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Letter

A classic key innovation constrains oral jaw functional diversification in fishes

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Abstract

Modifications to the pharyngeal jaws—a prey processing system located posterior to the mouth cavity—are widely considered a key innovation that enhanced diversification within several prominent fish clades. Seen in cichlids, damselfishes, wrasses, and a few other lineages, these musculoskeletal alterations are believed to increase the evolutionary independence and, thus, the diversification of the oral and pharyngeal jaw systems. To test this classic hypothesis, we conducted comparative phylogenetic analyses to assess the effect of the pharyngeal novelty on the diversification of feeding morphology and kinematics across a taxonomically diverse sample of spiny-rayed fishes. We quantified movements of the oral jaws and other craniofacial structures from 689 suction-feeding strikes using high-speed videos collected from 228 species with and without the pharyngeal jaw novelty. Contradicting long-held predictions, we find significantly greater disparity across all traits and faster rates of oral jaw functional evolution in fishes without the specialized prey processing system. The modified pharyngeal jaw is undoubtedly a functional innovation as it enhances the strength of the prey processing system, facilitating exceptional transition rates to feeding on hard and tough prey. However, it also restricts the diversification of the feeding system, revealing that the impact of pharyngognathy is more nuanced than previously thought. In light of these and other recent findings, a reinterpretation of the macroevolutionary consequences of the pharyngeal jaw novelty is needed.

Keywords: pharyngognathy, geometric morphometrics, feeding kinematics, morphology, evolutionary integration, Acanthomorpha

Lay Summary

Thousands of fish species inhabit diverse aquatic environments due, in part, to the evolution of functional innovations. Such traits enable novel interactions with the environment, often facilitating increased diversification within the lineages in which they occur. Modifications to the pharyngeal jaws—a second jaw system located behind the mouth cavity that primarily functions to process prey—are widely considered innovations as multiple musculoskeletal changes allow fishes to process harder and tougher prey items (e.g., mollusks, algae). These modifications to the prey processing apparatus are predicted to increase the independence of the oral and pharyngeal jaws, enabling greater morphological and functional diversification in both systems. To test this classic hypothesis, we examined the diversification of oral jaw morphology and feeding motions in fishes with the modified pharyngeal jaw (133 species representing 4 families) and those without it (95 species representing 39 families). Contrary to long-held predictions, fishes with a specialized prey processing system show less variance across all traits and slower rates of functional evolution. Thus, although the novelty enhances the functional capacity of the pharyngeal jaws, it is also associated with restricted diversification of the feeding system. Our results highlight the importance of examining the consequences of specialized traits within a comparative framework, as their presence may not be uniformly advantageous to the diversification of functional systems.

Introduction

Key innovations are often credited as facilitators of organismal success across Earth's diverse ecological landscape (Bateman & DiMichele, 1994; Brusatte et al., 2015; German, 1982; Hodges & Arnold, 1995; Hunter & Jernvallt, 1995; Kirchberger et al., 2020; Miller & Stroud, 2022; Rainford et al., 2014; Wheat et al., 2007) as these traits enable new interactions with the environment and provide enhanced access to resources, leading to increased diversification (Alfaro, 2014; Heard & Hauser, 1995; Hunter, 1998; Mayr, 1963; Simpson, 1944). However, novel phenotypes affecting organismal performance, whether innovations or not, are subject to trade-offs that can complicate their macroevolutionary impacts (Higham et al., 2015; McGee et al., 2015; Wainwright & Price, 2016). Ray-finned fishes—one of the largest and most diverse vertebrate radiations (Hughes et al., 2018; Price et al., 2019)—showcase numerous functional innovations that enable

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survival in nearly all aquatic ecosystems (Wainwright & Longo, 2017). Several of these traits are morphological modifications that affect prey capture and manipulation (Ferry-Graham & Konow, 2010; Holzman et al., 2008; Konow et al., 2008; Motta, 1984; Stiassny & Jensen, 1987; Wainwright, 2005), making the feeding apparatus a rich system to examine the macroevolutionary impacts of functional novelties.

The fish feeding apparatus is a two-jaw system where oral and pharyngeal jaws independently perform prey capture (Alexander, 1967; Schaeffer & Rosen, 1961) and processing (Lauder, 1983; Wainwright, 2005) functions, respectively. Though the prey processing system is found throughout ray-finned fishes, pharyngognathy—a complex reconfiguration of the pharyngeal jaw bones and musculature that increases strength and mobility within the system (Figure 1A; Galis & Drucker, 1996; Hulsey & García De León, 2005; Kaufman & Liem, 1982; Lauder, 1983; Liem & Sanderson, 1986)—has independently evolved in several spiny-rayed fish clades (Acanthomorpha; Mabuchi et al., 2007; Wainwright et al., 2012). These structural changes include a fusion of the lower pharyngeal jaw bones into a single skeletal structure, a mobile joint between the dorsal face of each upper pharyngeal jaw bone and the base of the neurocranium, and a muscular sling suspending the lower pharyngeal jaw structure from the neurocranium. Occurring in cichlids, wrasses, surfperches, damselfishes, and a few other clades, species with a modified pharyngeal jaws (MPJ) can process more robust and tougher prey, like plants, algae, and mollusks (Kaufman & Liem, 1982; McGee et al., 2015; Stiassny & Jensen, 1987). In 1973, Karel Liem famously postulated that the MPJ had prompted such trophic diversification due to its potential impact on the coevolution of oral and pharyngeal jaws (Liem, 1973). For decades, the novelty has been regarded as a model key innovation that decoupled the evolution of prey capture and processing systems, enabling extensive ecomorphological diversification (Alfaro, 2014; Heard & Hauser, 1995; Salzburger, 2009; Stroud & Losos, 2016).

Liem proposed that the MPJ led to increased morphological and functional diversity of the feeding apparatus due to relaxed evolutionary integration between oral and pharyngeal jaws (Liem, 1973; Liem & Osse, 1975). Though several studies have shown how the novelty impacts morphological diversification (Burress & Muñoz, 2021; Burress et al., 2020; Conith & Albertson, 2021; Hulsey et al., 2006; Larouche et al., 2020; Roberts-Hugghis et al., 2023; Ronco & Salzburger, 2021), morphology and function may have varied evolutionary consequences (Corn et al., 2021;

