of extinction being at minimum 110% of speciation rates; if a trait markedly increases speciation rates, then the corresponding extinction rates are forced to be high, resulting in a large effect on net diversification. Indeed, we find that when net diversification is negatively affected by increased lability for $A = 1.1$, speciation rates show a strong positive effect of lability (Extended Data Figs. 6 and 9b). These patterns are consistent with the results of ref. 67, indicating that high lability has a greater absolute effect on net diversification than low lability.

Transition rate prior sensitivity

The inferred number of character transitions, character histories and transition rates may be influenced by the choice of the transition rate prior. To test for prior sensitivity, we estimated the parameters of the HR2-ARD model under five priors: 50, 150, 200, 250 and 400 transitions. Across priors, the relative difference between transition rates in both low- and high-lability categories is consistent, and the estimated number of transitions and transition rates are consistent across all priors when lability is low (Supplementary Table 4). We find that increasing the prior number of transitions above 200 results in inflated transition rates when lability is high, driven by rapid consecutive state changes along the same branch (Extended Data Fig. 2a). Increasing the prior decreases the number of lineages with high lability and further isolates African cichlids as the dominant lineages with high lability (Extended Data Fig. 2b,c). We replicated our FiSSE analyses to test for an effect of lability from the ancestral state reconstructions across all five priors. We find that the effect of lability on tip speciation rates is insensitive to the choice of prior on the transition rate; lineages with high lability have significantly higher tip speciation rates across all five priors (50: $\lambda_{low} = 0.114$, $\lambda_{high} = 0.28$, two-tailed $P < 0.05$; 150: $\lambda_{low} = 0.116$, $\lambda_{high} = 0.507$, two-tailed $P < 0.01$; 250: $\lambda_{low} = 0.117$, $\lambda_{high} = 0.744$, two-tailed $P < 0.005$; 400: $\lambda_{low} = 0.117$, $\lambda_{high} = 0.818$, two-tailed $P < 0.005$). We also tested the sensitivity of transition rates within African cichlids to the prior. We estimated parameters of the HR4-ER model under three priors; 50, 100 and 150 transitions. We find that the transition rate estimates are stable under different priors (Extended Data Fig. 3a–d).

Cichlid diet data

We categorized 875 species of cichlids into 6 diet categories on the basis of the dominant adult prey type of each species. Categorizations were based on primary literature (Supplementary Table 6) and FishBase[68]. We classified species into one of six groups: piscivore, zooplanktivore, zoobenthivore (insects and molluscs), herbivore, omnivore and carnivore specialist (lepidophagy and paedophagy). For all diet analyses, we used a tree pruned to include only the 875 species for which we had data on both diet and tooth complexity.

Diet evolution in cichlids

To test whether tooth complexity accelerated ecological diversification, we first expanded our dietary dataset to include an associated binary state for tooth complexity (simple or complex) resulting in 12 combined diet–tooth states. All dietary classifications included both simple and complex lineages (Fig. 3c). We used a reversible-jump MCMC in RevBayes v1.2.1 to estimate transition rates between dietary categories within simple and complex lineages. We included a 'null' model in which the transition rate between any state was assumed to be 0 (as some transitions probably never occur; that is, simple piscivore to simple herbivore), and an ARD model that assumes the transition rate between any state is greater than 0, with a prior of 300 transitions. We set a prior probability of 0.25 that any transition rate is equal to 0. The MCMC was run for 10,000 generations, sampling every generation with 10% burn-in. We verified convergence of the transition rate estimates using checkConvergence in the R package convenience ($\alpha = 0.01$; effective sample size > 625 for all transition rate parameters). Mean rates were calculated from the posterior distribution for further analyses. We directly estimated the posterior probability that any rate was equal to 0; rates were fixed to be 0 if the posterior probability was estimated to be >0.75. We log + 0.01-transformed mean rates to fulfil assumptions of normality (Shapiro–Wilk test; $W = 0.96$, $P > 0.05$) and used an ANOVA test to compare rates when lineages have complex teeth ($n = 30$) to when lineages have simple teeth ($n = 30$). We estimated the effect size with Cohen's d. To test for correlated evolution between complex teeth and herbivory, we first converted our dietary classifications into a binary trait of herbivores and non-herbivores. We then used the fitPagel function in the R package phytools v2.0-4[61] to fit independent and dependent trait evolution models[69] and compared the fits with a likelihood-ratio test. Our results are robust to an alternative binarization of herbivory (herbivores versus herbivores and omnivores; Supplementary Table 12).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All the data generated and analysed in the current study, including tooth complexity classifications for 30,915 species of ray-finned fishes, are available via figshare at https://doi.org/10.6084/m9.figshare.25661859 (ref. 51).

Code availability

All RevBayes scripts used for phylogenetic analyses are available at https://github.com/npeoples/fish_tooth_complexity.

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Author contributions The study was conceptualized and designed by N.P. and P.C.W. N.P. collected the data on tooth complexity and diet and performed all analyses. Data interpretation was carried out by N.P. with support from P.C.W., M.M. and M.D.B. N.P. wrote the manuscript with contributions from all authors.

Competing interests The authors declare no competing interests.

