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Functional Trade-Offs Asymmetrically Promote Phenotypic Evolution

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Abstract.—Trade-offs are thought to bias evolution and are core features of many anatomical systems. Therefore, trade-offs may have far-reaching macroevolutionary consequences, including patterns of morphological, functional, and ecological diversity. Jaws, like many complex anatomical systems, are comprised of elements involved in biomechanical trade-offs. We test the impact of a core mechanical trade-off, the transmission of velocity versus force (i.e., mechanical advantage), on rates of jaw evolution in Neotropical cichlids. Across 130 species representing a wide array of feeding ecologies, we find that the velocity–force trade-off impacts the evolution of the surrounding jaw system. Specifically, rates of jaw evolution are faster at functional extremes than in more functionally intermediate or unspecialized jaws. Yet, surprisingly, the effect on jaw evolution is uneven across the extremes of the velocity–force continuum. Rates of jaw evolution are 4- to 10-fold faster in velocity-modified jaws, whereas force-modified jaws are 7- to 18-fold faster, compared to unspecialized jaws, depending on the extent of specialization. Further, we find that a more extreme mechanical trade-off resulted in faster rates of jaw evolution. The velocity–force trade-off reflects a gradient from specialization on capture-intensive (e.g., evasive or buried) to processing-intensive prey (e.g., attached or shelled), respectively. The velocity extreme of the trade-off is characterized by large magnitudes of trait change leading to functionally divergent specialists and ecological stasis. By contrast, the force extreme of the trade-off is characterized by enhanced ecological lability made possible by phenotypes more readily co-opted for different feeding ecologies. This asymmetry of macroevolutionary outcomes along each extreme is likely the result of an enhanced utility of the pharyngeal jaw system as force-modified oral jaws are adapted for prey that requires intensive processing (e.g., algae, detritus, and mollusks). The velocity–force trade-off, a fundamental feature of many anatomical systems, promotes rapid phenotypic evolution of the surrounding jaw system in a canonical continental adaptive radiation. Considering that the velocity–force trade-off is an inherent feature of all jaw systems that involve a lower element that rotates at a joint, spanning the vast majority of vertebrates, our results may be widely applicable across the tree of life. [Adaptive radiation; constraint; decoupling; jaws; macroevolution; specialization.]

Trade-offs are fundamental to an array of biological systems, ranging from life history implications of limited resources to functional implications of anatomical conflict (Reznick 1983; Stearns 1989; Fleming and Gross 1990; Adamo et al. 2001; Zera and Harshman 2001; Godin and McDonough 2003; Sadras 2007; Olofsson et al. 2009; Cox et al. 2010; Schwenke et al. 2016; Koch and Hill 2018). Since trade-offs are pervasive in nature and are core features of many functional and mechanical systems, they may have far-reaching macroevolutionary consequences, perhaps sculpting patterns of morphological, functional, and ecological diversity. Trade-offs inherently constrain evolution by limiting the compatibility of traits and their emergent functions, and subsequently, may also limit their rate of evolution (Futuyma and Moreno 1988; Arnold 1992; Koehl 1996; Wainwright 2007; Walker 2007). Yet, macroevolutionary signatures of trade-offs can be positive. For example, traits involved in trade-offs often evolve faster than other traits (Holzman et al. 2012; Muñoz et al. 2017, 2018). Further, some emergent properties of trade-offs, such as extreme functions, may be associated with rapid phenotypic evolution (Borstein et al. 2019; Burress et al. 2020; Corn et al. 2020). Therefore, the macroevolutionary signatures of trade-offs may be contradictory to their functional properties.

Anatomical systems must meet the performance demands of their functions. This necessity may limit the evolution of a system in which performance trades off across dimensions of the phenotype. Lever systems present a trade-off (Fig. 1) in which they cannot be simultaneously specialized for transmitting both velocity and force (Uicker et al. 2003). In other words, some combinations of traits (and their mechanical properties) are not possible. Simple levers underpin an array of biomechanical systems, including fish jaws (Westneat 1994; Wainwright and Richard 1995), mammal jaws (Freeman and Lemen 2008; Zelditch et al. 2017; Missagia et al. 2020), bird beaks (Herrel et al. 2009; Navalón et al. 2020), tetrapod limbs (Biewener 1989), and raptorial appendages of mantis shrimp (Patek et al. 2007; Muñoz et al. 2017). Since jaws and limbs provide vital functions, like food acquisition and locomotion, underlying mechanical trade-offs could have far-reaching consequences.

The functional and ecological implications of such trade-offs are often profound. Limbs are subject to the velocity–force trade-off, which imposes constraints on stamina (Vanhooydonck et al. 2001), mobility (i.e., sprinting, jumping, and swimming performance), and stability (i.e., clinging and climbing performance; Losos and Sinervo 1989; Losos et al. 1993; Losos 1990;