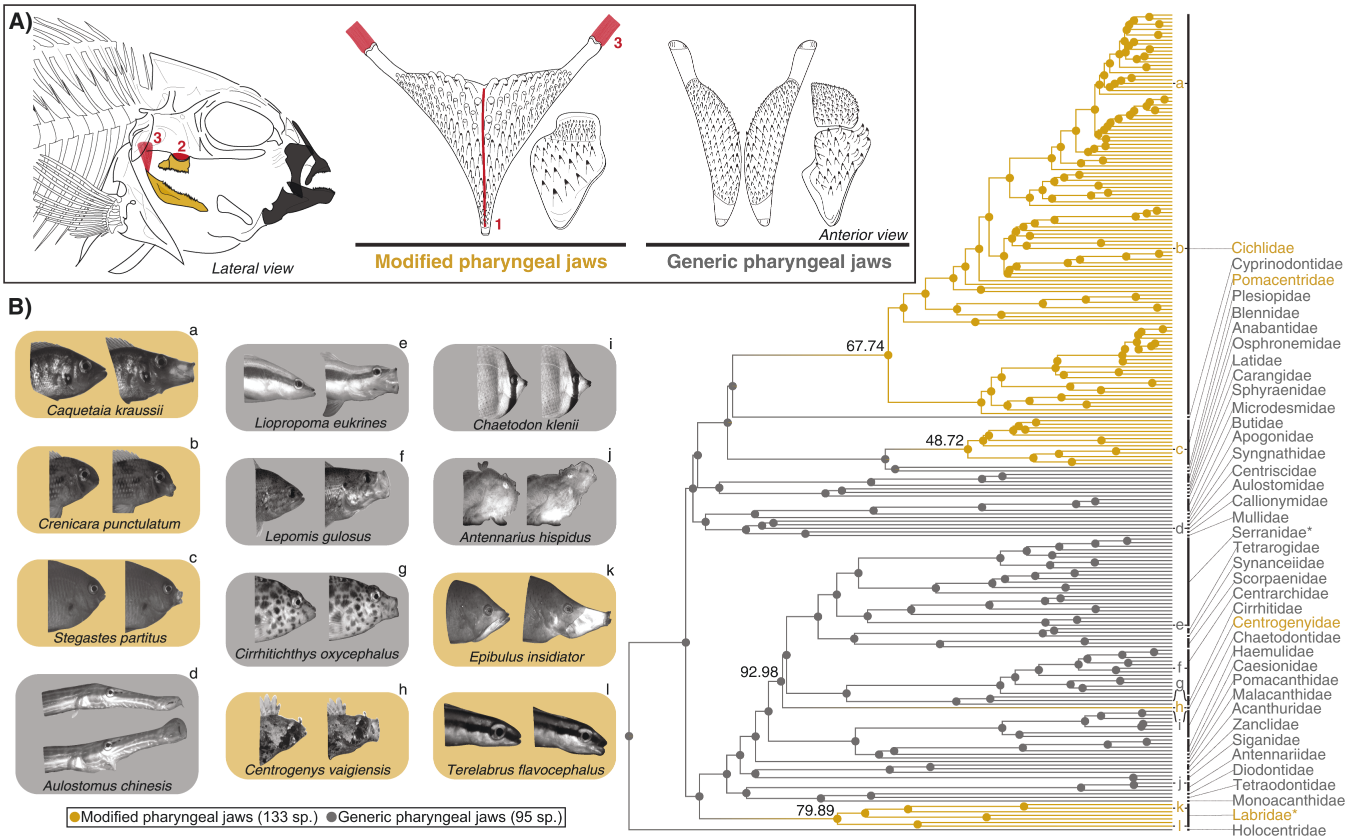

Figure 1. (A) Illustrations depicting the oral (lateral view; shaded in black) and pharyngeal (lateral view; shaded in gold) jaw structures involved in prey capture and processing functions, respectively. Though the prey processing system is similar across spiny-rayed fishes, several lineages exhibit a modified pharyngeal jaw (MPJ) where major musculoskeletal changes enable greater strength and mobility in prey manipulation and transport. Modifications include (1) fusion of the paired lower pharyngeal jaw bones into a single skeletal structure, (2) a mobile joint between each of the paired upper pharyngeal jaw bones and the neurocranium, and (3) a muscular sling suspending the lower pharyngeal jaw structure from the neurocranium. Bars below pharyngeal jaw structures represent 10mm scales. (B) A representative stochastic character map shows the relatedness of the 228 study species across 43 acanthomorph families and the evolutionary character history of the MPJ. Note that Serranidae includes Epinephelidae, Liopropomatidae, and Anthiadidae; Labridae includes Scaridae. Pie charts show the frequency of the MPJ and non-MPJ states at each node across 1,000 stochastic character maps and changes in branch color reveal that the novelty independently evolved four times across our sampled species between ~48 and 93 Ma. Images display closed mouth (left) and maximum gape (right) stages of feeding motions for a subset of MPJ and non-MPJ species.

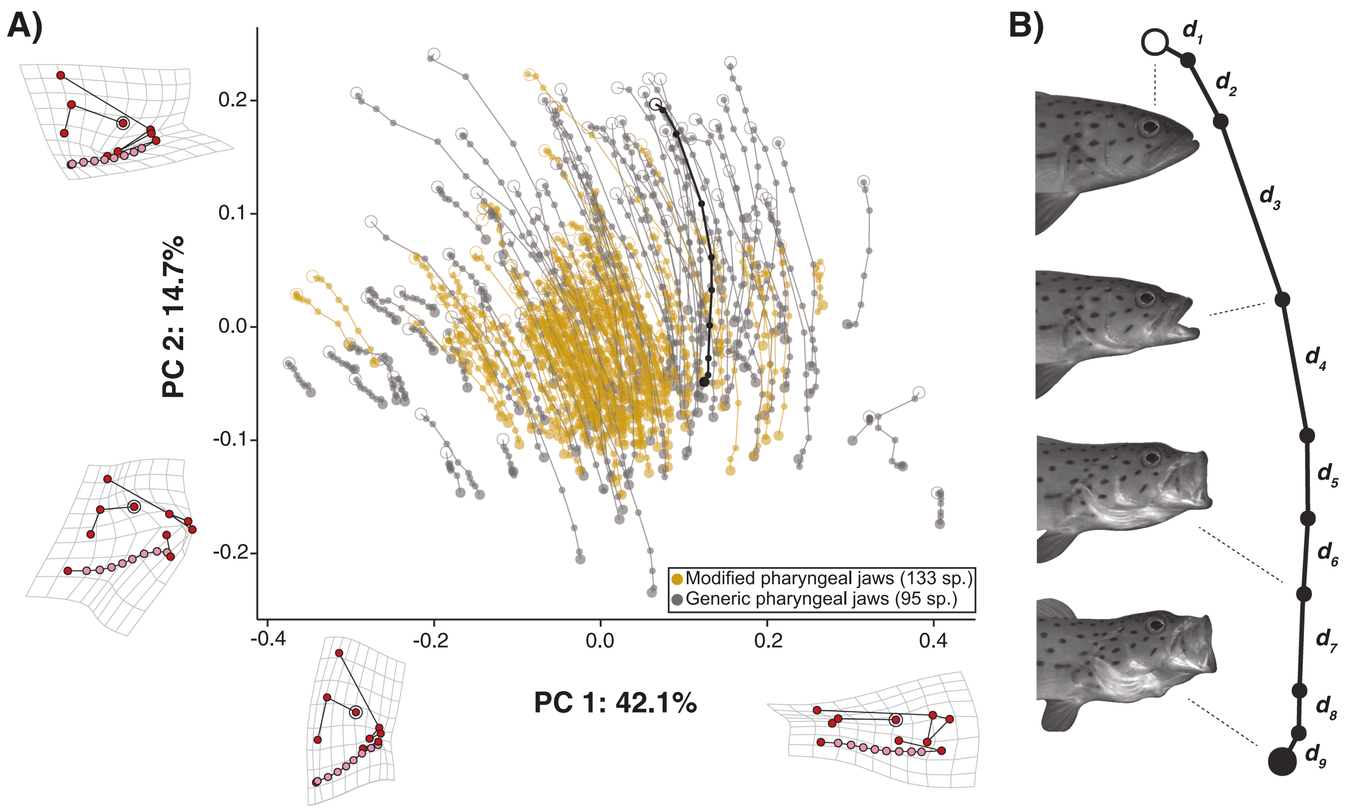

Figure 2. (A) Average shape trajectories for suction-based feeding motions in fishes with modified or unmodified pharyngeal jaws. Trajectories are comprised of 10 craniofacial shapes sampled at equally spaced time points from closed mouth to maximum jaw expansion. Deformation grids show theoretical shapes at the extremes of PCs 1 and 2, where filled circles represent 10 fixed landmarks (red) and 8 sliding semi-landmarks (pink; along the ventral margin of the head) used to track feeding movements. PC1 primarily captures variation in interspecific head shape, while PC2 describes motion-based shape change. (B) Average motion trajectory for *Plectropomus laevis* (Grouper; non-MPJ; highlighted in black in panel A). Images depict craniofacial shapes at different time points throughout the feeding motion. Total craniofacial kinesis is the sum of Procrustes distances (d_i) between successive shapes, describing the amount of shape change achieved during prey capture. Kinesis skew is the natural logarithm of kinesis across the last five motion shapes ($\sum(d_6{:}d_9)$) divided by total craniofacial kinesis ($\sum(d_1{:}d_9)$). Note that kinesis and kinesis skew are computed with full-dimensional shape data but are shown here in two-dimensions for visualization.

Koehl, 1996; Martinez et al., 2024). Thus, we sought to determine whether the presence of a specialized pharyngeal jaw affects *functional* diversification of the feeding system by exploring the MPJ's impact on the evolution of prey capture kinematics—a set of metrics describing how a predator uses its feeding morphology during prey acquisition (Gidmark et al., 2012; Lauder, 1985). Most fishes acquire prey using suction feeding—a behavior involving a rapid, highly coordinated (Camp & Brainerd, 2015; Copus & Gibb, 2013; Durie & Turingan, 2004) expansion of the mouth and oral cavity to draw in prey (Camp & Brainerd, 2022; Day et al., 2015; Lauder, 1982). Though the suction-feeding kinematic sequence is generally conserved, there is phylogenetic variation in aspects of these motions, reflecting the complexity of craniofacial mechanisms and strategies for successfully overcoming diverse prey defenses (Higham et al., 2006; Oufiero et al., 2012; Staab et al., 2012). Using morphometric data from high-speed video recordings of suction feeding strikes in 228 species with and without the MPJ, we compare variations in craniofacial morphology and movements to gain deeper insight into the impacts of the novelty on functional diversification in fishes. We ask whether fishes with MPJs show differential patterns in diversity, integration, and/or rates of evolution in craniofacial morphology and functions compared to fishes lacking the functional novelty. If the MPJ acts as a key innovation that spurs diversification in spite of mechanical trade-offs, we expect to see greater diversity, reduced integration, and/or higher rates of diversification in the feeding morphology and mechanisms of fishes with MPJ.