Additional information

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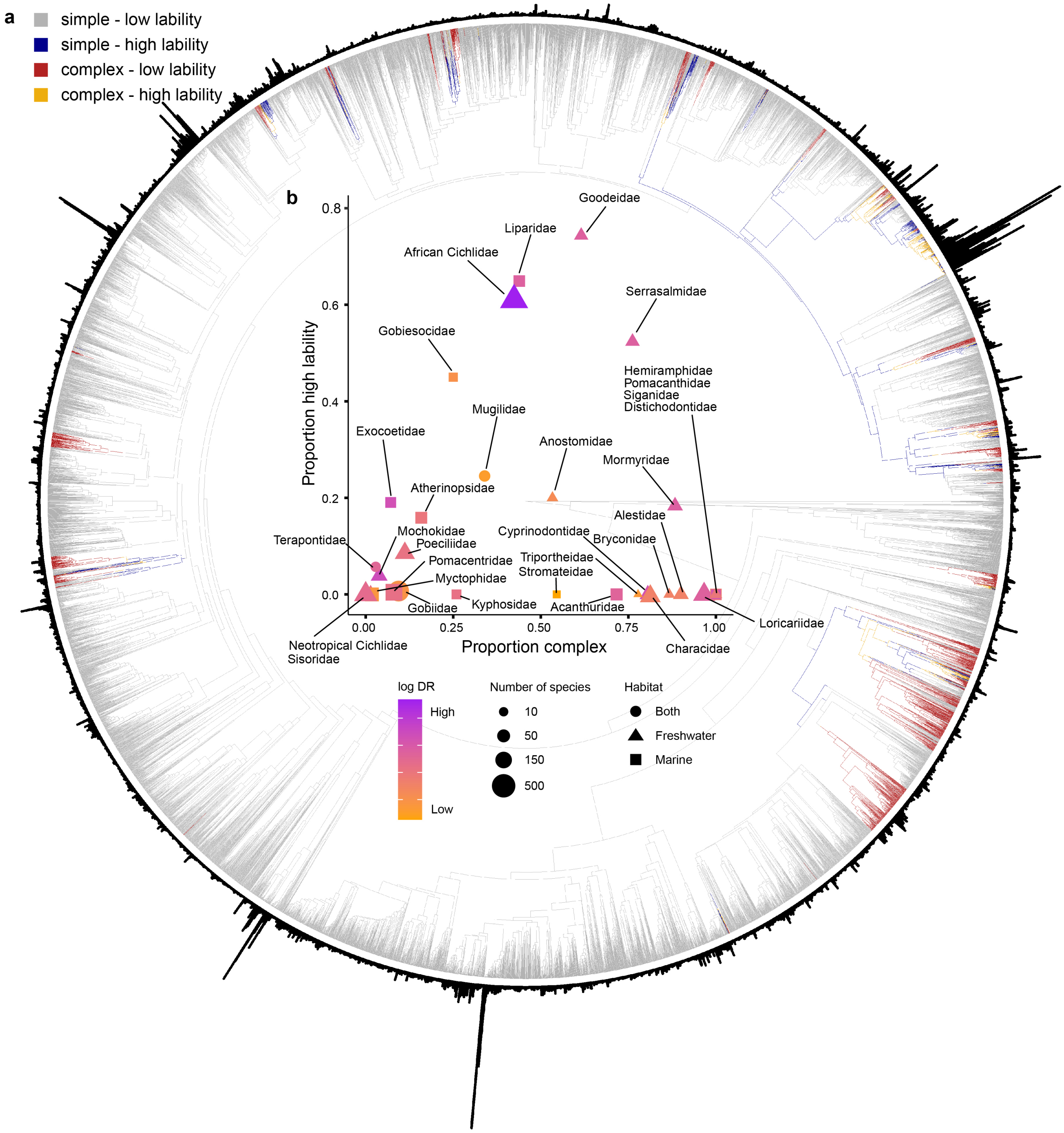
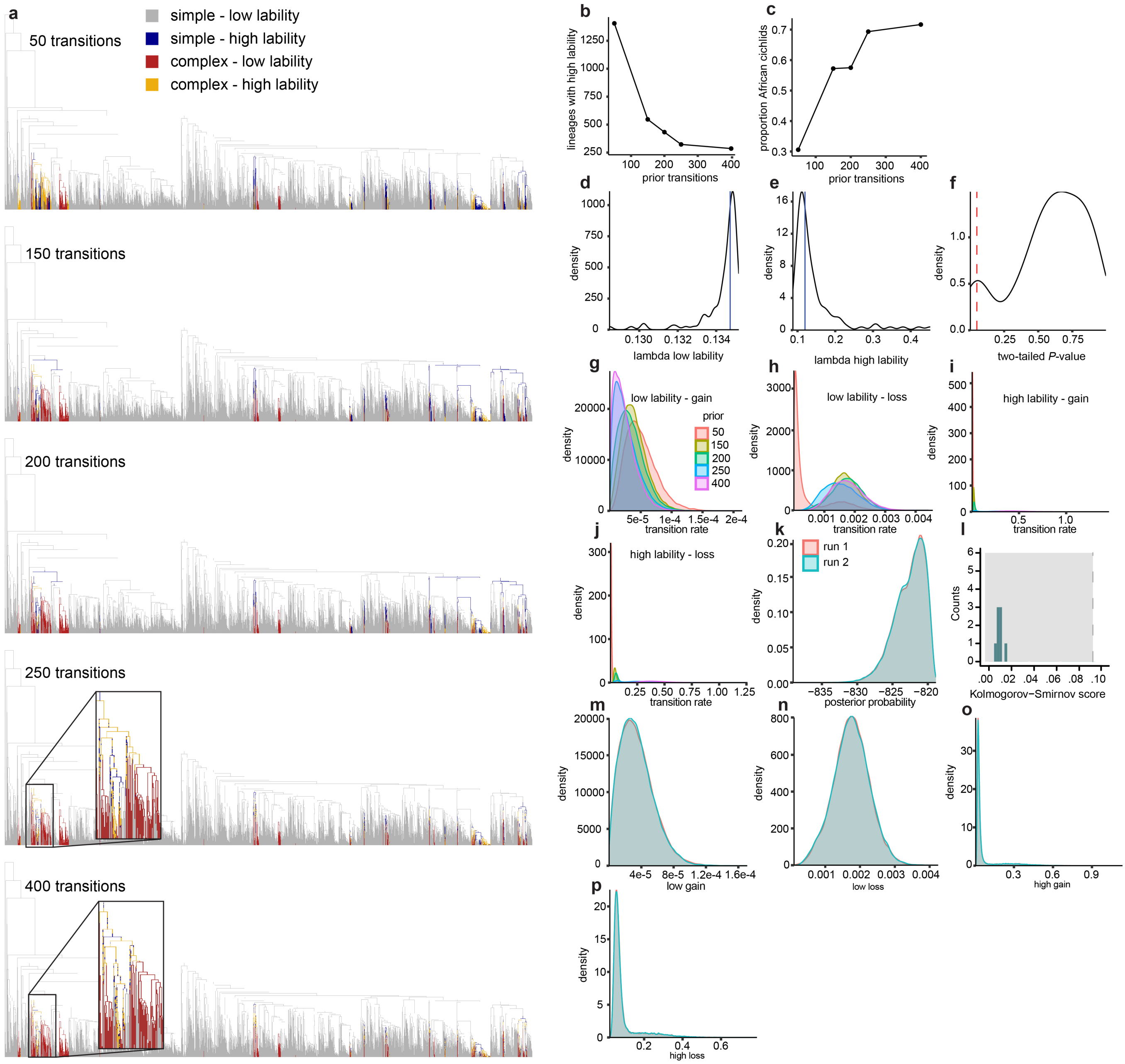
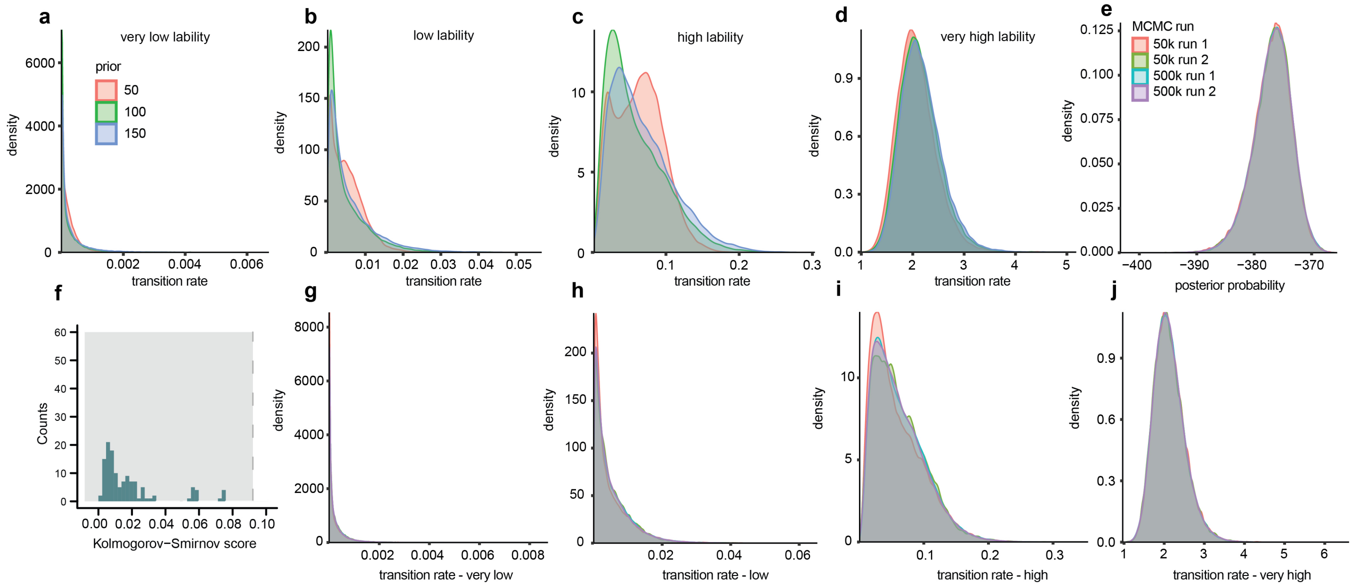


