OXFORD

Phenotypic rate and state are decoupled in response to river-to-lake transitions in cichlid fishes

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Abstract

Geographic access to isolated ecosystems is an important catalyst of adaptive radiation. Cichlid fishes repeatedly colonized rift, crater, and volcanic lakes from surrounding rivers. We test the "lake effect" on the phenotypic rate and state across 253 cichlid species. The rate of evolution was consistently higher (~10-fold) in lakes, and consistent across different dimensions of the phenotype. Rate shifts tended to occur coincident with or immediately following river-to-lake transitions, generally resulting in 2- to 5-fold faster rates than in the founding riverine lineage. By contrast, river- and lake-dwelling cichlids exhibit considerable overlap in phenotypes, generally with less disparity in lakes, but often different evolutionary optima. Taken together, these results suggest that lake radiations rapidly expand into niches largely already represented by ancestral riverine lineages, albeit in different frequencies. Lakes may provide ecological opportunity via ecological release (e.g., from predators/competitors) but need not be coupled with access to novel ecological niches.

Keywords: adaptive radiation, shape, ecological opportunity, ecosystem, feeding kinematics, functional morphology

Introduction

Geographic setting plays a key role in shaping the evolutionary trajectories of organisms and the lineages in which they arise (Schluter, 1996a, 1988; Losos & Ricklefs, 2009; Stroud & Losos, 2016). Colonization of a new environment is often a critical precursor to adaptive radiation (Gavrilets & Losos, 2009; Schluter, 2000; Simpson, 1953; Stroud & Losos, 2016). Islands, for example, provide release from competition and predation, as well as enhanced access to novel resources, in turn promoting rapid phenotypic specialization (Schluter, 1988, 2000). Indeed, many of the most conspicuous adaptive radiations are found on islands, including Darwin's Galápagos finches (Grant & Grant, 2008; Lack, 1947), Hawai'ian honeycreepers (Lerner et al., 2011; Lovette et al., 2002) and stick spiders (Gillespie et al., 2018), Malagasy vangas (Jønsson et al., 2012), and Caribbean anole lizards (Losos, 2009). Lakes are analogous to islands in the aquatic realm and also host many conspicuous adaptive radiations, including East African cichlids (Seehausen, 2006), Ethiopian barbs (de Graaf et al., 2008), and Indonesian silversides (Pfaender et al., 2016).

Diversification in insular environments is particularly prolific in cichlids: riverine lineages have repeatedly colonized isolated lakes and produced some of the most striking examples of adaptive radiation (Seehausen, 2006, 2015). Perhaps most recognizable among these are the species-rich assemblages of Lakes Tanganyika, Malawi, and Victoria (Joyce et al., 2011; Meier et al., 2017; Ronco et al., 2021), but several notable radiations also occur in myriad smaller lakes throughout Africa (Martin et al., 2015; Meier et al., 2019; Schliewen et al., 2001; Wagner et al., 2012) and Middle America

(Barluenga et al., 2006; Elmer et al., 2010, 2014; Kautt et al., 2016). Geographic transitions generally lead to speciation (Seehausen, 2006). An underappreciated facet of this speciation process is the heterogeneity in its timing: whereas in some cases, speciation rapidly follows habitat transition, in others, it involves some period of evolutionary lag (Burress & Tan, 2017). The extent of lake radiation is influenced by several environmental, historical, and evolutionary factors. For example, species richness of lake radiations increases with lake size (Wagner et al., 2014) and decreases with predation pressure (McGee et al., 2020) and with clade age (Seehausen, 2006). The role of hybridization is increasingly appreciated as a catalyst of cichlid diversity (Salzburger, 2018; Svardal et al., 2021), including in each of the East African Great Lakes (Irisarri et al., 2018; Joyce et al., 2011; Meier et al., 2017; Malinsky et al., 2018; Svardal et al., 2020), as well as smaller lakes throughout Africa (Martin et al., 2015; Meier et al., 2019) and Middle America (Kautt et al., 2016). Putting these features together, there are myriad co-varying factors that nuance the richness of lake assemblages, and the timing by which such diversity arises.

In addition to high species richness, lake assemblages are known for rapid phenotypic evolution (Hulsey et al., 2010a) and high phenotypic diversity (Ronco et al., 2021). Conspicuously, however, the riverine lineages from which they evolved are also ecologically and morphologically diverse (Arbour & López-Fernández, 2016; Burress et al., 2017, 2022; López-Fernández et al., 2013; Winemiller et al., 1995). Although it has yet to be quantified at a broad scale, several authors have remarked about the high degree of phenotypic

overlap between lake and riverine assemblages (Burress, 2015; Seehausen, 2015), suggesting the viability of similar niches in both ecosystems. Under classic views of adaptive radiation, the invasion of insular environments is thought to prompt rapid evolution as species phenotypically specialize to niches that were previously unavailable (i.e., the invasion of novel "adaptive zones"; Schluter, 2000; Simpson, 1953). At its core, this view has two tangible features. First, the geographic transition could accelerate the rate of evolution (Freckleton & Harvey, 2006; Glor, 2010; Harmon et al., 2010; Mahler et al., 2010; Yoder et al., 2010). Second, geographic transitions may also lead to a shift in the mean phenotype as the lineage adapts to different environmental conditions. For example, river-to-lake transitions in stickleback result in rapid changes in body shape, defense morphology, and feeding morphology (Berner et al., 2008; Bolnick et al., 2009; Kaeuffer et al., 2012; Ravinet et al., 2013). Similarly, coral reefs fueled rapid changes in fish form and function as biting emerged as a viable feeding mode (Corn et al., 2022). Despite a clear signal of elevated lineage diversification in cichlids (Burress & Tan, 2017; McGee et al., 2020; Seehausen, 2006), it is uncertain how river-to-lake transitions have influenced the rate and pattern of phenotypic evolution, and how repeatable these features are across independent transitions.