Results

Morphological and functional diversity

We explored a diversity of prey capture morphologies and motions using high-speed video sequences of 689 suction feeding strikes (Supplementary Table 1), representing 133 and 95 species with and without MPJ, respectively (Figures 1 and 2; Supplementary Table 2). MPJ fishes herein comprise an ecomorphologically diverse sampling of species from four of the seven clades that independently evolved the MPJ condition, including wrasses and parrotfishes (crown age of Labridae: 79.9 Ma), damselfishes (crown age of Pomacentridae: 48.7 Ma), the only false Scorpionfish (crown age of the monospecific clade, Centrogenyidae: 93.0 Ma), and cichlids (crown age of Cichlidae: 67.7 Ma; Figure 1B). To capture the complexity and diversity of feeding mechanics across this broad taxonomic sample, we examined several morphological and functional traits, including (1) craniofacial shape exhibited when a fish is in the closed mouth position at the start of a feeding sequence (referred to as "starting or interspecific head shape"); (2) six components of the feeding motion that describe the rotational movements and linear displacements of craniofacial structures during a suction feeding sequence, thus capturing the contributions of key bones

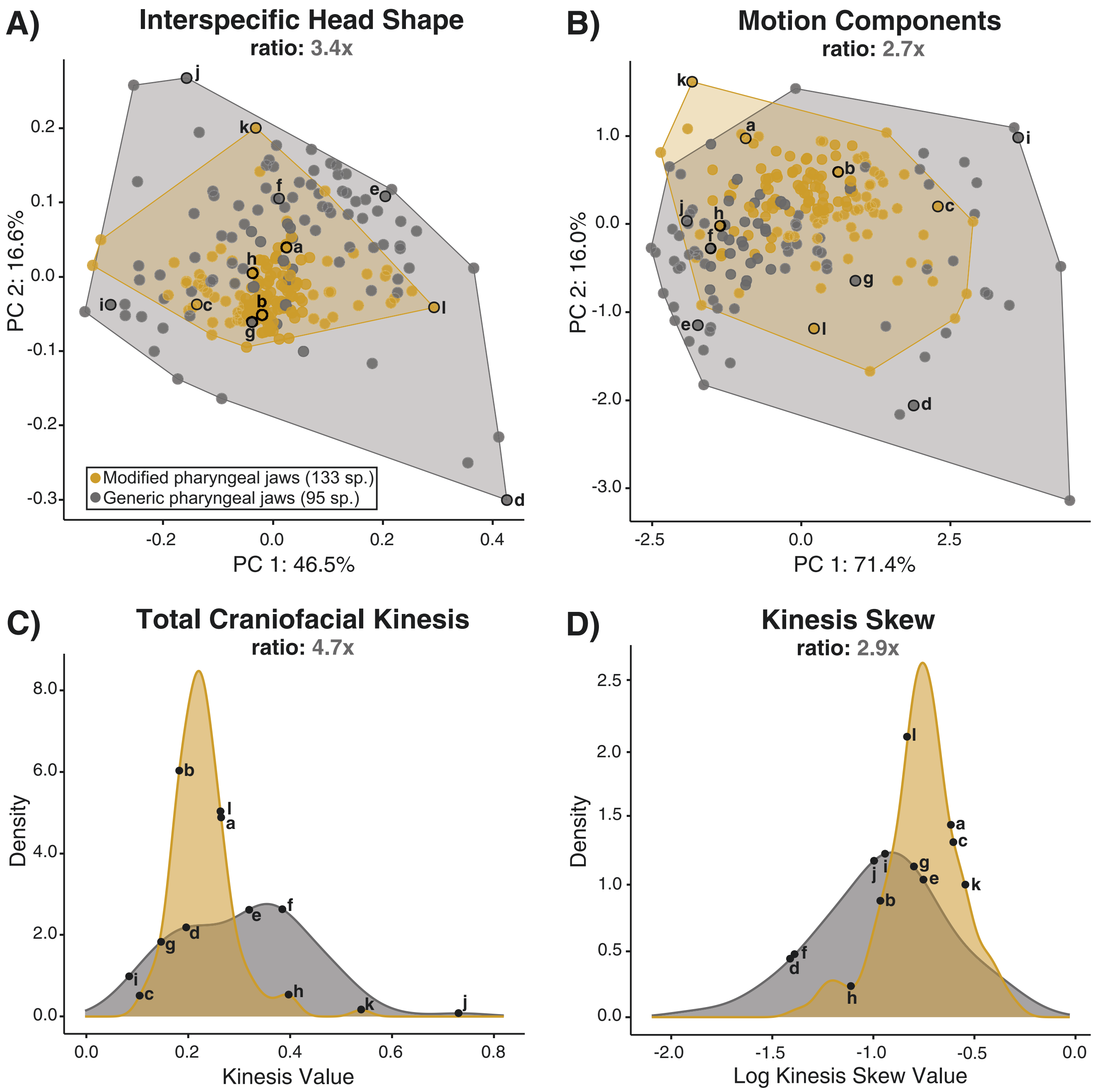

Figure 3. Species lacking modified pahryngeal jaws show greater disparity than species with a specialized prey processing system for all traits, including (A) interspecific craniofacial shape (3.4-fold more disparity), (B) the movements of key skeletal structures that contribute to feeding kinematics (2.7-fold more disparity), (C) total craniofacial kinesis (4.7-fold more disparity), and (D) kinesis skew (2.9-fold more disparity). Select species exemplifying morphological and functional diversity in MPJ and non-MPJ fishes include (a) *Caquetaia kraussii* (Cichlid), (b) *Crenicara punctulata* (Cichlid), (c) *Stegastes partitus* (Damselfish), (d) *Aulostomus chinensis* (Trumpetfish), (e) *Liopropoma eukrines* (Painted Basslet), (f) *Lepomis gulosus* (North American Sunfish), (g) *Cirrhitichthys oxycephalus* (Hawkfish), (h) *Centrogenys vaigiensis* (False Scorpionfish), (i) *Chaetodon kleinii* (Butterflyfish), (j) *Antennarius hispidus* (Frogfish), (k) *Epibulus insidiator* (Wrasse), and (l) *Terelabrus flavocephalus* (Wrasse; all species depicted in Figure 1B).

that underly cranial shape change during feeding (referred to as "motion components"; Martinez et al., 2024); (3) the total amount of craniofacial shape change that occurs during a feeding strike (referred to as "total craniofacial kinesis" or "kinesis"); as well as (4) the proportion of kinesis associated with shape change in the latter half of the feeding strike (referred to as "kinesis skew"; Figure 2; Supplementary Figure 1). While kinesis explains the capacity for cranial mobility, kinesis skew helps identify whether craniofacial kinesis is disproportionately concentrated during early vs. latter motion phases. We averaged trait values by specimen and then by species before comparing patterns of disparity (i.e., uni- or multivariate variance) between fishes with and without an MPJ. With data representing 43 acanthomorph families (Figure 1B), we find that fishes lacking the specialized pharyngeal jaw have more diverse craniofacial morphologies and feeding motions (Figure 3; Supplementary Table 3).

Principal component analyses (PCAs) run separately on interspecific head shape and the six motion components show that shape and functional spaces occupied by fishes with modified pharyngeal jaws are almost entirely a subset of the spaces occupied by fishes that lack the pharyngeal jaw novelty (Figure 3A and B). Among the motion components, MPJ fishes are only more extreme in their capacity to protrude their oral jaws away from their head towards their intended prey (Figure 3B; Supplementary Table 2). Though phylogenetic analyses of variance on the full-dimensional trait data show no significant differences in multivariate (MANOVA) or univariate (ANOVA) mean trait values, density plots of kinesis and kinesis skew reveal that, on average, species with modified pharyngeal jaws have slightly, but not statistically lower values of cranial mobility (i.e., less kinesis; Figure 3C), and slightly, but not statistically greater movement during the latter half of the feeding strike (i.e., greater kinesis skew; Figure 3D). Overall, disparity analyses on the full-dimensional trait data show that non-MPJ fishes have greater variance in starting head shape (3.4-fold), motion components (2.7-fold), total craniofacial kinesis (4.7-fold), and kinesis skew (2.9-fold; Figure 3; Supplementary Table 3).

Examining the distribution of species in craniofacial morphospace, the first principal component axis in a PCA of starting head shape accounts for 46% of interspecific diversity, while the second captures 16% of variation (Figure 3A; Supplementary Table 4). PC1 primarily describes variation associated with head depth. Fishes with deep, laterally compressed head shapes, such as *Chaetodon kleinii* (Butterflyfish; non-MPJ) and *Stegastes partitus* (Damselfish; MPJ), are found on one end of this axis. In contrast, species with more elongate head shapes, such as *Aulostomus chinensis* (Trumpetfish; non-MPJ) and *Terelabrus flavocephalus* (Wrasse; MPJ), are on the opposite end of PC1. PC2 primarily distinguishes species based on overall mouth size. Here, species such as *Epibulus insidiator* (Wrasse; MPJ) and *Antennarius hispidus* (Frogfish; non-MPJ) with larger mouths are on one end of this secondary axis of variation. Fishes with smaller mouths, such as *A. chinensis* (Trumpetfish; non-MPJ) and *T. flavocephalus* (Wrasse; MPJ), are found on the opposite end of PC2.