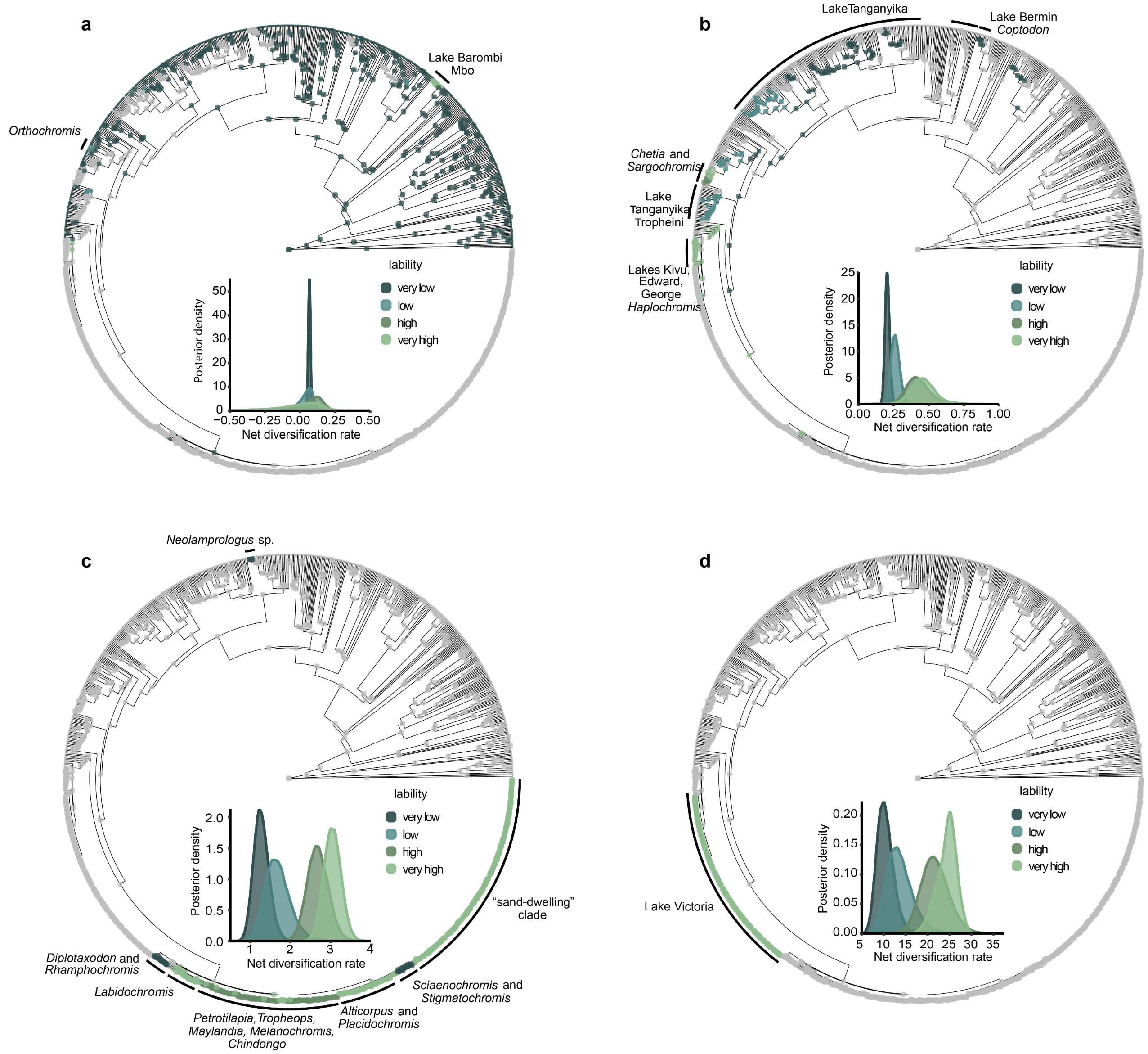
Extended Data Fig. 1 | The phylogenetic distribution of complex teeth and high lability across ray-finned fishes. a, Maximum a posteriori stochastic character map of tooth complexity and its evolutionary lability for 11,508 species of ray-finned fishes under a HR2-ARD model. Lineages with simple teeth are light grey (low labiltiy) and dark blue (high lability); lineages with complex teeth are red (low lability) and gold (high lability). DR statistic values, a measure of species' tip speciation rate, are plotted at the tips; longer bars indicate higher speciation rates. **b**, The proportion of lineages with complex teeth and high lability across families of ray-finned fishes that have at least one complex lineage (n = 31 families). The color of the points corresponds to family mean speciation rate, estimated using the DR statistic. The shape of the points represent habitat (freshwater, marine, both) and the size of the points are scaled by the total number of species. African and Neotropical cichlids are indicated separately to highlight the difference between these groups.