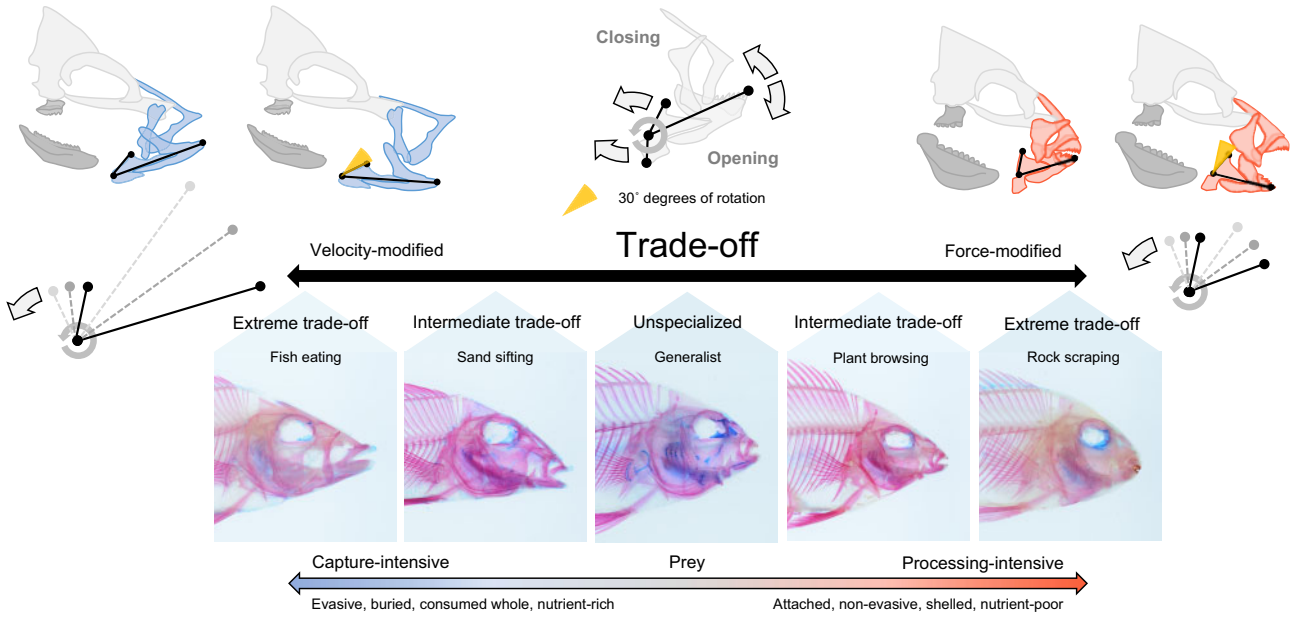

FIGURE 1. Anatomical, functional, and ecological implications of the velocity–force trade-off in fish jaws. The levers depicted along each side show the comparative length of the in- and out-levers that determine the relative transmission of velocity and force. Inset images depict differing degrees of velocity–force trade-off associated with prominent cichlid feeding ecologies: fish-eating (e.g., *Crenicichla*, *Cichla*, *Caquetaia*), sand-sifting (e.g., *Satanoperca*, *Gymnogeophagus*, *Geophagus*), plant-browsing (e.g., *Symphysodon*, *Uaru*, *Mesonauta*), rock-scraping (e.g., *Hypsophrys*, *Tomocichla*, *Talmancaheros*), and no trade-off (e.g., *Nannacara*). Outlines depict general phenotypes and feeding motions associated with the velocity–force trade-off. Pharyngeal jaws are depicted in dark gray.

James et al. 2007; Nauwelaerts et al. 2007; Moreno-Rueda et al. 2020). In jaw systems, there is a trade-off between a rapid versus strong bite (Westneat 1994, 1995), which has broad ecological implications, particularly for dietary niche (Fig. 1). In rodents, for example, faster jaw movements are useful when chewing soft insects, whereas cracking hard nuts and seeds requires more forceful bites (Zelditch et al. 2017; Missagia et al. 2020). In fishes, feeding on evasive prey requires the generation of sufficient suction to draw prey into the predator's mouth, which is facilitated by large, protrusible jaws (Bellwood et al. 2015). Prey attached to substrate, such as coral, snails, or epilithic algae, by contrast, require direct grasping and prying, which is facilitated by a powerful bite (Bellwood and Choat 1990).

Little is known about how trade-offs *directly* influence the evolution of the surrounding anatomical system at macroevolutionary scales, convoluting the causal link between specialization and rate of evolution, as most work has centered on the *indirect* effects of trade-offs by focusing on their emergent attributes. For example, some mechanically specialized feeding ecologies are associated with faster evolving phenotypes than others (Borstein et al. 2019; Burress and Wainwright 2020; Corn et al. 2020). These macroevolutionary outcomes raise the question if mechanical trade-offs might provide a causal link between extreme functions and rapid evolution. Jaw systems can have very different shapes, considering both the upper and lower jaw elements, yet have the same underlying mechanical advantage (MA) (Wainwright et al. 2004; Burress et al. 2020), and by extension, fall along the same point of the velocity–force trade-off (Wainwright et al. 2005). In other words, at any given point along the velocity–force trade-off, there is some capacity for the surrounding jaw system to diversify. Here, we test whether this capacity is uniform along the trade-off, or rather, if certain regions constrain or promote the evolution of the jaw system. Using contemporary phylogenetic comparative methods, we test whether (i) trade-offs act as a constraint or driver of jaw evolution (i.e., has a consistently negative or positive effect), (ii) if this effect is symmetrical (or asymmetrical) along both mechanical extremes of the trade-off (i.e., in velocity- and force-modified jaws), and (iii) if the intensity of the trade-off scales with the evolution of the jaw system (i.e., if a stronger trade-off has a smaller/larger effect). To tease apart these patterns, we test for several alternative relationships between the velocity–force trade-off and the rate of jaw evolution (Supplementary Fig. S1a–d available on Dryad at http://dx.doi.org/10.25338/B8HK9D) in a large continental radiation of cichlid fishes. Neotropical cichlids have extensively explored the velocity–force trade-off, ranging from some of the most velocity-modified jaws found in fishes (Ferry et al. 2019) to compact force-modified jaws adapted to scrape algae from rock surfaces (Winemiller et al. 1995; Burress 2016; Říčan et al. 2016). Neotropical cichlids exhibit high ecological diversity, consuming an array of prey, including fishes, crabs, snails, bivalves, algae, plants,

detritus, fruits, and seeds (Winemiller et al. 1995; Burress 2016), making them an ideal group to evaluate the macroevolutionary consequences of mechanical trade-offs on jaw evolution.