In this study, we comprehensively assess the core "lake effect" during the evolutionary history of cichlid fishes across different dimensions of the phenotype—head shape as well as the functional morphology and mechanical properties of the oral jaws—while controlling for alternative sources of rate heterogeneity (e.g., lake size, hybridization, clade age, predation pressure, etc.). We further evaluate the temporal nature of the "lake effect" on phenotypic rates by assessing whether it manifests immediately (i.e., coincident with the geographic transition) or after some degree of evolutionary lag (i.e., delayed response). We then compare phenotypes between species that occupy rivers and lakes. We hypothesized that lakes may provide ecological opportunity via competitive release from competitors and/or predators. In this case, we expect rates of phenotypic evolution to be elevated relative to rivers. Second, we hypothesized that lakes may provide ecological opportunity via access to novel niches. In this case, we expect the phenotype, on average, to differ between species that occupy lakes and rivers and that lake assemblages have expanded phenotypic disparity, both resulting from lacustrine species expanding into trait space unoccupied by their riverine counterparts. Lastly, we place our results within the broader conceptualization of adaptive radiation and in the fundamental role of geographic setting in shaping the rate and patterns of how such radiation unfolds.

Materials and methods

Specimens and measurements

We examined radiographs of 894 specimens representing 253 species (one to five individuals per species) representative of the group's ecological and morphological diversity (Burress, 2015; Kocher et al., 1993; López-Fernández et al., 2012; Muschick et al., 2012). Our sampling also includes all major lineages distributed in India, Madagascar, the Americas, and Africa (except Lake Victoria; Burress & Tan, 2017; Irisarri et al., 2018; López-Fernández et al., 2010; Matschiner et al., 2017; McMahan et al., 2013). We measured three classes of traits: (a) mechanical properties of the oral jaws,

(b) functional morphological traits of the oral jaws, and (c) general characterizations of head shape (Supplementary Table S1). Mechanical traits included kinematic transmission (KT; Westneat, 1994), kinesis, and kinematic asynchrony (KA), which are properties of the oral jaw four-bar linkage system. KT, kinesis, and KA were calculated based on methods by Martinez and Wainwright (2019). See Martinez and Wainwright (2019) for detailed descriptions and illustrations of how these traits were calculated from the four-bar linkage system. KT is the ratio of output rotation of the oral four-bar's maxillary link to input rotation of the mandible (Martinez & Wainwright, 2019; Martinez et al., 2018). Higher KT values describe jaw systems modified for the transmission of velocity, whereas lower values depict jaws modified for the transmission of force. Kinesis is a measure of mobility of the four-bar linkage system, which was calculated after 20 °C of input rotation. Higher values of kinesis reflect a greater magnitude of movement during the feeding motion. KA reflects the degree of temporal asynchrony of the four-bar shape during motion (i.e., deviation from a linear motion—approximating the efficiency of the feeding strike; Martinez & Wainwright, 2019). Lower KA values reflect a more linear (i.e., efficient) feeding motion. These mechanical properties characterize the motion during feeding and are known correlates of jaw protrusion (Hulsey et al., 2010b) and feeding ecology in fishes (Burress et al., 2020; Price et al., 2011). These traits are analyzed separately from other traits in part because they are ratios (KT and KA) and are on different scales than the remaining traits (i.e., residuals; see below). Functional morphological traits included: lengths of the dentigerous arm of the premaxilla, ascending process of the premaxilla, maxilla, and mandible (articular and dentary). Shape traits included: head length, head depth, and snout length. The head length was measured as the distance from the anterior tip of the premaxilla to the joint between the neurocranium and spine. Head depth was measured as the vertical distance through the orbit. Snout length was measured as the linear distance between the anterior tip of the premaxilla to the center of the orbit. Shape traits are generally multifunctional, relating to various dimensions of fish biology, including feeding ecology, microhabitat use, and locomotion (Webb, 1984; Winemiller et al., 1995). Measurements were taken from images using the measure function in tpsDig2 (Rohlf, 2006) or were measured directly from specimens with digital calipers. Standard length was measured as the linear distance between the anterior tip of the premaxilla to the posterior edge of the hypural plate. Data are available on the Dryad Digital Repository (https://doi.org/10.5061/dryad.fbg79cp1n).

We then classified species based on the ecosystem they principally inhabit. The discrete nature of lakes facilitated a strict definition of associated species. Species endemic to lakes or otherwise limited to only immediate surrounding outflows from lakes were classified as "lake" (109 species). Given the more continuous and labile nature of rivers, this category was more inclusive, reflecting the broad range of flowing and stagnant water conditions that occur in rivers. Species that occur principally in rivers, including a few widespread species that broadly occur in rivers, lakes, and other types of habitats (e.g., marshes, etc.) were classified as "river" (144 species). Sampled riverine species are distributed in the Amazon, Orinoco, La Plata, Congo, Nile, and Zambezi Rivers, among others, whereas sampled lake species are distributed in Lakes Tanganyika, Malawi, Victoria, George, Albert, Barombi Mbo,

Bermin, Ejagham, Nicaragua, Xiloá, and Apoyo. This sampling includes 10 cases in which the lineage subsequently radiated within the lake and seven cases in which it did not.