Regarding the distribution of species in functional space, the first principal component axis in a PCA of the six motion components captures 71% of interspecific diversity, while the second contains 16% of the variation (Figure 3B; Supplementary Table 5). PC1 primarily captures variation in the magnitude of cranial rotation and depression of the mouth cavity floor. Species such as *Liopropoma eukrines* (Painted Basslet; non-MPJ) and *E. insidiator* (Wrasse; MPJ) that exhibit high cranial rotation and hyoid depression are on one end of the axis. Species with much smaller values for these traits, such as *C. kleinii* (Butterflyfish; non-MPJ) and *S. partitus* (Damselfish; MPJ), are on the opposite end of this axis. PC2 primarily distinguishes species based on oral jaw protrusion. Here, species such as *E. insidiator* (Wrasse; MPJ) and *A. hispidus* (Frogfish; non-MPJ) with high protrusion are on one end of this secondary axis of variation. Fishes with minimal protrusion, such as *A. chinensis* (Trumpetfish; non-MPJ) and *T. flavocephalus* (Wrasse; MPJ), are found on the opposite end of PC2.

Trait coevolution and craniofacial evolutionary integration

Examining how kinesis and kinesis skew covary with individual motion components, we find that MPJ fishes show stronger evolutionary correlations between (1) kinesis and premaxillary protrusion and (2) kinesis and lower jaw rotation (Figure 4). In contrast, non-MPJ fishes only show stronger coevolution between kinesis and kinesis skew. Strong positive pairwise relationships are found among nearly all motion components in both MPJ and non-MPJ fishes (Figure 4A), with individual motion components correlating more strongly with premaxillary protrusion in MPJ fishes and with maxillary rotation in non-MPJ fishes (Figure 4B). Despite some differences in pairwise patterns, the level of evolutionary integration within the oral jaw system did not differ between MPJ and non-MPJ fishes when estimated with morphological or functional data (effect size < 0.5 and $p > 0.05$ for the pairwise difference between the two groups in separate analyses of starting head shape and motion components).

State-dependent evolution and rate heterogeneity

We used a relaxed clock, state-dependent model of multivariate Brownian evolution—the MuSSCRat model (May & Moore, 2020)—to examine the impact of the modified pharyngeal jaw system on rates of morphological and functional evolution. Implemented in a Bayesian framework within RevBayes (Hohna et al., 2016), this approach allows us to determine whether rates of continuous character diversification are impacted by the presence of the MPJ. This method permits rate variation among branches and accounts for rate heterogeneity that is not due to the evolution of the specified discrete character. With separate models fit to interspecific head shape, motion components, total craniofacial kinesis, and kinesis skew, we only find an effect of the MPJ on the Brownian rate parameter for total craniofacial kinesis. Here, we recover a 98.3% posterior probability of state-dependence where fishes with the generalized pharyngeal jaw configuration show 2.3-fold faster state-dependent evolution of craniofacial movements during feeding than fishes with the MPJ (Figure 5; Supplementary Figure 2).

Though extant MPJ taxa have slower or equivalent rates of state-dependent, continuous character evolution compared to non-MPJ species, it is possible that trait diversification rates have shifted over time. Local polynomial regressions of overall branch rate estimates from MuSSCRat against node age reveal minor positive and negative rate shifts throughout the evolutionary history of MPJ and non-MPJ fishes, with major rate increases in the last 20 million years (Supplementary Figure 2). However, we note that this scaling pattern is found across micro- and macroevolutionary studies of diversification (Harmon et al., 2021). Further, linear models fit between phylogenetic independent contrasts and node age confirm rate increases in all four trait categories, though only MPJ fishes show significant, positive relationships (Supplementary Figure 2; Supplementary Table 6).

Discussion

The modified pharyngeal jaw system is often characterized as a key innovation (Alfaro, 2014; Heard & Hauser, 1995; Salzburger, 2009; Stroud & Losos, 2016) and is thought to have stimulated ecological and phenotypic diversification within several prominent fish families (Kaufman & Liem, 1982; Liem & Osse, 1975; McGee et al., 2015; Stiassny & Jensen, 1987; Wainwright et al., 2012). However, contrary to these predictions, we find that fishes with modified pharyngeal jaws show reduced functional and morphological diversification compared to fish without this novelty. In fishes that lack the MPJ, trait disparity is 3.4-fold greater for head shape, 2.7-fold greater for motion components, 4.7-fold higher for total craniofacial kinesis, and 2.9-fold more for kinesis skew. The older age—and thus greater time for diversification—of non-MPJ lineages only partially accounts for these differences, as there is a 2.3-fold faster rate of state-dependent evolution of kinesis in taxa without the pharyngeal jaw novelty. We find that

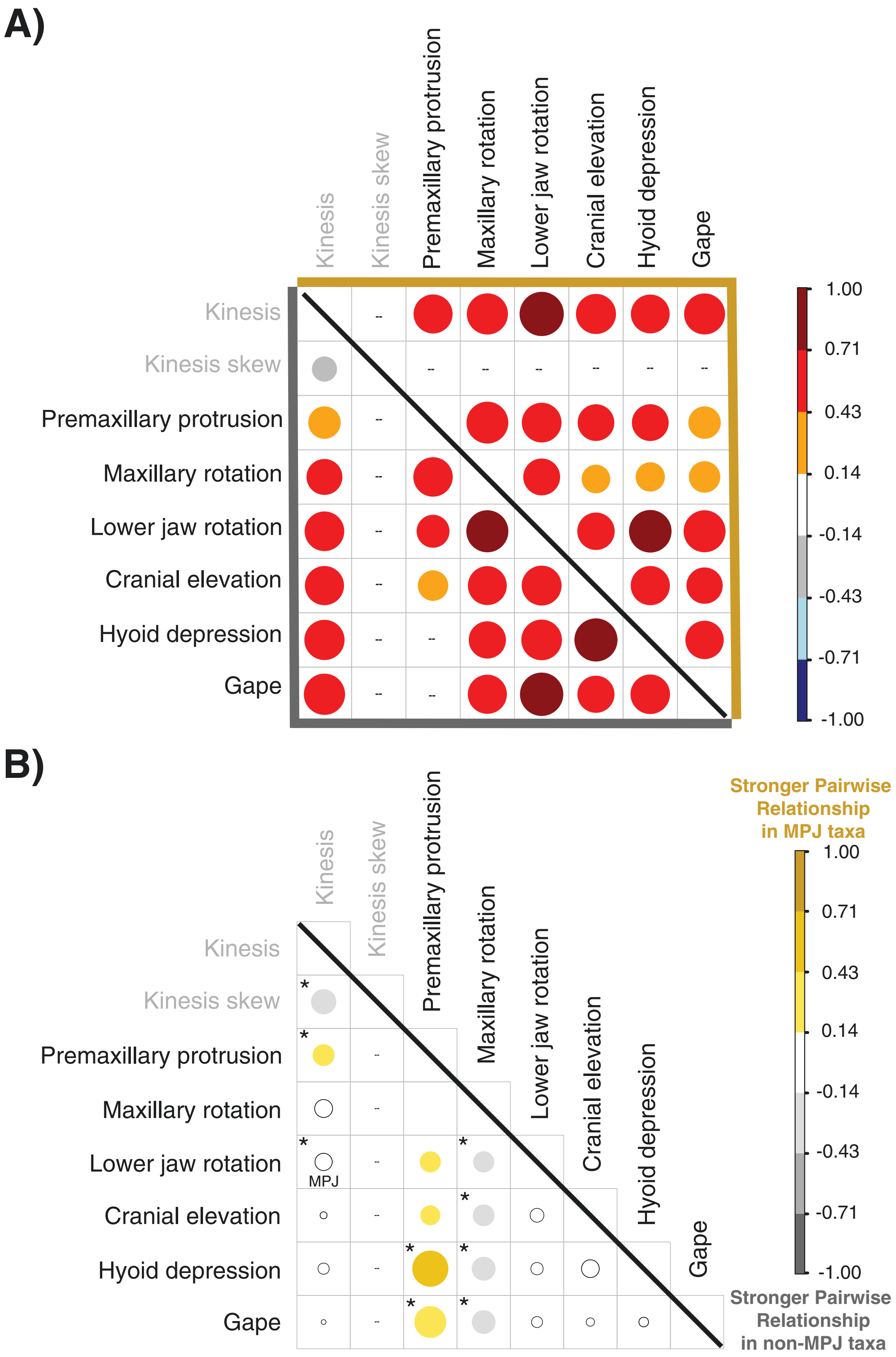

Figure 4. (A) Evolutionary correlation matrices reveal that MPJ (top triangle) and non-MPJ (bottom triangle) taxa have strong pairwise relationships between total craniofacial kinesis and all six motion components. Dashes indicate that pairwise relationships are not greater than those found between traits simulated under Brownian Motion. (B) A matrix depicting the difference in absolute values of pairwise correlations between MPJ and non-MPJ fishes reveals that species with a modified pharyngeal jaw show stronger coevolution of kinesis with premaxillary protrusion and lower jaw rotation. Circle size, color, and asterisks represent the difference in correlation strength, the group with the stronger correlation, and a significant difference between the two pairwise correlations ($p \leq 0.05$), respectively.