Materials and Methods

Sampling, Study Group, and Measurements

We measured 358 individuals representing 130 species of Neotropical cichlid (Supplementary Table S1 available on Dryad) that span all major lineages (López-Fernández et al. 2010; McMahan et al. 2013) and reflect their ecological diversity (Winemiller et al. 1995; López-Fernández et al. 2012; Říčan et al. 2016). Specimens were either cleared and stained or radiographed, permitting direct measurement of jaw bones. Fish jaws are complex and comprised of many lever systems (Westneat 1994). To characterize the trade-off between velocity- and force-modified jaw systems, we measured the lever mechanism of the lower jaw and calculated MA as the in-lever divided by the out-lever (Westneat 1994, 2004; Wainwright and Richard 1995). MA depicts the potential force transfer to the tip of the lower jaw as the adductor mandibulae muscle contracts and closes the jaws (Wainwright et al. 2004; Fig. 1). MA of the jaw closing and opening levers were significantly correlated based on phylogenetic least squares regression ($r = 0.225$; $t = 2.779$; $p = 0.006$); therefore, we simply used the closing MA values to characterize the velocity–force trade-off for all subsequent phylogenetic comparative analyses (hereafter, MA is generally referred to as the trade-off).

The lower jaw lever is part of a broader anatomical system that participates in feeding motion. To characterize the size, shape, and protrusible nature of the surrounding jaw system, we measured the length of the mandible, maxilla, dentigerous arm of the premaxilla, and ascending process of the premaxilla (Supplementary Table S1 available on Dryad; see the Supplementary material available on Dryad for detailed descriptions). These traits have well-established associations with feeding performance and/or feeding ecology (Winemiller et al. 1995; Waltzek and Wainwright 2003; Hulsey and García de León 2005; Hulsey et al. 2010a; Bellwood et al. 2015; Burress et al. 2020). Traits were ln-transformed and regressed against ln-transformed standard body length and phylogenetically size-corrected using the phyl.resid function implemented in PHYTOOLS (Revell 2012). We also visualized the distribution of MA across different jaw shapes using principal components analysis implemented with the prcomp function. During this procedure, we used the mandible, maxilla, premaxilla, and ascending process phylogenetic residuals as input.

Owing to subjectivity in determining the point at which one function "meaningfully" trades off for another (i.e., becomes specialized), we used a sliding window approach to classify species as engaging in a trade-off in terms of jaws that are specialized for the transmission of velocity or force. We used five different intervals to classify species as velocity-modified and force-modified based on the closing MA of the lower jaw: the 5th and 95th percentiles, 10th and 90th percentiles, 15th and 85th percentiles, 20th and 80th percentiles, and 25th and 75th percentiles (Supplementary Fig. S2 available on Dryad). These sliding windows reflect varied degrees of trade-off, from more to less (on average), respectively. Technically, all jaws trade-off velocity and force to some degree, but species in the intermediate category (i.e., between the 25% and 75% percentile) have less specialized jaws in terms of transmission of velocity and force and may be considered generalists or "jack-of-all trades" rather than specialists (Fig. 1).

Phylogenetic Tree

During phylogenetic comparative analyses, we used an existing phylogeny that densely sampled cichlids (Burress and Tan 2017; Burress et al. 2019) and is consistent with recent phylogenomic hypotheses of the Cichlinae (Burress et al. 2018; Ilves et al. 2018). There is a more recent phylogeny that broadly sampled cichlids (McGee et al. 2020); we demonstrate that our results are consistent using this alternative phylogeny (see Supplementary material available on Dryad).

State-Dependent Rates of Evolution

We then estimated rates of jaw evolution for each of the discrete states that reflect the velocity–force trade-off using a Bayesian, state-dependent, relaxed-clock model of multivariate Brownian motion (MuSSCRat; May and Moore 2020) implemented in RevBayes (Höhna et al. 2016). This method accounts for background rate heterogeneity, which prevents all rate heterogeneity from being attributed to the discrete character of interest, reducing the risk of type-I error. Many factors can moderate the rate of phenotypic evolution, including genetic (Schluter 1996) and ecological features (Simpson 1953; Hunter 1998; Mahler et al. 2010). By accounting for background rate variation and thereby reducing the risk of erroneously interpreting the signal of these alternative factors (May and Moore 2020; Burress and Muñoz 2022), we were able to home in on rate variation attributable to the velocity–force trade-off. We scrutinized the robustness of the MuSSCRat model in several ways (see Supplementary material available on Dryad for additional information). Briefly, we repeated each model using different priors, different rate models, an alternative phylogeny (McGee et al. 2020), and we conducted a thorough simulation exercise to assess the sliding-window procedure.

Selection

We estimated the degree of selection (α) towards velocity- and force-modified jaws using OUwie function employed in the OUwie R package (Beaulieu et al. 2012; Beaulieu and O'Meara 2015). We estimated the evolutionary histories of the discrete characters using

stochastic character mapping (Huelsenbeck et al. 2003) with the make.simmap function implemented in the PHYTOOLS package (Revell 2012). During this procedure, we allowed all transitions to have different rates (i.e., the all-rates-different model transition model), and we fitted a multipeak Ornstein–Uhlenbeck evolutionary model that permits different α for each state of the selective regime (i.e., OUMA) with the regimes depicting velocity-modified jaws, jaws with no trade-off, and force-modified jaws. We estimated α across each of the aforementioned sliding windows and repeated these estimates across 100 trees randomly sampled from the posterior distribution to account for phylogenetic uncertainty.