Phylogenetic comparative methods

For phylogenetic comparative methods, we used a recent phylogeny (McGee et al., 2020) with broad sampling across the Cichlidae and strategically utilized constraints based on recent phylogenomic hypotheses (e.g., Burress et al., 2018; Irisarri et al., 2018; McGee et al., 2016). Analyses in R were performed with version 4.2.1 (R Core Team., 2022). For linear traits (functional and shape traits detailed above), we ln-transformed each measurement and calculated phylogenetic residuals with Brownian motion (BM) by regressing each trait against ln-transformed standard length using the phyl.resid function in the R package phytools (Revell, 2012). These size-relative traits were then used as input for subsequent analyses. For each class of traits, we calculated morphological disparity of lake and riverine cichlids using the disparity function implemented in geiger R package (Harmon et al., 2008). During this procedure, disparity was calculated as the Euclidean distance among all pairs of data points. Owing to the overwhelming evidence that fish trait evolution is often best fitted by Ornstein-Uhlenbeck (OU) models of evolution (López-Fernández et al., 2013; Burress et al., 2019; Friedman et al., 2016; Larouche et al., 2022; Muñoz et al., 2018; Muschick et al., 2014), we employed evolutionary model selection. We tested the effect of environment (river vs. lake) on head shape, functional morphology of the jaws, and mechanical properties of the jaws using mvMORPH (Clavel et al., 2015, 2019), which uses penalized maximum likelihood during model fitting. We fitted three alternative models: Brownian motion (BM1), a single optima OU (OU1), and a multi-optima OU (OUM) model in which river- and lake-dwelling cichlids have different trait optima. Each class of traits was analyzed in a multivariate framework (as defined above). To assess the relative fit of the models, we used a modified Akaike Information Criterion (AICc) that incorporates a correction for small sample size (Burnham & Anderson, 2002; Burnham et al., 2011). To distinguish model fits, we use the criterion that more complex models must have AICc scores > 2 less than simpler models to consider the fit improvement significant (Burnham & Anderson, 2002; Burnham et al., 2011; Butler & King, 2004). Otherwise, we default to simpler models when appropriate. These analyses were repeated across 1000 stochastic character histories estimated using the make.simmap function implemented in phytools (Revell, 2012) to account for regime uncertainty (for the OUM model). During the estimation of the stochastic history of ecosystem (river and lake), we used a transition model in which all rates are different ("ARD") and set the root state as riverine (Burress & Tan, 2017; Salzburger et al., 2005; Seehausen, 2015). To visualize the phenotypic data, we employed principal component analyses using the prcomp function in R.

Second, we tested for a "lake effect" on the rate of trait evolution. To do this, we estimated the environment-dependent rates of multivariate evolution for each class of traits using MuSSCRat (May & Moore, 2020). This method is an extension of BM, but with several of its core assumptions relaxed: the model jointly estimates the evolutionary history of the discrete and continuous characters, permits the continuous characters to have different rates, dynamically estimates the correlation matrix, and incorporates background rate variation (i.e., avoiding attributing all rate variation to the discrete character). Since rates are estimated for every branch, the model allows rates to vary through time and across the phylogeny (major assumptions of BM). As described above, rates of cichlid speciation, and presumably phenotypic evolution, are likely nuanced among lakes by covarying factors (Burress & Tan, 2017; Seehausen, 2006). For example, hybridization between divergent riverine lineages may have spurred exceptionally rapid adaptive radiation in some lake assemblages (Joyce et al., 2011; Meier et al., 2017, 2019). By accounting for background rate heterogeneity, we can tease apart these idiosyncrasies of individual lake assemblages and home in on a core "lake effect" on cichlid phenotypic evolution. We let state changes in each direction (i.e., lake-to-river, river-to-lake) have different transition rates while estimating the stochastic history of the discrete character (i.e., freeK model). The Markov chain Monte Carlo was run for 100k generations with 10% burnin. We ran MuSSCRat using a random local clock (RLC) and uncorrelated lognormal clock (UCLN) (May & Moore, 2020) to assess the influence on the posterior probability that the rates were dependent on the environment (the character being either "river" or "lake"). Rates estimated with the RLC model have phylogenetic structure, whereas rates estimated with the UCLN model do not. We repeated analyses with different priors on the number of rate shifts (i.e., 25, 50, and 75 shifts) to evaluate its impact on posterior estimates of key parameters, including the number of transitions between environments, number of rate shifts, posterior probability that the rates were dependent upon the environment, and lake- and river-specific evolutionary rates.

Owing to the diversity of cichlids and that we sampled only a fraction of the described species, we evaluated the probability that our sampling could lead to type-I error. To do so, we simulated 100 datasets across the full McGee et al. (2020) phylogeny (1712 species) using a Brownian motion process with the fastBM function employed in phytools (Revell, 2012). To inform the simulated data, we used the mean rate from the observed data ($\sigma^2 = 0.62$), and set variance ($\alpha = 0.023$) and bounds (–0.515, 0.428) using a randomly chosen observed trait (i.e., snout length). We then pruned these datasets to match our empirical taxon sampling (253 species) and used these reduced simulated datasets to test for significant differences (i.e., type-I error) with MUSSCRat. Another consideration is that evolutionary rates may simply scale with time (Gingerich, 1983; Harmon et al., 2021). In other words, younger clades may be inferred to have faster evolutionary rates. Since such patterns may be artifactual (i.e., non-biological), we directly assessed time-scaling by calculating mean rates for 29 non-overlapping clades that range in age from 1.1 to 68.2 My (Supplementary Table S2). We then regressed the observed and simulated clade rates against clade age to assess time-scaling. If, for example, the clade rates inferred from BM-simulated (i.e., constant rate) data scaled negatively with clade age, then the observed elevated rates for the generally younger lake lineages could be artifactual rather than biological.

To evaluate lake-specific effects, we estimated the branch-specific rates of phenotypic evolution with a second model that was naive of the discrete character history (all other priors and parameters as above; Burress et al., 2020). We summarized the magnitude of rate shifts as the rate ratio between the mean rate of the lake branch (see below) divided

by the mean rate of the founding riverine branch (i.e., the lake-specific background rate). We specified the lake branches in two ways. First, we defined an immediate lake effect using the branch coincident with the river-to-lake transition (i.e., the rootward branch relative to the oldest node fully resolved as the lake state). Second, we also considered a delayed lake effect using up to two subsequent (tipward) branches (modified from Burress & Tan, 2017; Supplementary Figure S1). These rate ratios allow us to evaluate heterogeneity in the magnitude of rate shifts associated with river-to-lake transitions as well as the relative timing of the rate shift.