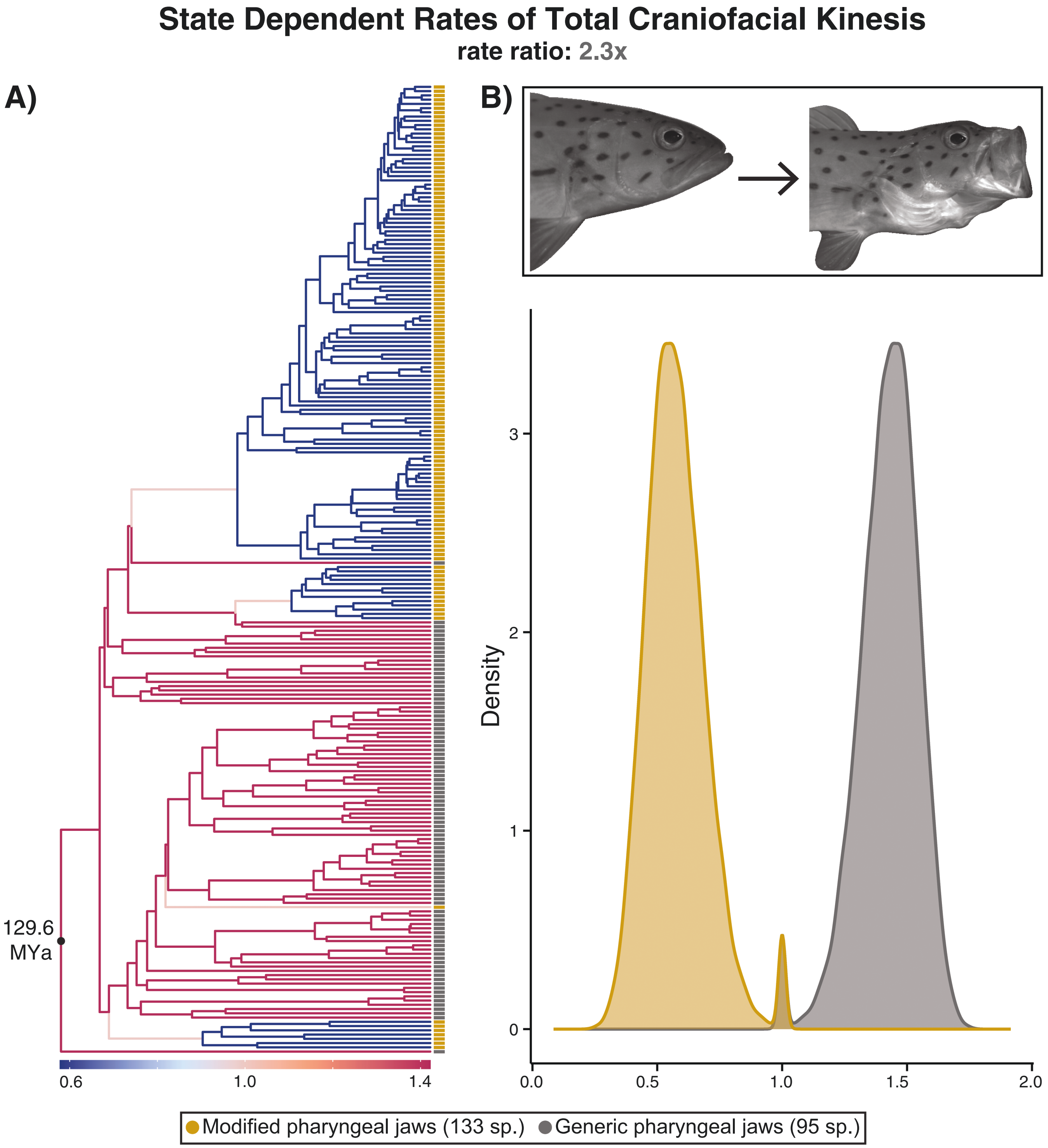

Figure 5. (A) Branch-specific estimates of the Brownian rate parameter for total craniofacial kinesis show 2.3-fold faster, state-dependent evolution in fish species with generic pharyngeal jaws compared to fishes with modified pharyngeal jaws. (B) Posterior estimates of the Brownian rate parameter in each group show minimal overlap, suggesting that the state-dependent rate of craniofacial kinesis evolution (total shape change along a motion trajectory between the closed mouth and maximum gape positions as depicted in non-MPJ species *Plectropomus laevis*) is significantly impacted by the state of the discrete trait—pharyngeal jaw configuration. We recover a 98.3% posterior probability of state-dependence, where 491,500 of 500,000 generations in our model return significantly different evolutionary rates of total craniofacial kinesis for the MPJ and non-MPJ groups.

the modified pharyngeal jaw system has had a marked, although unexpected, impact on the evolution of the fish feeding apparatus as its presence seems to constrain morphological and functional diversification relative to lineages lacking the novelty rather than promote it.

Our results contribute to a growing body of evidence that the macroevolutionary consequences of the MPJ, while substantial, require reinterpretation. Though the modified pharyngeal jaw was believed to spur ecomorphological diversification (Alfaro, 2014; Heard & Hauser, 1995; Salzburger, 2009; Stroud &

Losos, 2016), our study and other recent work suggests that the functional novelty increases prey processing capacity, but limits morphological and functional diversification of the feeding apparatus. Previous work has shown that MPJ lineages more frequently evolve diets that include hard-bodied and tough prey, but that the stronger jaw comes at the cost of a restricted pharyngeal gape that negatively affects the size of consumable prey (McGee et al., 2015). Others support this finding, showing that fishes with the MPJ occupy greater areas of ecological space, but similar degrees of body shape diversity compared to their non-MPJ sister clades (Larouche et al., 2020). Thus, while the MPJ allows an ecological expansion into durophagy and various forms of herbivory, it comes with a reduced frequency of piscivory and related morphologies. The reduced occurrence of piscivorous MPJ lineages may be a significant factor herein, as this feeding mode is often associated with high cranial kinesis (Corn et al., 2021). Indeed, we find that the eight species with the highest total craniofacial kinesis in our study are all piscivores, with all but one being non-MPJ taxa (Supplementary Table 2). By placing constraints on piscivory via a restricted pharyngeal jaw gape, often a diet-limiting factor for these fishes (Burress et al., 2016; Mihalitsis & Bellwood, 2017), the MPJ may reduce the frequency of species with high kinesis which is often associated with larger mouths, extreme oral jaw gape, and notable jaw protrusion.

As diet imposes similar selective pressures on both the oral and pharyngeal jaw systems, we must also consider how our results relate to coevolutionary patterns within the feeding apparatus. It has long been presumed that increased evolutionary decoupling of the prey capture and processing systems (Burress et al., 2020; Conith & Albertson, 2021; Hulsey et al., 2006; Liem, 1973; Liem & Osse, 1975; Ronco & Salzburger, 2021) underlies the purported increase of ecomorphological diversification in MPJ fishes. However, several studies have shown that the coevolution of the oral and pharyngeal jaws is statistically significant in MPJ lineages (Burress et al., 2020; Conith & Albertson, 2021; Larouche et al., 2023; Ronco & Salzburger, 2021)—though we note some variation in the strength of the relationships recovered—and is greater than in groups lacking the functional novelty (Roberts-Hugghis et al., 2023). Further, recent work on labrids—an iconically diverse MPJ family—determined that the oral and pharyngeal jaws compose the slowest evolving functional module in the skull (Larouche et al., 2023). The strength of integration between the oral and pharyngeal jaw units is strongly associated with diet, as both systems respond in predictable ways to common prey types (Burress & Muñoz, 2021; Burress et al., 2020). Thus, a picture emerges where these complex musculoskeletal modifications to the prey processing system endow fishes with a stronger pharyngeal jaw and a greater ability to feed on hard prey, like mollusks and plant material (Galis & Drucker, 1996; Hulsey, 2006; Hulsey & García De León, 2005; Kaufman & Liem, 1982; Lauder, 1983; Liem & Sanderson, 1986; McGee et al., 2015). However, the presence of the MPJ does not decouple the evolution of the oral and pharyngeal jaws, nor does it promote the diversification of craniofacial morphologies and motions. Instead, the functional novelty appears to result in stronger evolutionary integration—induced by the correlated adaptation of the two jaw systems to specific prey types—as well as repeated evolution into constrained areas of shape and functional space.