Ecological Lability

We were interested in the degree of ecological lability along the velocity–force trade-off. We classified three feeding guilds associated with velocity-modified jaws: piscivory, substrate sifting, and zooplanktivory (Hulsey and García de León 2005; Martinez et al. 2018; Burress et al. 2020). We also classified three guilds associated with force-modified jaws: algivory, detritivory, and herbivory (Říčan et al. 2016; Burress et al. 2020). We assigned species to feeding guilds based on a combination of primary dietary and feeding kinematic literature (Winemiller et al. 1995; Wainwright et al. 2001; Waltzek and Wainwright 2003; Hulsey et al. 2010a; Burress 2016; Říčan et al. 2016) as well as cross-validation with our estimates of MA. For this analysis, all other species were classified as not exhibiting trade-offs. We defined an equal number of guilds to prevent one side of the velocity–force trade-off from arbitrarily having more opportunities for transitions. Since mollusks are mostly secondary or tertiary prey items (Winemiller et al. 1995; Burress 2016 and references therein), all species that eat mollusks in our dataset were represented by one of the other force-modified guilds that better reflect their primary diets. We estimated transition rates using stochastic character mapping as described above (Huelsenbeck et al. 2003; Revell 2012). We summarized three types of transitions: (i) transitions into a trade-off (no trade-offs to velocity- or force-associated feeding ecology), (ii) transitions from a trade-off (velocity- or force-associated feeding ecology to no trade-offs), and (iii) transitions within a trade-off (among feeding ecologies associated with the same trade-off).

Phenotypic Disparity and Evolutionary Optima

To assess phenotypic disparity in multivariate oral jaw shape along the velocity–force trade-off, we calculated jaw shape disparity for each of the sliding windows (i.e., 95%, 90%, etc.) using the disparity function implemented with the GEIGER package (Harmon et al. 2008). Disparity was calculated using mean squared distance. Lastly, we estimated the adaptive landscape on either side of the velocity–force trade-off, specifically the distribution of adaptive peaks, using the l1ou package (Khabbazian et al. 2016). Using the *estimate_shift_configuration* function, we fitted multipeak OU models to our four continuous characters that characterize the shape and size of the oral jaws. We then summarized the proportion of optima (i.e., selective regimes) represented within each sliding window (i.e., 95%, 90%, etc.). Our intent in doing so was to quantify the implications of the velocity–force trade-off in terms of viable evolutionary optima, specifically a loss of viable optima towards the extremes of the trade-off and potential asymmetries in this loss in each direction. We repeated this exercise across 100 trees randomly sampled from the posterior distribution to account for phylogenetic uncertainty.

Results

Mechanical extremes of the velocity–force trade-off were well-distributed across the phylogeny, including numerous origins of velocity- (e.g., *Petenia*, *Caquetaia*, *Crenicichla*, *Parachromis*) and force-modified jaws (e.g., *Hypsophrys*, *Tomocichla*, *Symphysodon*, *Paraneetroplus*; *Amatitlania*; Fig. 2a). Species were normally distributed in terms of MA (Fig. 2b), and selection (i.e., estimates of α) did not differ between force- and velocity-modified jaws (Supplementary Fig. S3a available on Dryad). Further, along both mechanical extremes, selection generally increased with the extent of the trade-off (Supplementary Fig. S3b,c available on Dryad). The velocity–force trade-off (i.e., MA) was not correlated with the multivariate shape of the jaws ($R^2 = 0.049$; $F = 0.015$; $P = 0.904$; Fig. 3c), indicating no auto-correlation between our predictor (velocity–force trade-off; MA) and response (jaw shape) variables.

Both mechanical extremes of the velocity–force trade-off were associated with faster evolution of the jaw system (Fig. 3a). Yet, this effect was asymmetrical, as it was ∼2-fold stronger in force-modified jaws than in velocity-modified jaws (Fig. 3a). The effect also scaled bidirectionally with the extent of the trade-off, meaning that the fastest rates of jaw evolution were consistently associated with phenotypes at the extremes of the trade-off continuum (Fig. 3b,c). These results were robust across analyses with different priors and rate models (Supplementary Table S2 available on Dryad; Supplementary Figs. S4–S6 available on Dryad). The disparity of jaw shape is nominally greater in force-modified than velocity-modified jaws, but jaw shape disparity varied symmetrically along both extremes of the velocity–force trade-off (Fig. 4a). Along both extremes of the trade-off, viable evolutionary optima were symmetrically lost (Fig. 4b; Supplementary Fig. S7 available on Dryad). In the strictest sliding window for trade-offs (5th and 95th percentiles), the average proportion of viable optima represented was only 20% of the total estimated across the phylogeny (Fig. 4b). There was also a large discrepancy in ecological lability along either extreme of the velocity–force trade-off (Fig. 4c). There was a 1.8-fold higher transition rate into