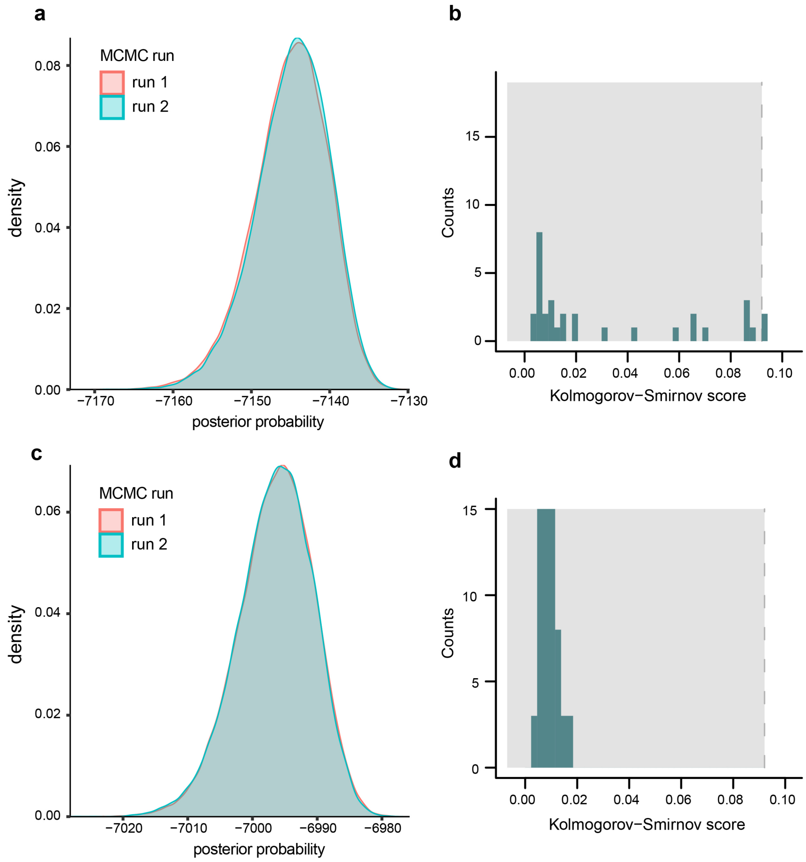
Extended Data Fig. 2 | The evolution of tooth complexity and effect of lability are robust to assumptions on the prior transition rate in ray-finned fishes. **a**, Maximum a posteriori ancestral state reconstruction of tooth complexity and its evolutionary lability across ray-finned fishes (n = 11,508 species) under the HR2-ARD model, under five different priors (50, 150, 200, 250, 400) for the total number of transitions. The insets for 250 and 400 highlight that rapid consecutive state changes on long branches inflate the transition rates in the "high lability" state under these priors. **b**, The total number of lineages with high lability and **c**, the proportion of lineages with high lability that are African cichlids under five different prior number of transitions. **d-f**, Simulated data shows no effect of lability on speciation rates. Distribution of FiSSE tip speciation rates for **d**, low lability and **e**, high lability over 100 ancestral state reconstructions simulated under the observed HR2-ARD model. Median rates are indicated with blue lines. **f**, Distribution of FiSSE two-tailed p-values for 100 simulated character histories; the red line marks the significance level of 0.05. **g-j**, Transition rates are robust to assumptions on the prior number of transitions. Posterior distribution of estimated rates for **g**, low lability gain, **h**, low lability loss, **i**, high lability gain and **j**, high lability loss under the HR2-ARD model for five priors (50, 150, 200, 250, 400) on the number of transitions. **k-p**, Convergence of the HR2-ARD model. **k**, Posterior probability distribution of two replicate MCMC runs of the HR2-ARD model. **l**, Histogram of Kolmogorov-Smirnov (KS) scores for model parameters. The grey dotted line marks the threshold for the KS test of 0.0921 ($\alpha = 0.01$, ESS > 625), indicating that the model parameters were drawn from the same distribution for both replicate runs. Posterior distribution of transition rates across replicate MCMC runs for **m**, low lability gain, **n**, low lability loss, **o**, high lability gain, and **p**, high lability loss.