Results

We detected 20.2 state changes on average, with 13.4 being transitions from river-to-lake and 6.8 being transitions from lake-to-river (Figure 1). Most time was spent in the ancestral river state, 76.4%, on average. Riverine cichlids had considerably higher disparity in head shape (DR = 1.48; Figure 2), occupying the phenotypic extremes in terms of small, elongate heads and deep, robust heads (Figure 2A). River and lake ecosystems had different evolutionary optima in terms of head shape (Table 1), which was principally driven by head depth (Supplementary Table S3). Notably, head length had nearly identical evolutionary optima (Table 1). Riverine cichlids exhibited greater overall disparity in functional jaw morphology (DR = 1.21), notably occupying a unique region of morphospace associated with large jaws with a long ascending process (Figure 2B). River and lake ecosystems had different evolutionary optima in their jaw functional morphology (Table 1). Riverine species tended to have larger jaws, with a longer ascending process (Supplementary Table
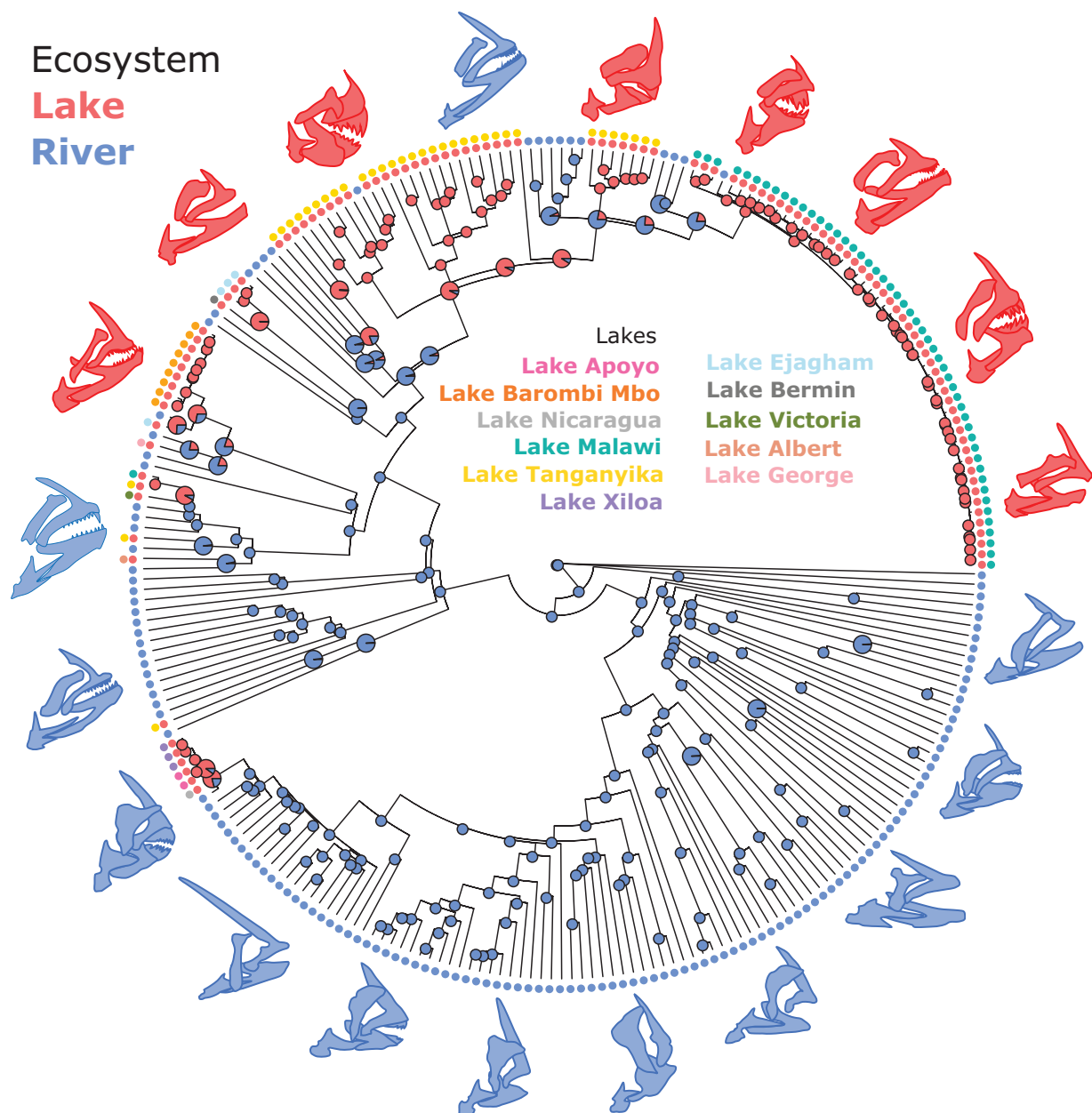
Figure 1. Geographic transitions between river and lake ecosystems during the evolutionary history of cichlid fishes. Pies at nodes depict the probability of each state. Dots around the tips depict the ecosystem (inner) and lake (outer) assignment for each species. Illustrations depict the oral jaws of an adjacent species.
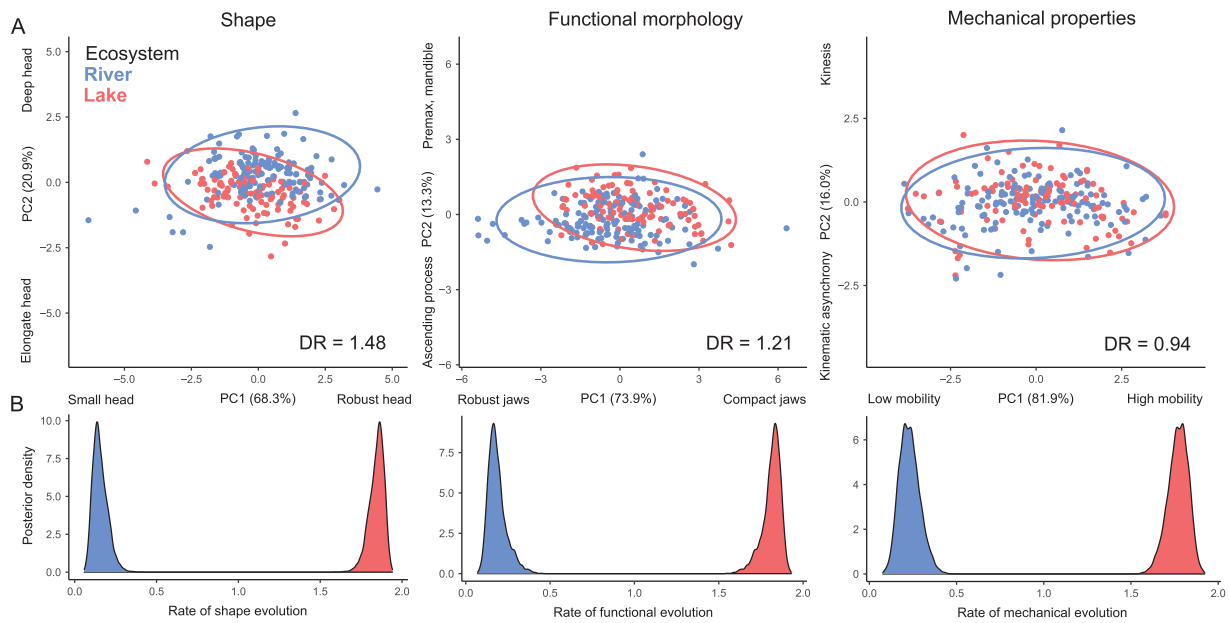
Figure 2. Dimensions of oral jaw diversity in cichlid fishes: general head shape, functional morphology of the jaws, and mechanical properties of the jaws across 253 riverine and lacustrine cichlids (A). Descriptions along the axes depict the loadings along each PC. Ellipses depict the 95% CI for each ecosystem type. Each point represents a species. Ecosystem-specific rates of phenotypic evolution for each dimension of phenotypic diversity (B).

