Figures and figure supplements

Strong biomechanical relationships bias the tempo and mode of morphological evolution

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**Figure 1.** Four-bar linkage systems have evolved independently multiple times across animals and are comprised of four rotatable links that transmit motion and force.  
(A) Four-bar linkages consist of a fixed link (black) and three mobile links: input (orange), output (red), and coupler (blue).  
(B) In the raptorial appendages of mantis shrimp (Stomatopoda), rotation of the input link (meral-V, m-V, which is part of the merus segment, me) causes the output link (carpus, ca) to rotate outward, which then rapidly rotates the dactyl (da).  
(C) In the oral four-bar system that evolved independently in labrid and cichlid fishes, the input link (lower jaw, lj) rotates ventrally, causing rotation in the nasal (na) and in the output link (maxilla, mx), resulting in premaxillary (pmx) protrusion.  
(D) In the opercular four-bar linkage system of centrarchid fish, the input link (opercle and subopercle, op) swings posteriorly, as does the interopercle (iop). This motion is transmitted to the output link (retroarticular process in the mandible, ra), which causes the mandible to rotate ventrally and open the lower jaw.  
(B–D) Dashed lines denote the closed configuration of input (orange), output (red), and coupler (blue) links, whereas solid lines denote their open configuration following motion. Arrows denote the direction of motion. Distal/anterior is to the right and dorsal is toward the top of the page.

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Figure 2. Across the four focal systems, evolutionary rate is consistently faster in the links to which the mechanical output is most mechanically sensitive (asterisks). The evolutionary rate parameter, $\sigma^2$ (± 95% confidence interval), is depicted for each link in each system. Orange circles denote the input link, red circles denote the output link, and blue circles denote the coupler link. Shared letters denote rates that are not statistically different from each other (statistical results are in Table 1).

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Figure 3. Three well-supported transitions in KT (black circles) occurred across the phylogeny of wrasses. With each of these transitions in KT, either the input (orange circle) or output link (red circle) also experienced a strongly-supported shift in magnitude (sign indicates directionality of trait shift). The Figure 3 continued on next page.
coupler link (blue circle) did not exhibit a strongly-supported shift. These analyses were performed using reversible-jump MCMC which detected significant shifts (optimal trait value, θ) based on the distribution of traits across the phylogeny (KT trait distribution is overlaid as a color map on the tree branches; see Figure 3—figure supplement 1 for color maps of the other trait distributions). The sizes of the circles represent posterior probability (threshold posterior probability for a strongly supported transition was set at > 0.5).

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Figure 3—figure supplement 1. Results of reversible-jump MCMC analysis of evolutionary trait shifts for the input link (A), output link (B), coupler link (C), and KT (D). Color in each phylogeny denotes trait values with the range of values (theta) for each trait given in each legend. Circles denote branches where shifts in trait values were supported (posterior probability >0.5). Circle size denotes posterior probability of trait shifts.

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Figure 4. The three conceptual frameworks of many-to-one mapping, mechanical sensitivity and constraints converge at the intersection of biomechanics and morphological evolution, highlighting the importance of analyzing these systems at multiple levels. Many-to-one mapping (multiple configurations yield similar mechanical outputs) can occur in any linkage system, yet mechanical sensitivity defines the tight correlations between link size and kinematic transmission (KT). From a biomechanical perspective, mechanical sensitivity occurs because length changes in short links have disproportionately large effects on KT. From an evolutionary perspective, rate of evolutionary change (tempo) is accelerated in the links to which KT is most mechanically sensitive. Many-to-one mapping again emerges from analyses of evolutionary mode (pattern), in which statistically significant shifts in link length and KT across the topology of the phylogeny can occur through multiple configurations, yet only in the links to which the system is most mechanically sensitive.

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