It may be that strong covariance between oral and pharyngeal jaw structures (Burress & Muñoz, 2021; Roberts-Hugghis et al., 2023), likely induced by functional trade-offs related to feeding ecology (Burress & Muñoz, 2021; McGee et al., 2015), is the mechanism by which diversification in MPJ fishes in constrained. While modularity and integration are key concepts in evolutionary morphology, it remains controversial whether substantial integration generally constrains or facilitates trait diversification. For example, strong integration can result in increased diversification within a system due to the efficiency of genetically aligned change (Burns et al., 2023; Cheverud, 1996; Goswami et al., 2014; Knapp et al., 2023; Marroig & Cheverud, 2005; Muñoz et al., 2018; R. L. Miller & Olson, 1958; Schluter, 1996; Schwenk & Wagner, 2001), but such strong trait covariance can limit diversification as disruption to a highly integrated system can cause instability (Bright et al., 2016; Felice & Goswami, 2018; Raup & Gould, 1974; Schwenk & Wagner, 2001). Further, weak trait covariance (often referred to as "decoupling") and modularity can enhance diversification due to the increased capacity for relatively independent evolution of distinct functional systems (Breuker et al., 2006; Evans et al., 2017, 2019; Felice et al., 2018; Larouche et al., 2018; Roberts et al., 2018; Schaefer & Lauder, 1996; Vermeij, 1973). Though the two groups examined here do not differ in strength of evolutionary integration within the oral jaw system, MPJ fishes do show stronger pairwise relationships between kinesis and individual motion components, along with slight differences in their average mechanical patterns, and only a few examples of more extreme feeding kinematics compared to fishes lacking the pharyngeal jaw novelty (Figures 3 and 4). Thus, our results support a scenario where the MPJ is associated with moderately strengthened coevolution within the feeding system (Roberts-Hugghis et al., 2023) and constrained evolution of form (Larouche et al., 2023) and function (Cooper & Westneat, 2009) such that the diversity of both fails to extend beyond the ranges observed in non-MPJ fishes.

The presence of the MPJ may also coincide with shifts in other evolutionary patterns. It is possible that lineages underwent rapid trait diversification shortly after the development of the pharyngeal jaw novelty, then experienced a slowing of trait diversification rates once ecological and functional niche space was filled. Such patterns of "early burst"—where trait evolution initially accelerates due to ecological opportunity enabled by the development of a novel trait or function (Burress, 2016)—could be present if the musculoskeletal alterations to the prey processing system aligned strongly with the fitness landscape, essentially facilitating rapid evolution along a 'genetic line of least resistance' (Schluter, 1996). Though we do not find evidence for early bursts in functional or morphological evolution (Supplementary Figure 2), future research should aim to determine whether early bursts in species proliferation (e.g., cichlids; López-Fernández et al., 2013) and/or increased transition rates between trophic guilds (e.g., damselfishes; Cooper & Westneat, 2009) are seen broadly across MPJ clades, as these patterns would further elucidate the macroevolutionary impact of the modified pharyngeal jaw.

As phenotype arises from complex interactions at multiple biological levels of organization, patterns of morphological and functional constraint likely reflect cellular, genetic, and/or developmental limits and restrictive biases (Alberch, 1983; Wake & Larson, 1987), whereas diversity may reflect plasticity and facilitative biases (Kavanagh, 2020; Uller et al., 2020) in these same processes. Thus, the constrained phenotypic diversity and stronger trait coevolution seen here in MPJ taxa may indicate increased integration within this group's regulatory processes relative to non-MPJ species. Previous research on African cichlids revealed conservation of the gene network underlying tooth development (Fraser et al., 2009) and the gene coexpression networks between the two jaw systems (Singh et al., 2021). Further, these studies found genetic and morphological coupling of oral and pharyngeal jaw shape (Conith & Albertson, 2021), even though each system materializes from distinct developmental regions (Fraser et al., 2009) and transcriptional pathways (Singh et al., 2021). Though these studies detail the interplay of integration and modularity at morphological, developmental, and genetic levels within MPJ feeding systems, here again, we lack comparative analyses examining whether regulatory pathways leading to modified vs. generic pharyngeal jaw morphologies differ. By collating results from comparative studies at several biological levels, future work can shed light on the potential origins and the complex, multifaceted consequences of key innovations (Hernandez & Cohen, 2019; Jablonski, 2020; Vermeij, 2001). Moreover, such interdisciplinary studies would allow us to link our understanding of phenotypic diversification and evolutionary integration to broader biological concepts such as developmental bias—the notion that intrinsic mechanisms disproportionately produce certain phenotypic variants compared to others (Arthur, 2004; Maynard-Smith et al., 1985)—and its ability to facilitate or constrain organismal evolvability, thus shaping biodiversity (Jablonski, 2020; Uller et al., 2018).

The modified pharyngeal jaw is undoubtedly a functional innovation as it results in a mechanically stronger jaw that can process hard prey. This capacity has influenced the trophic diversification of major MPJ lineages, as feeding on hard-bodied and tougher prey is a hallmark of labrid fishes and substrate biting has evolved in numerous cichlids and pomacentrids. However, because the novelty also limits the diversification of prey capture morphologies and functions, we propose that the impact of this innovation may be more nuanced than previously thought. Though some novel traits support diversification via access to new adaptive zones, competitive advantage, and/or speciation via reproductive isolation (Alfaro, 2014), others may prompt increased performance, but minimally or even negatively impact diversification due to functional trade-offs (Larouche et al., 2020; McGee et al., 2015; Wainwright & Price, 2016) as we find here. We recommend that the macroevolutionary, phenotypic, and ecological consequences of novelties be carefully quantified and compared to clades lacking these specialized traits, as their presence may not be uniformly advantageous to all forms of diversification (Schweizer et al., 2014; Vermeij, 2001). We also underscore the point that morphology is not always an appropriate proxy for function (Corn et al., 2021; Koehl, 1996; Martinez et al., 2024), as we find dissimilar results regarding the evolutionary rates of morphologies and motions linked to prey capture (non-significant and significant state-dependent evolution, respectively). We, therefore, emphasize the importance of extending future studies of morphological diversity within jaw systems to include analysis of the movements that those feeding structures generate during prey capture.

Materials and Methods

Feeding videos and morphometric data

Totaling 689 feeding strikes, this dataset spans a wide swath of the diversity of suction feeding motions in spiny-rayed fishes (Acanthomorpha; Supplementary Table 1). Specimens of 133 and 95 species with and without modified pharyngeal jaws, respectively (Supplementary Table 2), were obtained from commercial sources and housed in laboratory aquaria at room temperature where they were filmed feeding on mobile prey. We sampled a total of 43 acanthomorph families, including wrasses and parrotfishes (Labridae including Scaridae), damselfishes (Pomacentridae), the only false scorpionfish (Centrogenyidae), and cichlids (Cichlidae) to represent four of the seven clades in which all known species exhibit a modified pharyngeal jaw (Figure 1B).

Though our sampling of MPJ fishes does not include surfperch (Embiotocidae), halfbeaks (Hemiramphidae), or flying fishes (Exocoetidae), previous work exploring the ecomorphological diversity in six taxon-rich MPJ families found that these three clades show reduced body shape diversity and, on average, slower rates of body shape evolution compared to their non-MPJ sister clades. Further, these three MPJ families overlap significantly in body shape and/or ecological space with cichlids, damselfishes, and wrasses. Halfbeaks and flying fishes—species typically more elongate in body and head shape—do occupy distinct body shape space compared to other MPJ fishes. However, authors found (1) complete overlap in diet space, (2) 1.4 to 3.1-fold less morphological disparity, and (3) significantly slower rates of evolution in seven out of eight body and head shape traits among these two clades compared to the four other MPJ clades included in the study (Larouche et al., 2020). Thus, the addition of halfbeaks, surfperch, and flying fishes may have affected our estimates of multivariate variance in MPJ fishes, but it is unlikely that their inclusion would significantly impact our overall findings. Additionally, we note that our sampling of Cichlidae only includes Neotropical and African riverine cichlids. Recent examination of the diversification of prey capture mechanisms across Neotropical and African Rift Lake cichlids found (1) that Neotropical cichlids have the most variance in craniofacial morphology, but similar or lower variance for most functional traits compared to cichlids from Lake Tanganyika; and (2) a negative relationship between age and rates of evolution such that young lake radiations display faster diversification than the older Neotropical cichlid radiation (Martinez et al., 2024). Thus, the exclusion of Rift Lake cichlids may reduce our estimates of functional diversity and rates of evolution. Still, the Neotropical and African riverine cichlids included herein represent much of the ecomorphological and functional variation found throughout Cichlidae (Burress, 2014; Burress et al., 2017; Martinez et al., 2024). Further, by excluding Rift Lake cichlids, we avoid conflating the impact of the MPJ with the influence of other factors, such as hybridization (Joyce et al., 2011; Meier et al., 2017, 2019, 2023) and lake effects (Seehausen, 2006) which have been shown to drive increased evolutionary rates in African Rift Lake cichlids.