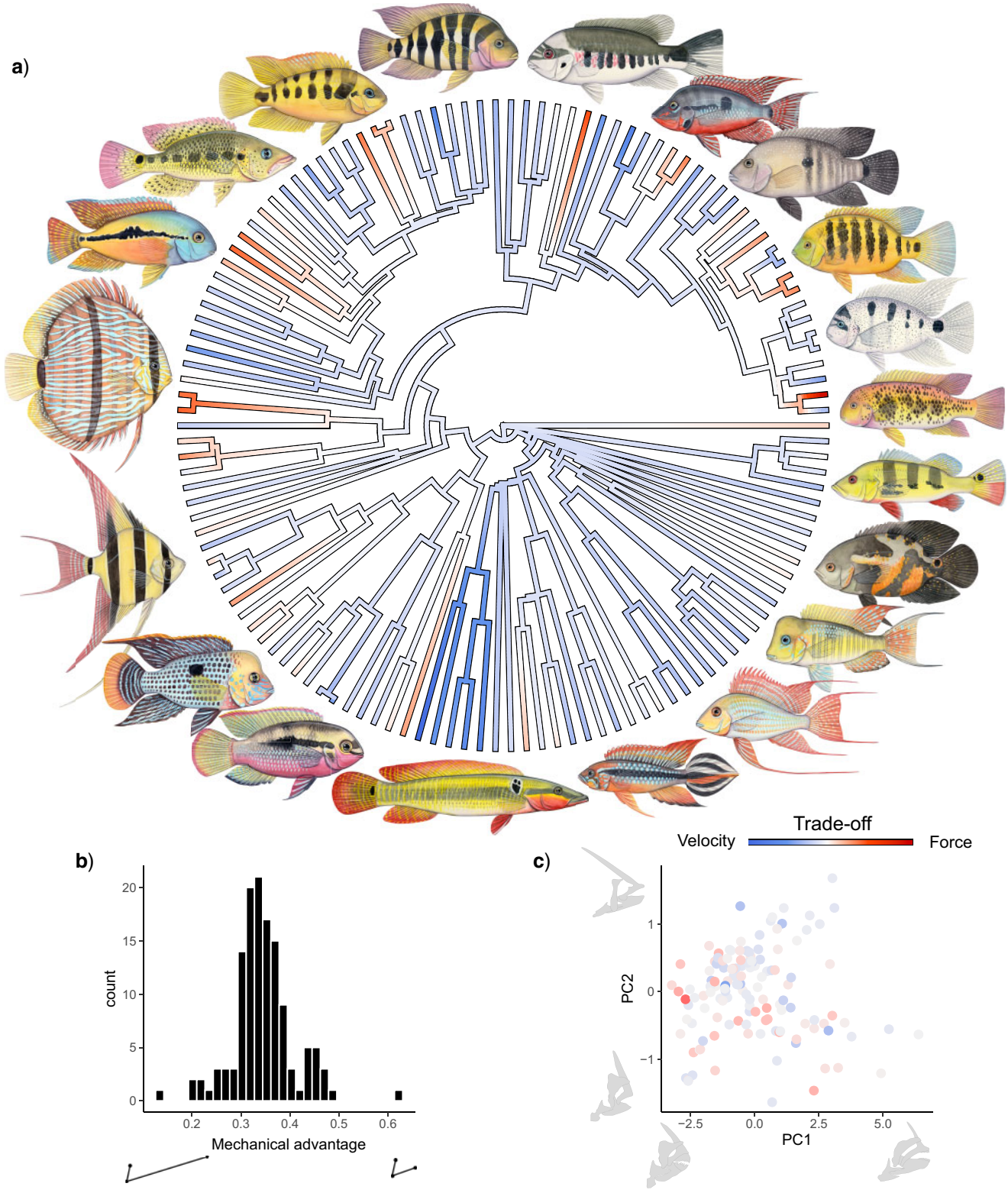

FIGURE 2. Exploration of the velocity–force trade-off among American cichlids. Distribution of mechanical advantage across the phylogeny (a) and among species (b). Illustrations depict an adjacent lineage (clockwise from bottom): *Crenicichla*, *Laetacara*, *Andinoacara*, *Pterophyllum*, *Symphysodon*, *Hypsorphrys*, *Petenia*, *Amatitlania*, *Amphilophus*, *Tomocichla*, *Thorichthys*, *Herichthys*, *Cincelichthys*, *Vieja*, *Paraneetroplus*, *Cichla*, *Astronotus*, *Gymnogeophagus*, *Geophagus*, and *Apistogramma*. Distribution of mechanical advantage across different jaw shapes (c). Each point depicts a species. Outlines depict jaw shapes associated with the extremes of each axis.

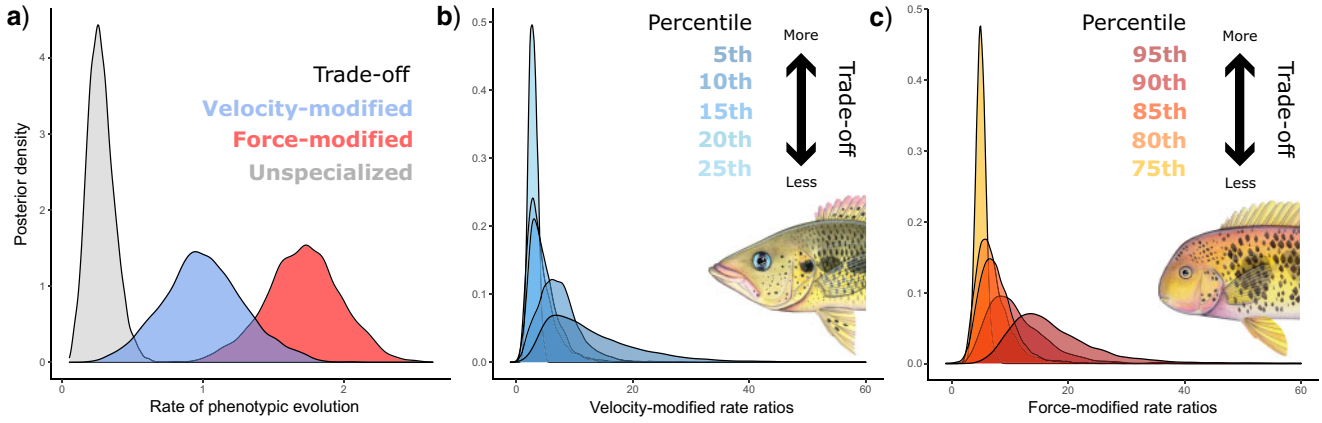

FIGURE 3. Diversification of fish jaws across the velocity–force trade-off. Rates of phenotypic evolution in velocity- and force-modified jaws (a). Rate ratios of (b) velocity- and (c) force-modified jaws relative to jaws lacking a trade-off. Percentiles depict the sliding windows used to classify species engaged in a trade-off (darker colors reflect a stronger trade-off). Illustrations depict a representative species that reflect each side of the velocity–force trade-off.

feeding ecologies associated with velocity-modified jaws (Fig. 4c). There was a 4.7-fold higher transition rate away from feeding ecologies associated with force-modified jaws (Fig. 4c). There was a 13.2-fold higher transition rate among feeding ecologies that share an association with force-modified jaws (Fig. 4c). Therefore, there were far fewer transitions away from feeding ecologies associated with velocity-modified jaws.