Table 1. Evolutionary model fitting for head shape, jaw functional morphology, and mechanical properties of the jaws across river- and lake-dwelling cichlid fishes.

| Class of traits	Model	logLikelihood	AICc	ΔAICc	Prop.
Shape	BM1	−263.97	546.18	372.50	0.00
	OU1	468.76	−906.87	11.81	0.00
	OUM	**477.80**	**−918.68**	**0.00**	**1.00**
Functional	BM1	−483.20	994.83	1458.21	0.00
	OU1	250.11	−451.00	12.38	0.00
	OUM	**260.54**	**−463.38**	**0.00**	**1.00**
Mechanical	BM1	859.51	−1701.03	1268.61	0.00
	OU1	**1500.14**	**−2969.64**	**0.00**	**0.46**
	OUM	1503.61	−2970.30	0.66	0.54

Note. Brownian motion (BM1), single-optimum (OU1) and multiple optima (OUM) Ornstein-Uhlenbeck models, Akaike Information criterion corrected for small sample size (AICc), proportion of the stochastic character histories for which the model was best fit (Prop.) The best-supported model is indicated in bold.

S3). Lacustrine cichlids had nominally higher disparity in mechanical properties of the jaws than their riverine counterparts (disparity ratio; DR = 0.94), with near complete overlap in morphospace (Figure 2C) and river and lake ecosystems shared a single evolutionary optimum for mechanical properties of the jaws (Table 1 and Supplementary Table S3).

Rates of shape, functional, and mechanical evolution were faster in lakes than rivers (all models posterior probability; PP = 1.0; Figure 2D–F). Shape, functional, and mechanical traits evolved 12.8, 10.6, and 7.7-fold faster in lacustrine species than their riverine counterparts, respectively (Figure 2D–F). These differences in evolutionary rates were consistent across models with different priors (Supplementary Figure S2) and a different underlying model (Supplementary Figure S2). Simulated data did not produce false positives, indicating that these results were not an artefact of sampling (all PP < 0.10). Considering that lake assemblages were

disproportionately under sampled, our results likely provide a conservative estimate of the lake effect on evolutionary rates. Although the observed clade rates scaled negatively with clade age, clade rates inferred from BM-simulated data exhibited no time-scaling (Figure 3; Supplementary Table S3). This result indicates that the inferred evolutionary rates for the lake radiations is not an artefact of their younger ages relative to riverine lineages.