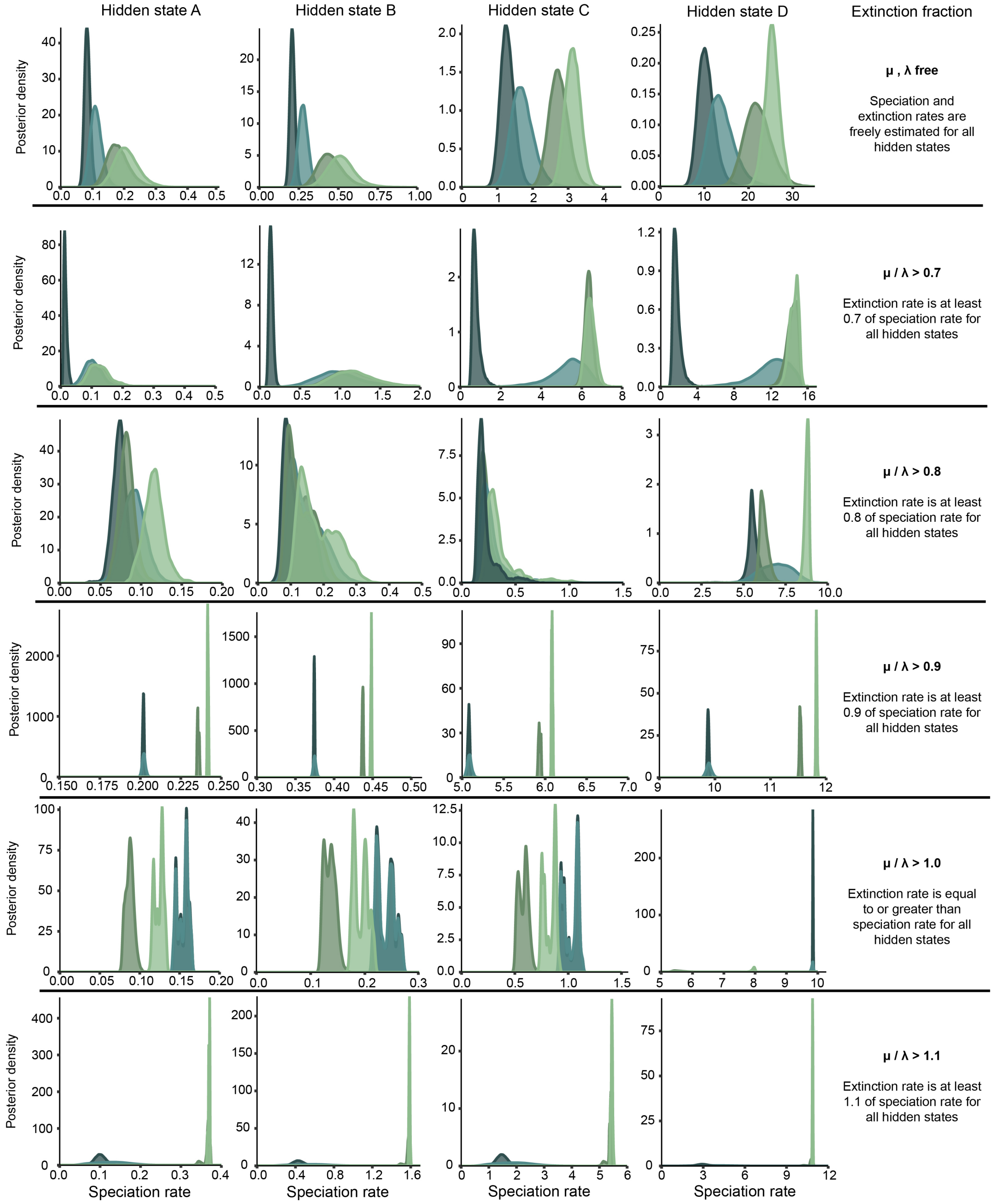
Extended Data Fig. 3 | Convergence and prior sensitivity analyses for the HR4-ARD model in African cichlids. Posterior distribution of estimated transition rates under the HR4-ER model for three different priors (50, 100, 150) on the total number of transitions; **a**, very low lability, **b**, low lability, **c**, high lability, and **d**, very high lability. **e**, Posterior probability distribution of four replicate MCMC runs of the HR4-ER model; two chains ran for 50,000 generations and two chains ran for 500,000 generations. **f**, Histogram of Kolmogorov-Smirnov (KS) scores for model parameters. The grey dotted line marks the threshold for the KS test of 0.0921 ($\alpha = 0.01$, ESS > 625), indicating that the model parameters were drawn from the same distribution for all replicate runs. Running the chain longer resulted in the same posterior probability distribution and transition rate estimates despite ESS scores <625 for some parameters for 50,000 generations. Posterior distribution of transition rates across replicate MCMC runs for **g**, very low lability **h**, low lability **i**, high lability and **j**, very high lability.