Feeding strikes were filmed with a digital Fastec HiSpec 2G Monochrome high-speed camera at 2,000 frames per second and in 592 × 474 resolution. To ensure consistency in motion tracking across all strike sequences, videos were recorded from a lateral perspective and were only used if fishes exhibited a full-effort suction feeding attempt. We used landmark morphometrics to track oral jaw and craniofacial motions during each suction feeding sequence using 10 frames spanning the feeding strike. After identifying the video frames depicting the start (onset of mouth opening, designated as frame 1) and end (maximum oral jaw and mouth cavity expansion, prior to mouth closure; designated as frame 10) of each strike, we selected eight additional frames that were equally spaced in time between these two frames (Figure 2). We used either tpsDIG2 software (Rohlf, 2015) or the digitizeImage function in STEREOMORPH v.1.6.7 (Olsen & Haber, 2024; Olsen & Westneat, 2015) in R v.4.2.2 (R Core Team, 2022) to digitize 18 landmarks on feeding-related structures in each of the ten frames to capture the oral jaw motions and craniofacial shape change that occurred during each feeding sequence (Supplementary Figure 1A). Ten homologous fixed landmarks were used to track the motions of several oral jaw bones and the skull. Eight sliding semi-landmarks, bound by fixed landmarks on the insertion of the pelvic fin and a ventro-anterior point on the mandible, captured shape change along the ventral margin of the head due to buccal expansion. We used published landmark data for 155 species of cichlids (Martinez et al., 2024) and reef fishes (Corn et al., 2021). Landmark data for the remaining 73 species were new data collected for this study.

Using landmark coordinates, we calculated six "motion components", including premaxillary protrusion, hyoid depression, oral jaw gape, maxillary rotation, lower jaw rotation, and cranial rotation (Supplementary Figure 1B). These traits describe the rotational and linear motions of oral jaw bones and the skull during a suction-feeding sequence. To ensure that all motion components were commensurate, the rotational variables were converted to linear distances, as outlined in a recent study (Martinez et al., 2024). To account for the effect of size on feeding mechanics, each component was scaled by the centroid size of the fish's head when in the closed mouth position. All components were then log-transformed to achieve normal distributions. Finally, for each of the six motion components, we computed average trait values by specimen before calculating average trait values for each of our 228 species (on average, $n = 3$ strikes per species; Supplementary Figure 3).

In addition to examining diversification in the components of prey capture motions, we explored the evolution of two composite kinematic traits and cranial morphology. Using the gpagen function in GEOMORPH v.4.0.5 (Adams & Collyer, 2022; Adams et al., 2023; Baken et al., 2021; Collyer & Adams, 2018, 2021b), we performed a generalized Procrustes analysis which aligns morphometric data through an iterative process of scaling, rotating, and translating landmarks to minimize the Procrustes distances across motion shapes (Adams, 2014b). Aligned shapes create a trajectory through morphospace for each motion (Figure 2A; Adams, 2014a), and a trajectory's length provides a metric for "total craniofacial kinesis"—a univariate trait describing the magnitude of shape change that occurs due to movement of the oral jaw system's anatomical features during a feeding sequence (Martinez et al., 2018). Kinesis was computed for each prey capture event by summing the Procrustes distances between each pair of successive motion shapes (Figure 2B; Corn et al., 2021; Martinez et al., 2018). Kinesis skew was then calculated by taking the natural logarithm of kinesis across the last five motion shapes divided by total craniofacial kinesis (Figure 2B; Supplementary Figure 1A), providing information about the distribution of movement across a strike. Total craniofacial kinesis and kinesis skew values were computed for each of the 689 feeding strikes, before averaging by specimen and then by species (Supplementary Table 2). Finally, from each species' aligned and averaged morphometric data, we extracted starting head shape—the sole morphological trait included in this study—which describes craniofacial form when in the closed mouth position at the start of a feeding sequence (Supplementary Table 2).

Morphological and functional disparity

To conduct our analyses in a phylogenetic context, we trimmed a time-calibrated molecular phylogeny of ray-finned fishes (Rabosky et al., 2018) to the species in our dataset (Figure 1; Supplementary Table 2) using APE v.5.7-1 (Paradis & Schliep, 2019). For species in our kinematic dataset that were not present on the phylogeny, we used the closest related species within the same genus as a proxy. If no congeners were present, we selected a substitute species from within the taxon's clade at random, excluding any species sister to those in our dataset. In total, 30 substitutions were made (Supplementary Table 2).

To visualize the multivariate data in shape and kinematic space, we performed separate PCAs of (1) aligned morphometric data from all 10 frames, showcasing feeding sequences as trajectories of shape change; (2) aligned morphometric data from the first frame in the feeding sequence, which captures head shape in the starting, closed-mouthed posture; and (3) the six, size-scaled motion components. Here, PCAs were performed using covariance matrices in the gm.prcomp (Collyer & Adams, 2021a; Revell, 2009) and prcomp (Becker et al., 1988; Mardia et al., 1979; Venables & Ripley, 2002) functions within GEOMORPH and STATS v.4.2.2 (R Core Team, 2022) to analyze morphometric and motion component data, respectively. To compare the magnitude of interspecific variance among MPJ and non-MPJ morphologies and kinematic patterns, we used the full-dimensional trait data and the morphol.disparity function (Collyer & Adams, 2021a; Zelditch et al., 2012) in GEOMORPH to compute disparity—the sum of the diagonal elements of the variance-covariance matrix divided by the number of observations (Zelditch et al., 2012)—for interspecific head shape, the six motion components (both combined in a multivariate dataset, and individually as univariate traits), total craniofacial kinesis, and kinesis skew. To test whether MPJ and non-MPJ fishes have statistically different mean craniofacial morphologies, we performed a phylogenetic multivariate analysis of variance (phylogenetic MANOVA) on the full-dimensional starting head shape data over 10,000 iterations under a Brownian Motion (BM) model with the procD.pgls function (Adams, 2014a; Adams & Collyer, 2015, 2016, 2018; Collyer et al., 2015) in GEOMORPH. This same method was used to perform individual phylogenetic ANOVAs on the full-dimensional trait data for each of the six, individual motion components, total craniofacial kinesis, and kinesis skew to determine if, on average, there are significant differences in kinematic processes employed by MPJ and non-MPJ fishes.

Patterns of trait coevolution

To understand the impact of the modified pharyngeal jaw on patterns of trait coevolution, we examined (1) the overall strength of evolutionary integration for cranial morphology and jaw function and (2) pairwise trait correlations in MPJ and non-MPJ species. To do this, we first assessed the degree of evolutionary integration separately for interspecific head shape and motion components using the integration.Vrel function (Conaway & Adams, 2022; Pavlicev et al., 2009) in GEOMORPH. We then used the compare.ZVrel function (Conaway & Adams, 2022) in GEOMORPH, calculating covariances for head shape and motion components in each group (i.e., their relative eigenvalue variance, *Vrel*) and converting them to a standardized effect size. The function then compares these effect sizes using a two-sample test to determine if there is a significant difference in the strength of integration between MPJ and non-MPJ species. Second, we examined pairwise relationships between all functional traits (i.e., kinesis, kinesis skew, and all six motion components) to further understand if and how fishes with the pharyngeal jaw novelty use different mechanical strategies to successfully capture prey. We first produced evolutionary correlation matrices by calculating pairwise correlations between phylogenetic independent contrasts (PICs) for each functional trait using the pic and corr.test functions in APE and PSYCH v.2.4.3 (Revelle, 2024), respectively. We then removed pairwise correlations that were not stronger than expected under Brownian Motion. Here, we used the fastBM function in PHYTOOLS v.1.5-1 (Revell, 2012) to simulate trait data 1,000 times under a BM model of evolution, bound by each trait's empirical maximum and minimum values. As done with the empirical data, we estimated the pairwise relationships between PICs of the simulated data, resulting in null distributions of 1,000 simulated correlations for each pairwise trait comparison. Empirical correlations that did not fall at or above the 95th percentile of simulated correlations (15 of 56 pairwise relationships) were removed. We visualized each group's evolutionary correlation matrix and the difference between the absolute value of each matrix using the corrplot function (Friendly, 2002; Murdoch & Chow, 1996) in CORRPLOT v.0.92 (Wei & Simko, 2021). The strength of pairwise correlations in MPJ and non-MPJ fishes was statistically compared using the paired.r function in PSYCH.