Rate shifts across river-to-lake transitions varied in their magnitude and timing (Figure 4). Seven of the 10 lakes had an associated rate shift (Figure 4). Cases in which there were no rate shifts associated with a river-to-lake transition were generally due to evolutionary rates already being rapid in the founding riverine lineage (e.g., Lake Ejagham) or because rates were not particularly high throughout the lake (e.g., Lake Tanganyika). River-to-lake transitions that did not result in a radiation also did not result in elevated evolutionary rates (Figure 4), suggesting that
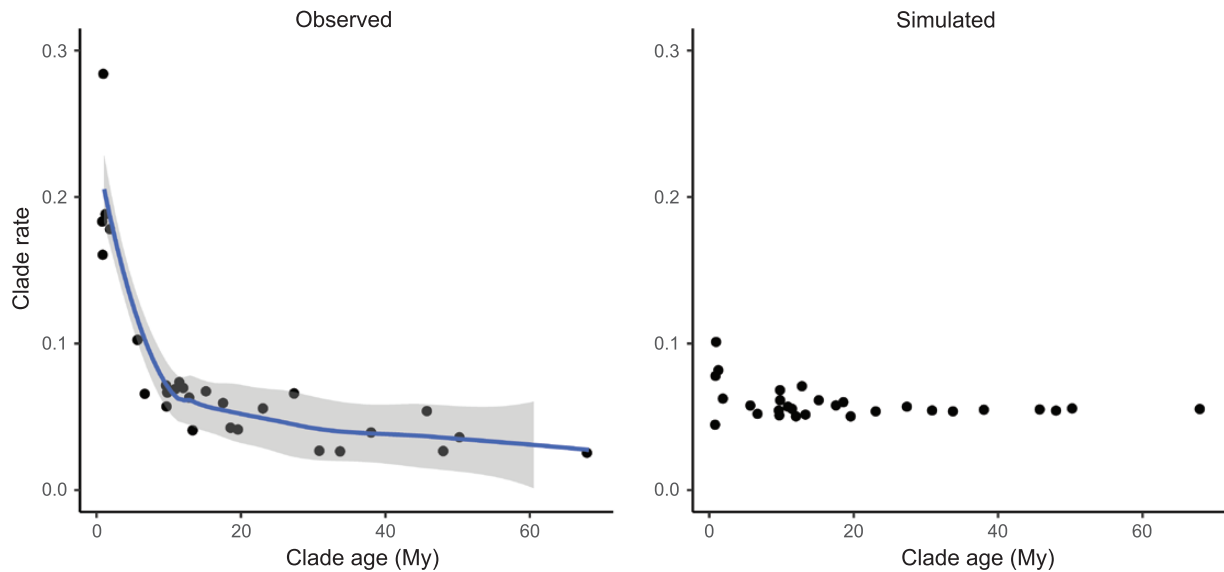
Figure 3. Time-scaling of phenotypic rates across 29 non-overlapping clades distributed across the cichlid phylogeny. The y-axis depicts the mean clade rates, whereas the x-axis depicts the clade ages. Each point represents a clade. Note that clade rate heterogeneity increases near the present in the simulated data, but the rates do not scale with clade age, as with the observed data.
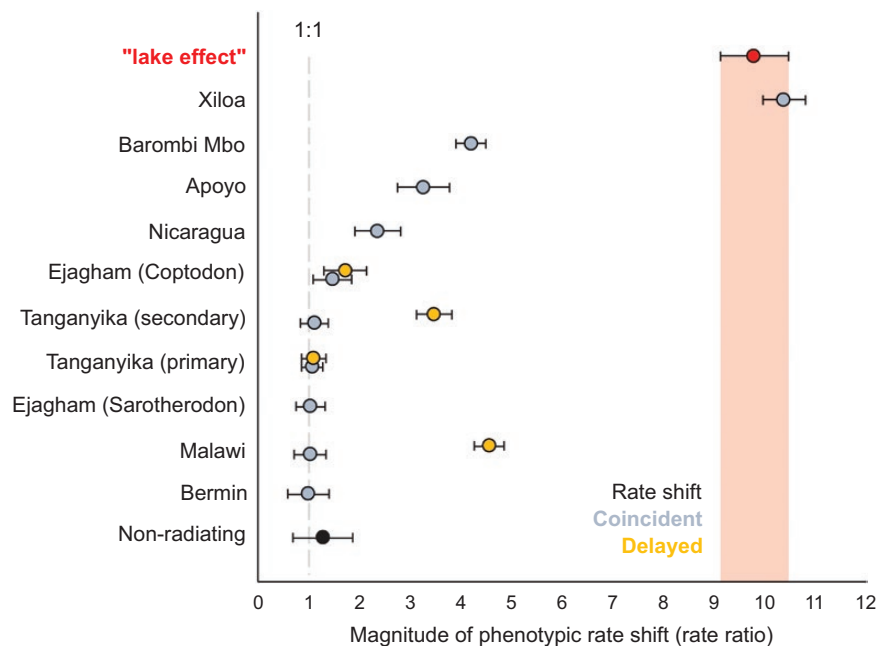
Figure 4. The magnitude (n-fold) of shifts in the rate of phenotypic evolution (mean ± 95% CI) across river-to-lake transitions. Lineages that subsequently radiated are listed separately by name. Lineages that did not radiate are summarized together as "non-radiating." The "lake effect" depicts the overall magnitude of rate change from MuSSCRat analyses. Note that the lake-specific rate ratios are calculated using the coincident and (if informative) immediately descending (i.e., delayed) branches relative to the founding riverine lineage, thereby homing in on the rather immediate impact of the river-to-lake transition, whereas the calculation of the "lake effect" rate ratio (shaded in red) involves all branches regardless of their proximity to transitions.

the lake effect results from cladogenesis rather than anagenesis. Interestingly, the magnitude of the initial rate shifts (2- to 10-fold) rarely matched the magnitude of the global "lake effect" (Figure 4), suggesting that a significant fraction of the "lake effect" accumulates well after the river-to-lake transition.

Discussion

Colonization of isolated ecosystems is often a defining ingredient of adaptive radiation (Gavrilets & Losos, 2009;

Schluter, 1988; Seehausen, 2006), but how such transitions impact phenotypic evolution at macroevolutionary scales is less well understood. Here, we affirm that lake colonization catalyzes cichlid evolution, accelerating both morphological and mechanical evolution 8- to 13-fold relative to riverine radiations. Nonetheless, as we unpack below, the signature of the "lake effect" is nuanced, both in the relative magnitude of rate change as well as the timing of rate shifts (i.e., whether it occurred immediately upon colonization, or following a lag period). Phenotypic evolution accelerated only

in lacustrine lineages that subsequently radiated, meaning that the "lake effect" is driven by cladogenesis rather than anagenesis. Notably, the magnitude of the "lake effect" is distinctly lower for jaw mechanical properties than for their underlying morphological traits. The diffused "lake effect" on mechanical traits may be a consequence of many-to-one mapping in which different morphological combinations converge on shared mechanical outputs (Muñoz, 2019; Wainwright et al,. 2005) (Supplementary Figure S3). Considering that river and lake cichlid jaws exhibit near complete overlap in their mechanical properties (Figure 2) and that many mechanically viable jaw functions are not realized (Martinez & Wainwright, 2019), both lacustrine and riverine lineages may have thoroughly explored the mechanical diversity feasible for the cichlid oral jaw system and its associated ecological constraints (e.g., dietary niche availability).

Lakes as motors for rapid phenotypic evolution, but not enhanced phenotypic novelty

Geographic transitions can catalyze adaptive radiation by providing release from ancestral predation and competition and/or by enhancing access to new or relatively untapped resources (Schluter, 1988, 2000; Simpson, 1953; Stroud & Losos, 2016), in turn facilitating rapid trait evolution as species specialize to novel niches. Biotic and abiotic factors likely work in concert to drive the "lake effect" of rapid phenotypic evolution observed in cichlids. First, the absence of top predators in recently colonized East African lakes likely facilitated the rapid speciation of those assemblages (McGee et al., 2020). Reduced predation enhances mobility and resource access that would otherwise be constrained by anti-predation behavior (Schluter, 1988).