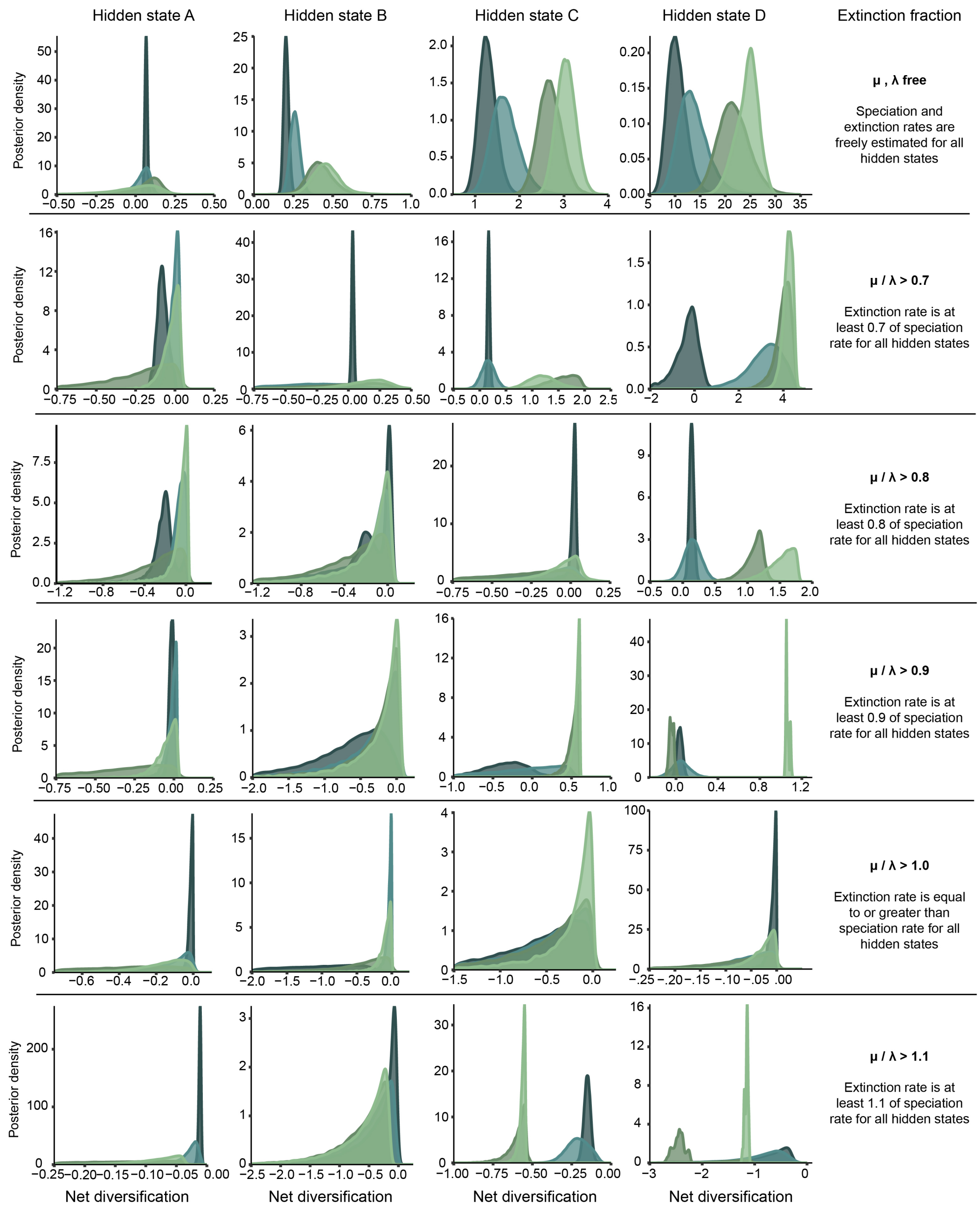
Extended Data Fig. 4 | Evolutionary lability of tooth complexity increases net diversification rates across four background rate regimes in African cichlids. Maximum a posteriori (MAP) ancestral state reconstruction of evolutionary lability for African cichlids (n = 1,069 species) under the MuHiSSE-4 model. Lineages in **a**, hidden state A, **b**, hidden state B, **c**, hidden state C, and **d**, hidden state D are highlighted separately. Selected clades are labeled for each hidden state. The posterior distribution of net diversification rates are reported for each level of lability, within each hidden state.