DISCUSSION

Mechanical Trade-Offs as Macroevolutionary Drivers

Mechanical trade-offs should constrain the evolution of anatomical systems by limiting the multifunctionality of performance traits (Futuyma and Moreno 1988; Koehl 1996; Wainwright 2007; Walker 2007). The velocity–force trade-off, in particular, prevents some combinations of traits and their emergent functions (Westneat 1994; Wainwright and Richard 1995; Burress et al. 2020). Yet, we found that this inherent functional implication of trade-offs does not necessarily extend to its macroevolutionary consequences. Rather, the mechanical extremes of the velocity–force trade-off promoted the evolution of the surrounding jaw system (Fig. 3). Importantly, this finding provides a causal link between rapid evolution and the extremes of feeding ecology, an emergent pattern widely observed in fishes (Borstein et al. 2019; Burress et al. 2020; Corn et al. 2020). Proximately, accelerated evolution with stronger trade-offs may underpin the pattern that adaptive radiations often exhibit (i) rapid phenotypic evolution and (ii) exploration of specialist feeding ecologies tied strongly to an underlying mechanical trade-off (Hulsey et al. 2010c; Martin and Wainwright 2011; Burress et al. 2018), and perhaps even the canonical pattern that adaptive radiation occurs via an early burst of phenotypic evolution as species rapidly diverge along the mechanical extremes of trade-offs (Simpson 1953). Our study also expands upon the pattern that traits involved in trade-offs tend to evolve more rapidly (Holzman et al. 2012; Muñoz et al. 2017, 2018) by showing that entire anatomical systems (not just the levers themselves) evolve more rapidly in response to extreme velocity–force trade-offs. This phenomenon is likely made possible by many-to-one mapping of morphology-to-mechanical properties (Alfaro et al. 2005; Wainwright et al. 2005) in which many differently shaped jaw systems can share the same underlying MA (i.e., position along the velocity–force trade-off), providing some capacity for the jaw system to rapidly evolve and meet similar performance demands.

Contrasting Adaptive Landscapes along the Velocity–Force Trade-Off

Stronger mechanical trade-offs resulted in faster rates of jaw evolution (Fig. 3). Surprisingly, the magnitude of this effect differed depending on whether jaws were specialized for transmitting force or velocity. Force-modified jaws had roughly 2- to 4-fold faster rates of jaw evolution than velocity-modified jaws (Fig. 4). Together, these results indicate that stronger trade-offs scale positively, but asymmetrically, with rates of trait evolution.

We ruled out several explanations for why the effect of the velocity–force trade-off on jaw diversification was asymmetrical. We characterized the trade-off with a simple ratio of input-to-output lever lengths, so the relative transmission of velocity and force are consistent across values of MA (i.e., are 1:1; Westneat 1994, 1995; Wainwright and Richard 1995). MA was also normally distributed among species (Fig. 2b). The intensity of selection is a major determinant of evolutionary rates (Smith 1976; Butler and King 2004); however, we found that selection towards both mechanical extremes of the velocity–force trade-off was equivalent (Supplementary Fig. S2 available on Dryad). Another issue is that some phenotypes may be feasible, yet unobserved, or mechanically precluded altogether, when conflicting functions cannot be co-optimized (i.e., Shoval et al.

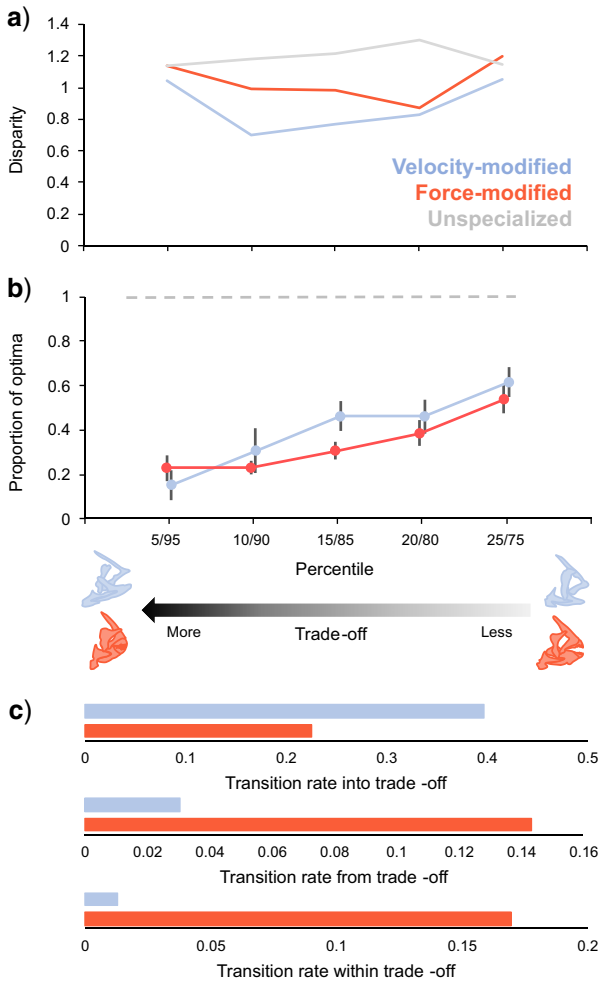

FIGURE 4. Distribution of morphological disparity across the velocity–force trade-off (a). Symmetrical loss of viable evolutionary optima along each extreme of the velocity–force trade-off (b). Transition rates into, from, and within feeding ecologies that involve velocity and force trade-offs (and those that do not involve a trade-off). Error bars in (b) depict the 95% CI from analyses on 100 randomly sampled trees.