In addition to predator release, lakes offer an expanded benthic-pelagic axis, likely facilitating more fine-scale niche partitioning and phenotypic specialization along the depth gradient (Friedman et al., 2020; Schluter, 1993; Seehausen & Wagner, 2014). In the terrestrial realm, for example, taller trees permit expanded niche partitioning by forest organisms (Leahy et al., 2021; Lister, 1976). Of course, many riverine fishes also diversify along the depth axis (Burress et al., 2017, 2022; Hollingsworth et al., 2013), but lakes tend to be deeper, often considerably more so, than rivers (exceptions include the vastly deep Congo River). Morphological and physiological adaptation of the jaws, fins, and digestive system accompany specialization along the depth gradient (Cooper et al., 2010; Elmer et al., 2014; Hulsey et al., 2013; Wagner et al., 2009). Many cichlid lineages, for example, are functionally aligned with substrate use, often specialized for grazing algae from rocks (Rüber et al., 1999), where they partition foraging sites based on depth (Albertson, 2008) and the rock surface angle (Genner et al., 1999). Certainly, this specialization is also present in riverine cichlids, evolving coincident with the same specialized dentition, but does not appear to be nearly as widespread as in lake assemblages (Burress et al., 2020; Casciotta & Arriata, 1993; Říčan et al., 2016). Similarly, planktivory is relatively common in lakes, including widespread species that occur in both lakes and rivers (Fryer & Iles, 1972), but this feeding ecology is comparatively limited in species found only in rivers (Winemiller et al., 1995). These asymmetries likely reflect the utility of an expanded depth dimension afforded by lakes (McGee et al., 2020).

While the expanded depth gradient might permit enhanced fine-scale specialization, it does not offer access to unique resources that enhance phenotypic disparity or favor the evolution of novel phenotypes relative to ancestral riverine lineages. In fact, both the most elongate and most deep-headed species occur in rivers, suggesting that, if anything, riverine species specialize (on both ends of the shape continuum) in ways that their lake counterparts do not. Deep bodies and short, stout caudal peduncles, and by extension deep heads, are associated with enhanced maneuverability (Webb, 1984), and may be particularly useful when navigating complex habitats at slow speeds. Certainly, lakes can also be spatially complex: East African Great Lakes, for example, have complex rocky reefs along their shores, which provide shelter, a substrate for food (e.g., algae), and often support high local cichlid diversity (Genner et al., 1999). A large proportion of these lakes, however, are relatively homogenous non-reef habitat comprising sandy substrate and open water. We argue that rivers provide many of the same habitats as lakes, as well as more complex and continually flowing habitat. This spatial discrepancy may have favored the evolution of morphologies associated with higher maneuverability (e.g., deep, short bodies [and heads], and short snouts; Webb, 1984), as observed in *Symphysodon*, *Pterophyllum*, and *Mesonauta*, fishes that occupy branches and wood tangles in stagnant portions of the Amazon River (Crampton, 2008; Pires et al., 2015). By contrast, fast water flow likely favored the evolution of elongate forms such as those found in the rapids of the Congo River (e.g., *Gobiocichla*, *Teleogramma*, and some *Steatocranus*; Alter et al., 2017; Schwarzer et al., 2012) and fluvial portions of the Amazon and La Plata Basins in South America (Astudillo-Clavijo et al., 2015; Burress et al., 2022; Varella et al., 2016). These factors likely contributed to the river and lake environments having different evolutionary optima for head shape and jaw functional morphology (Table 1), despite considerable overlap in morphospace. It is also noteworthy that similar phenotypes can have different functions in rivers and lakes. For example, low drag coefficients associated with elongate bodies may facilitate maintaining position in flowing water (rivers) or high-speed swimming in the pelagic zone of a lake (Webb, 1984; Hendry et al., 2011).

In this context, rivers differ from lakes in two important ways. First, their flowing nature means that they are labile and more prone to exchange with the surrounding terrestrial environment. For example, flooding provides periodic structural rearrangement of habitat and expands the available habitat into the floodplain. Second, the benthic-pelagic axis is physically constrained in rivers such that more of the water column is in immediate proximity to the benthos and structural habitat such as woody material and rocks. Flow imposes selection on morphology associated with swimming performance in fishes (Langerhans, 2008). For example, elongate phenotypes are suitable for steady-swimming through open water provided by lakes, and short, stout phenotypes are suitable for unsteady-swimming and complex maneuvers necessary to interact with structurally complex habitats that are prominent in rivers (Webb, 1984). Together, these factors help explain the greater head shape disparity observed in riverine cichlids (Figure 2). Although the more complex nature of riverine habitats may have permitted an expanded spectrum of phenotypes, the more heterogeneous conditions may have diluted selection necessary to elicit rapid evolution. In lakes, by contrast, reduced predation coupled with an expanded depth gradient (McGee et al., 2020) likely allowed the rapid, iterative proliferation of ecological niches, without

a simultaneous shift into novel regions of phenotype space. Such iterative evolution often results when a core set of phenotypes are widely adaptive across a radiation (Frédérich et al., 2013; Huie et al., 2021; Poe & Anderson, 2019; Slater, 2015; Van Valkenburgh, 1991).

A conspicuous feature of the "lake effect" is that a small fraction of its overall magnitude is attributable to the coincidence or immediate aftermath of the river-to-lake transition (Figure 4). This result indicates that most of the "lake effect" is driven by subsequent and ongoing phenotypic evolution (i.e., nearer the tips). One possibility is that lineages require time to phenotypically capitalize on the ecological opportunity afforded by lakes. In other words, whereas speciation and coloration can respond quickly to lake colonization (Burress & Tan, 2017; Seehausen, 2006; Wagner et al., 2012), adaptation of the jaw system and its functional properties may arise more slowly. For example, since adaptation often unfolds in a sequence (Hulsey et al., 2017; Kocher, 2004; Muschick et al., 2014; Ronco et al., 2021), the macroevolutionary signature of the "lake effect" protracts well beyond the initial colonization event.