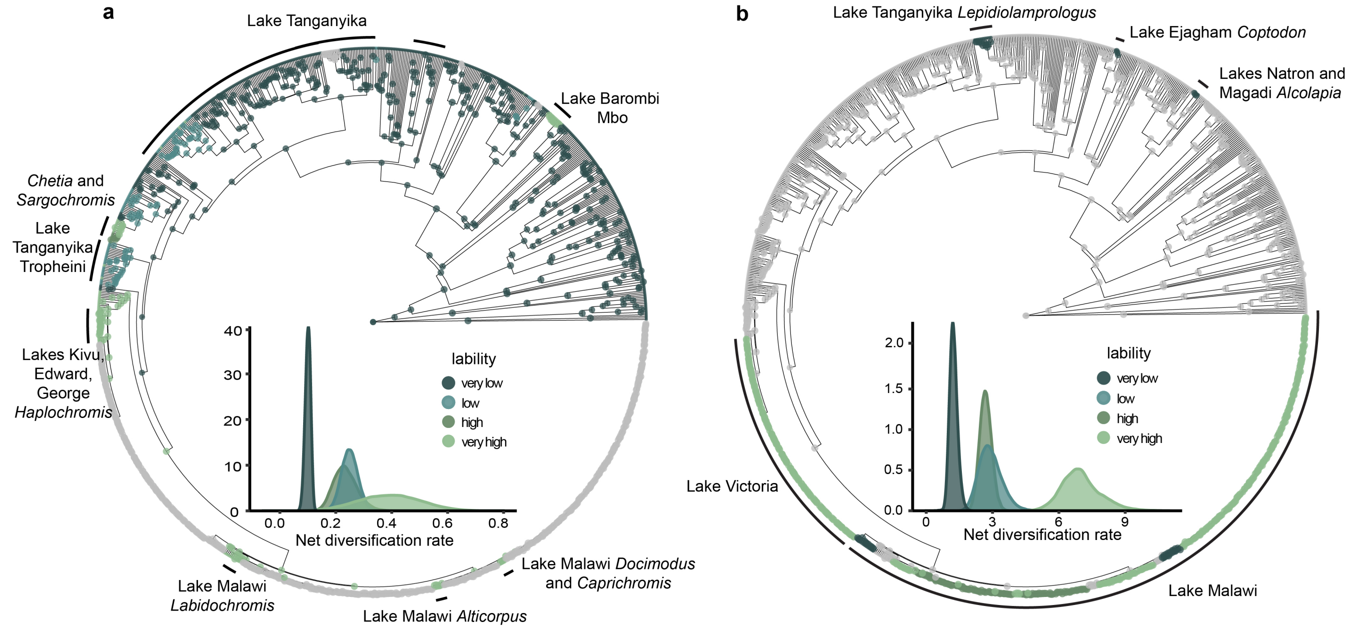
Extended Data Fig. 5 | Convergence of the MuHiSSE-2 and MuHiSSE-4 models, fit across African cichlids. a, Posterior probability distribution of two replicate MCMC runs of the MuHiSSE-2 model. **b**, Histogram of Kolmogorov-Smirnov (KS) scores for MuHiSSE-2 model parameters. The grey dotted line marks the threshold for the KS test of 0.0921 (α = 0.01, ESS > 625), indicating that the model parameters were drawn from the same distribution for both replicate runs. Two parameters fall just outside this threshold. **c**, Posterior probability distribution of two replicate MCMC runs of the MuHiSSE-4 model. **d**, Histogram of Kolmogorov-Smirnov (KS) scores for MuHiSSE-4 model parameters. The grey dotted line marks the threshold for the KS test of 0.0921 (α = 0.01, ESS > 625), indicating that the model parameters were drawn from the same distribution for both replicate runs.



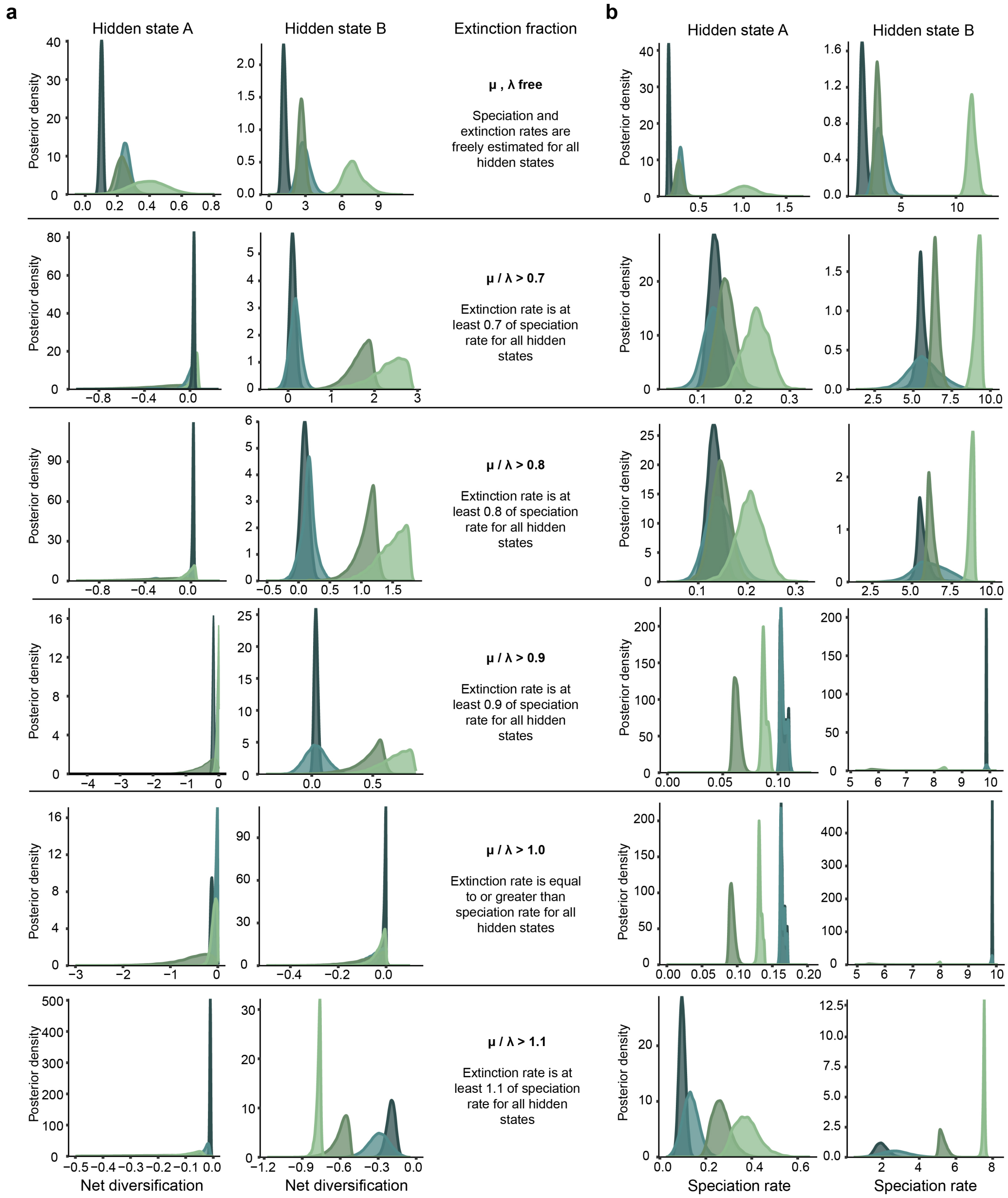
Extended Data Fig. 6 | Speciation rates for African cichlids under varying levels of lability and six relative extinction scenarios, estimated under a MuHiSSE-4 model. Posterior distributions of speciation rates for four levels of lability across four hidden states (A-D). Rates were estimated under six different relative extinction scenarios by setting lower bounds on the extinction rate (μ).