Rates of morphological and functional evolution

We examined the impact of the modified pharyngeal jaw system on rates of morphological and functional evolution of feeding structures using a Bayesian approach. After coding each species for the presence or absence of the MPJ, we tested for an effect of this discrete trait on interspecific head shape and kinematic traits using a relaxed clock, state-dependent model of multivariate Brownian Motion evolution implemented with the MuSSCRat model (May & Moore, 2020) in RevBayes (Hohna et al., 2016). MuSSCRat uses continuous-time Markov chain and Markov chain Monte Carlo (MCMC) processes to simultaneously estimate the evolution of discrete and continuous traits, respectively, to determine the impact of the discrete character on continuous character evolution. In its computation of the rate parameter for multivariate data that represent complex, functionally integrated systems and processes, this model accommodates branch-specific rate variation (i.e., rate heterogeneity) using a relaxed-clock model. Further, this model accounts for variation in rate that is not due to the discrete character (referred to as "background rate variation").

We ran separate MuSSCRat analyses for (1) scores for the first 10 principal component axes from a PCA of interspecific head shape, (2) the six motion components traits, (3) the univariate total craniofacial kinesis trait, and (4) the univariate kinesis skew trait (Supplementary Figure 2; Supplementary Table 2). We estimated evolutionary rates for interspecific head shape using scores from principal component axes that account for over 95% of shape variation due to computational limitations, as the model could not reach convergence on the morphometric data in its full dimensionality. In each of the four analyses, pharyngeal jaw configuration was used as the discrete character where the prior (i.e., expected) number of transitions from the unmodified to modified state was set to 4, and the magnitude of the associated rate shift was drawn from a lognormal distribution. Each MCMC was run for 500,000 generations with 10% burn-in; the prior probability of state-dependent continuous character evolution was set to 0.5; and the priors for the branch-specific background rates were drawn from an uncorrelated lognormal distribution (i.e., UCLN relaxed clock). We determined that varying priors had little effect on posterior parameter estimates by repeating these analyses under different prior specifications for (1) the number of discrete character state transitions, (2) lognormal distribution of the discrete character rate shift, and (3) the probability of state-dependence (Supplementary Table 7). We used Tracer software v.1.7.2 (Rambaut et al., 2018) to assess model convergence and code modified from REVGADGETS package v.1.1.0 (Tribble et al., 2022) to visualize the results on our phylogeny.

We assessed the degree of rate heterogeneity throughout the evolutionary history of each trait to determine if rates of functional and morphological diversification shift following transitions to a modified pharyngeal jaw. We performed local polynomial regressions between log-transformed, overall branch rate estimates from MuSSCRat and internal node ages to visualize if and how continuous character rates change over time. Additionally, we performed node height analyses using the nh.test function in GEIGER v.2.0.11 (Pennell et al., 2014), which fit linear models between log-transformed, absolute values of phylogenetic independent contrasts (PICs) and internal node ages. Univariate node height analyses were run for kinesis, kinesis skew, each of the six motion components, and head shape scores for each of the first 10 PC axes. For multivariate analyses of head shape and motion components, we used means of the absolute values of PICs of principal component scores and individual motion components, respectively. A significant positive relationship would indicate increases in rate through time, while a significant negative relationship would indicate that rates have slowed and potentially be consistent with an early burst in trait evolution (Freckleton & Harvey, 2006; Slater & Pennell, 2014).

Comparing rate estimates between maximum-likelihood and Bayesian frameworks

Although MuSSCRat presents multiple advantages for estimating rates of evolution, we also estimated rates of continuous character evolution under a variety of BM and Ornstein-Uhlenbeck (OU) models using the OUwie function within OUWIE v.2.10 (Beaulieu et al., 2012; Butler & King, 2004; Hansen, 1997; Ho & Ane, 2014; O'Meara et al., 2006; Thomas et al., 2006) to determine whether our findings are impacted by the underlying model of evolution. We generated a distribution of 100 stochastic character maps using PHYTOOLS, where the pharyngeal jaw condition was the discrete character. We then estimated evolutionary parameters under five models of evolution—single-rate Brownian Motion (BM1), multi-rate Brownian Motion (BMS), single-rate and single-optimum Ornstein-Uhlenbeck (OU1), single-rate and multi-optima Ornstein-Uhlenbeck (OUM), and multi-rate and multi-optima Ornstein-Uhlenbeck (OUMV)—and compared the fit of these models based on AICc scores. While we recovered a mix of best-fitting models, generally, the OUwie results did not differ from the MuSSCRat findings—when MPJ and non-MPJ fishes show significantly different rate parameters (8 of 13 traits), non-MPJ fishes typically evolve faster (7 of 8 traits; Supplementary Table 8). We note that the OUwie and MuSSCRat findings are not fully comparable as OUwie is only able to estimate univariate rates, whereas rates were estimated in multivariate ((A) interspecific head shape and (B) kinematic components; Supplementary Figure 2) and univariate ((C) kinesis and (D) kinesis skew; Supplementary Figure 2) formats within MuSSCrat. Because we do not recover significant, state-dependent evolution of kinematic components using MuSSCRat, it may be that individual motion components vary regarding which group evolves fastest, but this variation averages out to a non-significant difference in state-dependent rates overall. Similar to findings in other recent studies (Corn et al., 2021; Larouche et al., 2023), our results suggest that estimates of evolutionary patterns (e.g., rate, integration, modularity) within a Brownian Motion framework can still be informative even if a BM model is not the best-fitting evolutionary model. This also highlights some of the current limitations for evaluating models of multivariate trait evolution.

In addition to the above analyses, we conducted a simulation study to examine the appropriateness of conducting maximum-likelihood-based model-fitting analyses on this dataset. Here, we used the OUwie.sim function in OUWIE to simulate data under five models of evolution—BM1, BMS, OU1, OUM, and OUMV—across 100 stochastic character maps where the pharyngeal jaw condition was the discrete character. We then analyzed the fit of those same BM and OU models to each simulated dataset with the expectation that OUwie would return the model that the data was simulated under as the best-fitting model. In most cases (4 of 5 simulated datasets), OUwie did not return the correct model and often preferred a more complex model (Supplementary Table 9). Thus, we conclude that a Bayesian approach (e.g., the MuSSCRat model) is more appropriate for evolutionary rate estimation within this dataset as our data does not have the power to accurately distinguish models of evolution within a maximum-likelihood framework where rates of discrete and continuous character evolution are not estimated jointly.

Comparing parameter estimates between full and subsampled datasets

To ensure that cichlids ($n = 112$ of the 133 MPJ species) do not drive the patterns recovered, we estimated evolutionary parameters using a subset of the cichlid taxa. Here, we randomly selected 13 cichlid species, matching the next highest number of species examined from a single MPJ family, resulting in a dataset of 95 non-MPJ and 34 MPJ taxa. Using the morphol.disparity and compare.evol.rates (Adams, 2014b; Adams & Collyer, 2018, 2019; Denton & Adams, 2015) functions in GEOMORPH, we computed disparity and rates of evolution for interspecific head shape (all data used for disparity estimates; scores from PC axes 1–10 used for rate estimates following our treatment of the full dataset), motion components, total craniofacial kinesis, and kinesis skew. This analysis was repeated 100 times before comparing average disparity and rate estimates to those found using the full dataset of 133 MPJ species. On average, we found that estimates of functional and morphological disparity increased for all traits excluding kinesis skew, which showed no change, while rate estimates decreased for all traits excluding kinesis, which increased. Regardless of how parameter estimates shifted with a subsampled MPJ dataset, all patterns comparing MPJ to non-MPJ parameter estimates remained unchanged (Supplementary Figure 4). Thus, the results from the subsampling analysis align with our main findings, where non-MPJ fishes show significantly greater disparity for all traits and a significantly greater rate of evolution for total craniofacial kinesis.

Supplementary material

Supplementary material is available online at *Evolution Letters*.

Data and code availability

Data and code supporting the results reported in this manuscript are available on the open-access digital repository Data Dryad, under DOI: 10.5061/dryad.gmsbcc2x4. Additional results regarding the model-fitting analysis and simulation study in Ouwie, examination of rate shifts through time, comparison of intra- vs interspecific variation, and study of the impact of sampling on rate and disparity results are described in the Supplementary material file.

Author contributions

A.S.RH. and P.C.W. conceptualized the study. A.S.RH. and P.C.W. designed the study. All authors collected data from videos. A.S.RH. conducted all statistical analyses with guidance from K.A.C. and C.M.M. A.S.RH. wrote the manuscript with input from P.C.W. All authors reviewed and approved the final version of the manuscript.

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