Innovations do not explain evolutionary differences between riverine and lacustrine radiations

An alternative catalyst of adaptive radiation often cited in the literature is the origin of innovations that enhance functional versatility and capacity (Burress & Muñoz, 2022; Liem, 1973; Simpson, 1953; Heard & Hauser, 1995; Hunter, 1998; Stroud & Losos, 2016; Wainwright et al., 2012). Cichlids (both lacustrine and riverine) possess many such innovations, including specialized dentition and exaggerated snouts for scraping algae from rocks (Conith et al., 2018, 2019; Rüber et al., 1999), hypertrophied lips that facilitate feeding from crevices and interstitial rock gaps (Lukas et al., 2015), and mouth brooding, which increases mobility during parental care (Goodwin et al., 1998), among others. These innovations are perhaps best known from lake radiations, but most are also present in riverine lineages. Examples include specialized tricuspid dentition (Casciotta & Arriata, 1993), hypertrophied lips (Lucena & Kullander, 1992; Reis & Malabarba, 1987), and mouth brooding (Goodwin et al., 1998). Other innovations, like egg spots (Hert, 1989; Salzburger et al., 2005) are not shared among all lake-dwelling cichlids. Therefore, none of these innovations (at least on their own) suitably explain the rapid evolution associated with lake assemblages, although they may interact with lake features, like niche partitioning across depth, that magnify their utility. For example, hypertrophied lips are conspicuously associated with rapid sympatric speciation in lacustrine cichlids (Colombo et al., 2013; Elmer et al., 2010; Ford et al., 2016; Machado-Schiaffino et al., 2017) as well as other lake-dwelling fishes (de Graaf et al., 2008; Pfaender et al., 2016). In lakes, hypertrophied lips are linked to divergence along the depth gradient because their origin is often paired with a more pelagic form during ecological speciation (Elmer et al., 2010; Machado-Schiaffino et al., 2017). Hypertrophied lips, however, also arose in close association with rapid parallel adaptive radiation in riverine cichlids (Burress et al., 2018, 2022) as well as riverine barbs (Levin et al., 2020), although the ecomorphological link differs, as the innovation usually originates within a largely benthic clade (Burress et al., 2018, 2022; Levin et al., 2020). Therefore, innovations appear to impart functional and ecological versatility upon lineages (Burress et al., 2020;

Burress & Muñoz, 2021; Conith & Albertson, 2021; Ronco & Salzburger, 2021), but do not necessarily result in elevated rates of phenotypic evolution over macroevolutionary scales (Larouche et al., 2020, 2022; Seehausen, 2006). Interactions between existing functional innovations (e.g., pharyngeal jaws) and subsequent geographic transitions remains a fruitful line of inquiry (e.g., Wagner et al., 2012).

Decoupling of tempo and mode of trait evolution during adaptive radiation

Cichlids exhibit ecosystem-moderated decoupling in the rate and state of phenotypic evolution. River-to-lake transitions elicit a unified response of faster rates of evolution across multiple dimensions of the phenotype (i.e., head shape, jaw functional morphology, mechanical properties of the jaws). By contrast, there is no unified impact on the state of the phenotype across these same dimensions. While head shape and jaw morphology exhibit separate evolutionary optima for river and lake ecosystems, the mechanical properties of the jaws do not (Table 1). Further, not all head shape traits have different optima (Supplementary Table S3). These results suggest that rivers and lakes have a nuanced effect on adaptive evolution, with the outcome dependent on the traits in question. Lake assemblages exhibit largely the same trait values as well as similar (or a subset of) diversity represented by ancestral riverine lineages (Figure 2). While phenotypic evolution in lakes is rapid, it largely occurs via macroevolutionary recycling of phenotypes already present in river lineages. In this regard, cichlids join other canonical adaptive radiations—anoles, vangas, and labrids—that exhibit decoupled rate and state of phenotypic evolution based on geographic setting (Jønsson et al., 2012; Pinto et al., 2008; Price et al., 2011; Salazar et al., 2019). Decoupling of rate and state can also manifest among lineages that do not differ in geographic setting, reflecting evolutionary idiosyncrasies or lineage-specific constraints or innovations (e.g., Sidlauskas, 2008). Since lakes promote elevated rates, but not different phenotypes, river-to-lake transitions likely provide ecological release without also affording access to novel resources.

Beyond detecting the presence of decoupled rate and state, there is much that can be learned from dissecting how such decoupling unfolds and connecting the emergent pattern to the process(es) that might underlie it. Different underlying mechanisms (including genetic, mechanical, ecological, and behavioral features) can disrupt relationships between the rate and state of phenotypic evolution. Lineage-specific variation in genetic constraints can limit the range of potential phenotypes (both in mean and disparity), without necessarily also inducing shifts in evolutionary rate: evolution in certain G-matrix characteristics, for example, impacted ecomorph-specific phenotypic evolution in Caribbean anoles (McGlothlin et al., 2022). Greater time for divergence in older lineages can enhance disparity without a concomitant signature on evolutionary rate (Ricklefs, 2006). Theory posits some degree of coupling between the rate and state of phenotypic evolution during adaptive radiation, namely rapid phenotypic expansion (Simpson, 1953), yet adaptive radiation clearly proceeds with varying degrees and flavors of rate-state decoupling. This heterogeneity likely reflects a milieu of potential driving factors, including clade-specific innovations (Sidlauskas, 2008), geographic transitions (Salazar et al., 2019; Evans et al., 2019; this study), or both (Jønsson et al., 2012), as well as variable underlying mechanisms—ecological

release (Pinto et al., 2008), mechanical, life history, or genetic constraints (Castiglione et al., 2018; Schluter, 1996b; Stayton et al., 2018), or variance in time for evolution (Friedman et al., 2016). Despite the prevalence of such decoupling across diverse radiations, the relative prominence of different mechanisms and potential macroevolutionary outcomes remains unclear. We propose that unpacking how and why these phenomena arise is a fruitful framework with which to study phenotypic evolution and adaptive radiation.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Data are available on the Dryad Digital Repository (https://doi.org/10.5061/dryad.fbg79cp1n).

Author contributions

E.D.B. and M.M.M. designed the study. E.D.B. collected data and performed analyses in R and RevBayes. E.D.B. wrote the manuscript. M.M.M. helped revise the manuscript.

Conflict of interest: The authors declare no conflict of interest.

Acknowledgments

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