Extended Data Fig. 7 | Net diversification rates for African cichlids under varying levels of lability and six relative extinction scenarios, estimated under a MuHiSSE-4 model. Posterior distributions of net diversification rates, measured as speciation (λ) minus extinction (μ), for four levels of lability across four hidden states (A-D). Rates were estimated under six different relative extinction scenarios by setting lower bounds on the extinction rate (μ).



Extended Data Fig. 8 | Evolutionary lability of tooth complexity increases net diversification rates across two background rate regimes in African cichlids. Maximum a posteriori (MAP) ancestral state reconstruction of evolutionary lability for African cichlids (n = 1,069 species) under the MuHiSSE-2 model. Lineages in **a**, hidden state A and **b**, hidden state B are highlighted separately. Selected clades are labeled for each hidden state. The posterior distribution of net diversification rates are reported for each level of lability, within each hidden state.



Extended Data Fig. 9 | Speciation and net diversification rates for African cichlids under varying levels of lability and six relative extinction scenarios, estimated under a MuHiSSE-2 model. a, Posterior distributions of net diversification rates (speciation − extinction) for two levels of lability across two hidden states (A, B). **b**, Posterior distributions of corresponding speciation rates (λ). Rates were estimated under six different relative extinction scenarios by setting lower bounds on the extinction rate (μ).

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Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☐	☒	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	We did not use any software for data collection
Data analysis	We used R version 4.2.2 with packages ape v5.7.1, phytools v2.1.1, RevGadgets v1.2.1, and convenience v1.0.0. All functions required to run 'fisse' can be found at https://github.com/macroevolution/fisse/tree/master/run_fisse. We also used RevBayes v1.2.1, which can be downloaded from https://revbayes.github.io/download. RevBayes scripts are available at https://github.com/npeoples/fish_tooth_complexity/tree/main.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

All the data generated and analyzed in the current study, including tooth complexity classifications for 30,915 species of ray-finned fishes, are available at the figshare repository https://doi.org/10.6084/m9.figshare.25661859.

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	NA
Reporting on race, ethnicity, or other socially relevant groupings	NA
Population characteristics	NA
Recruitment	NA
Ethics oversight	NA

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We reconstructed the evolution of complex teeth, a vertebrate key innovation, across ray-finned fishes in order to test a key innovation hypothesis in a novel way. We find the rate at which complex teeth are gained and lost, but not tooth complexity itself, drives increased species diversification across fishes. We further show African cichlids change tooth complexity exceptionally fast when compared to all other fishes, and that within African cichlids, differences in this rate drive differences in net diversification rates. We also reported that tooth complexity increases the rate of ecological diversification within African cichlids. We provide evidence for a novel way that traits can affect species diversification.
Research sample	We collected data from all orders and families of Actinopterygii (ray-finned fishes). Our final datasets included classifications for 30,915 species of ray-finned fishes and 1,069 species of African cichlids (Cichlidae) (some of which were not present in our dataset across ray-finned fishes). We additionally generated a dataset of diet classifications for 875 species of African cichlids.
Sampling strategy	Our strategy was to classify tooth complexity for all species of ray-finned fishes present in the Fish Tree of Life (https://fishtreeoflife.org/). For this, we used existing literature as well as through observation of specimens purchased through the aquarium trade (for some cichlids and coral reef fishes).
Data collection	Nick Peoples collected all data on tooth complexity and diet through an extensive review of the literature. No software was used.
Timing and spatial scale	Data was collected over a period of two years (2021-2023).
Data exclusions	We excluded 19,407 species from our phylogenetic analyses across ray-finned fishes because these species were input into the phylogenetic tree using stochastic polytomy resolvers, which are well-known to break natural phylogenetic patterns. Trees built using these methods should not be used for analyses of trait evolution. We restricted our phylogenetic analyses to 11,508 species using a tree built only with genetic sequence data. We did not exclude any species from our analysis within African cichlids.
Reproducibility	All analyses can be reproduced, and RevBayes scripts are made available. We have also provided the output files of all power-

Reproducibility	posterior analyses and MCMC runs. Two tables are provided in the supplementary information that include references for all our tooth complexity and diet classifications.
Randomization	We used consistent criteria to classify fish teeth as being simple or complex. Most often, this explicit classification was reported in species descriptions/taxonomic review papers. Teeth are considered complex if there are two or more cusps present, with spacing between the cusps.
Blinding	No data blinding was performed.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☒	☐	Animals and other organisms
☒	☐	Clinical data
☒	☐	Dual use research of concern
☒	☐	Plants

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging

Plants

Seed stocks	NA
Novel plant genotypes	NA
Authentication	NA