2012; Sheftel et al. 2013; Tendler et al. 2015). Indeed, we found increasingly fewer viable adaptive peaks (i.e., jaw phenotype evolutionary optima) as the jaw system became more specialized for the transmission of velocity or force (Fig. 4b). This suggests that fewer phenotypes are functionally or ecologically viable as the strength of the velocity–force trade-off increases, consistent with theoretical (Olsson et al. 2020) and empirical (Martin and Wainwright 2013) estimates of feeding performance adaptive landscapes.

Our estimate of the adaptive landscape indicates that there are similar numbers of evolutionary optima along either extreme of the velocity–force trade-off (Fig. 4b). In other words, the loss of evolutionary optima is symmetrical as the jaws become increasingly specialized for the transmission of velocity or force. In terms of velocity-modified jaws, the adaptive landscape may have multiple peaks associated with different prey types with varied degrees of evasiveness (Olsson et al. 2020). Alternatively, multiple peaks may stem from the relative use of suction and predator approach (i.e., ram) during prey capture (Liem 1978; Longo et al. 2016). Both of these capture-intensive strategies are represented in American cichlids, including pursuit predators that feed via high ram velocity (e.g., *Crenicichla*) and ambush predators that use extreme jaw protrusion to generate suction (e.g., *Petenia* and *Caquetaia*; Wainwright et al. 2001; Waltzek and Wainwright 2003; Holzman et al. 2008; Hulsey et al. 2010a). These two feeding modes utilize velocity-modified jaws and likely represent distinct adaptive peaks (Arbour and López-Fernández 2014; Burress 2016; Burress et al. 2019; Arbour et al. 2020). In terms of force-modified jaws, there are numerous feeding ecologies that require different functional properties. Even in simple ecosystems, such as small isolated lakes, durophagy may have a distinct adaptive peak in fishes (Martin and Wainwright 2013). In Neotropical cichlids, there are numerous adaptive peaks associated with functional properties and feeding ecologies that characterize force-modified jaws (Arbour and López-Fernández 2014; Burress 2016; Burress et al. 2019), likely reflecting their diversity of feeding modes and prey (Winemiller et al. 1995). While these findings—normal distribution of species, symmetrical degree of selection, and symmetrical distribution of evolutionary optima along the extremes of the velocity–force trade-off—shed light on the evolutionary and ecological implications of the trade-off, none suitably explain the asymmetry in the effect of the trade-off on rates of jaw evolution.

Extremes of Trade-Off Favor Alternative Modes of Evolution

There may be underlying asymmetries along the velocity–force trade-off that manifest in the observed asymmetrical evolutionary rates. Despite the restrictive nature of trade-offs, in most cases, their effects can be relaxed or circumvented altogether. For example, functional innovations may allow previously antagonistic tasks to be co-optimized (Burress et al. 2020; Olivier et al. 2021). Ray-finned fishes possess two jaw systems: the oral jaws that perform the task of prey capture and the pharyngeal jaws that perform the task of prey processing (Lauder 1982, 1983). Recent work has shown that the two jaw systems evolve somewhat independently (Burress et al. 2020; Conith and Albertson 2021; Ronco and Salzburger 2021) and, in particular, that adaptation of the pharyngeal jaws can occur independently of the oral jaws (Burress and Muñoz 2021). Importantly, the utility of a second set of jaws, dedicated to prey processing, is strongly skewed along the velocity–force trade-off. When the oral jaws are modified for the transmission of velocity, prey items tend to be functionally demanding in terms of prey capture (Fig. 1). For example, evasive prey requires the generation of sufficient suction to draw prey into the mouth (Bellwood et al. 2015) or prey buried underneath substrate requires excavation by mobile oral jaws (López-Fernández et al. 2014). Since the pharyngeal jaws are only involved in the processing of prey, rather than its capture, they are of limited use if the prey is

minute (i.e., plankton) and require little or no processing or a functional nuisance if large prey is simply swallowed whole (i.e., fishes), as their physical presence restricts gape and thus the size of prey that can be swallowed (McGee et al. 2015; Burress and Wainwright 2020).

By contrast, force-modified oral jaws tend to be associated with prey that is functionally demanding by requiring significant processing prior to ingestion (Fig. 1). Since pharyngeal jaws perform all crucial functions related to prey processing (Liem 1973), their utility is expanded in these circumstances. Many cichlids have pharyngeal jaw shapes and corresponding dentition adapted to crush, grind, or shear hard and tough prey ranging from mollusks, shelled macrocrustaceans, plants, algae, detritus, seeds, and fruits (Casciotta and Arratia 1993; Winemiller et al. 1995; Burress 2016). While these items may require initial forceful grasping or prying actions by the oral jaws, afterwards the pharyngeal jaws do the heavy lifting of prey processing. For example, the pharyngeal jaws may engage in the prolonged and oscillating generation of force necessary to grind and rupture algae cells, thereby facilitating their digestion (Xie 2001; Carr et al. 2006) or generate acute bouts of sufficient force to crush mollusk shells (Hulsey 2006; Hulsey et al. 2008). The asymmetry in the utility of the pharyngeal jaws at the extremes of the velocity–force trade-off likely has broad macroevolutionary consequences.

We found that velocity- and force-modified jaws, particularly those on the extremes of the mechanical trade-off, exhibit marked differences in ecological lability (Fig. 4c). The evolution of highly protrusible oral jaws permits fish to rapidly reduce the physical distance to prey (Bellwood et al. 2015; Wainwright et al. 2015), thereby facilitating the capture of evasive organisms (Waltzek and Wainwright 2003; Holzman et al. 2008; Hulsey et al. 2010a). The magnitude of morphological and functional changes to the feeding apparatus tends to be large when the jaw system is modified for the transmission of velocity, especially when associated with the evolution of piscivory (Arbour and López-Fernández 2014; Arbour et al. 2020; Burress et al. 2020) and substrate sifting (Winemiller et al. 1995; Burress 2016). Consequently, reversals away from feeding ecologies associated with velocity-modified jaws are rare (McGee et al. 2015; Burress and Wainwright 2019; Arbour et al. 2020; Fig. 4c). This pattern is consistent with the notion that piscivory is functionally demanding, favors specialization, and is prone to ecological stasis (Mittelbach and Persson 1998; Collar et al. 2009; Arbour et al. 2020). Further, there appears to be a limited capacity for cichlids to transition easily among piscivory, substrate sifting, and zooplanktivory (i.e., feeding ecologies generally associated with velocity-modified jaws; Fig. 4c), likely in response to the divergent functional demands imposed on both jaw systems by these feeding ecologies (Winemiller et al. 1995; Wainwright et al. 2001; Hulsey and García de León 2005; Burress 2016; Weller et al. 2017; Martinez et al. 2018) and reduced utility of the core functions provided by the pharyngeal jaws (as prey require minimal processing prior to ingestion; Liem 1973; Burress 2016). In other words, co-opting velocity-modified jaws for alternative feeding ecologies is functionally challenging, ultimately leading to ecological stasis.

By contrast, force-modified jaws are often used to pluck or dislodge prey that is attached directly to hard substrates, such as coral reefs (Wainwright et al. 2004) or rocks (Rüber et al. 1999). American cichlids have exploited the force-modified side of the mechanical trade-off in an iterative fashion, readily swapping back and forth among different feeding ecologies tied to prey that requires intensive processing such as mollusks, algae, and detritus (Hulsey 2006; Hulsey et al. 2008; Říčan et al. 2016; Burress et al. 2019; Figs. 2a and 4c). This degree of ecological lability is likely made possible by an enhanced functional utility of the core functions provided by the pharyngeal jaws across different feeding ecologies (Liem 1973; Burress 2016; Burress et al. 2020). Thus, force-modified jaws may be more easily co-opted for alternative feeding ecologies in response to expanded functional support from the pharyngeal jaw system, ultimately leading to elevated rates of oral jaw evolution relative to velocity-modified jaws (Figs. 1, 3, and 4).

Conclusions

Despite that trade-offs limit evolution in myriad ways (Futuyma and Moreno 1988; Koehl 1996; Wainwright 2007; Walker 2007), we found that a core mechanical trade-off, inherent to all jaw systems that involve a lower jaw element that rotates at a joint (i.e., the vast majority of vertebrates), led to a positive macroevolutionary signature on jaw evolution. An underlying mechanical trade-off between the transmission of velocity and force asymmetrically promoted the evolution of the surrounding jaw system in a major continental radiation of cichlid fishes (Fig. 3). We ruled out several alternative explanations for the asymmetry—a biased distribution of species along the velocity–force trade-off, asymmetries in the selection, phenotypic disparity, and the viability of adaptive peaks along each extreme of the trade-off. Rather, we found that each mechanical extreme of the velocity–force trade-off was characterized via divergent macroevolutionary patterns. Velocity trade-offs were exploited through mechanical specialization that led to ecological stasis, whereas force trade-offs were explored through an iterative fashion in response to enhanced ecological lability. Conspicuous adaptive radiations often feature the rapid evolution of phenotypes that exemplify the extremes of functional trade-offs (e.g., Caribbean anoles, Losos 2009; Malawian cichlids, Hulsey et al. 2010b; Hawaiian honey creepers, Navalón et al. 2020; and Tanganyikan cichlids, Ronco et al. 2021). We propose that this coupling of extreme phenotypes and rapid evolution may occur in response to trade-offs directly promoting phenotypic evolution of the surrounding anatomical systems (Fig. 3). Our study fills a critical gap in recent literature linking the extremes of feeding ecology with rapid phenotypic evolution at macroevolutionary scales (Borstein et al. 2019; Burress et al. 2020; Corn et al. 2020) by directly implicating the

underlying mechanical trade-off as a key evolutionary catalyst. We also expand the understanding of how the rate of evolution of individual traits vary in response to trade-offs (Holzman et al. 2012; Muñoz et al. 2017, 2018) by showing that mechanical trade-offs can elicit rapid evolution of the entire surrounding anatomical system, rather than just the levers themselves or specific traits. This phenomenon (faster evolution at functional extremes) may be widespread, extending to other trade-offs. For example, limb length confers a trade-off in agility versus stability (Losos and Sinervo 1989; Losos 1990; Losos et al. 1993) and is a major axis of adaptive specialization explored by Caribbean anoles (Losos 2009). This effect may likewise influence nonmechanical trade-offs. Physiological evolution is governed by specialist–generalist trade-offs (Angilletta 2009) that might be associated with more rapid evolution. For example, thermal trade-offs driven by latitude (Rabosky et al. 2018) and ocean depth (Martinez et al. 2021) have asymmetrical effects on rates of fish diversification. Therefore, the macroevolutionary reach of trade-offs may correspondingly be broad, and remains a fruitful arena for further inquiry.

Supplementary Material

Data available from the Dryad Digital Repository: http://dx.doi.org/10.25338/B8HK9D.

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