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Speciation through the lens of biomechanics: locomotion, prey capture and reproductive isolation

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Speciation is a multifaceted process that involves numerous aspects of the biological sciences and occurs for multiple reasons. Ecology plays a major role, including both abiotic and biotic factors. Whether populations experience similar or divergent ecological environments, they often adapt to local conditions through divergence in biomechanical traits. We investigate the role of biomechanics in speciation using fish predator–prey interactions, a primary driver of fitness for both predators and prey. We highlight specific groups of fishes, or specific species, that have been particularly valuable for understanding these dynamic interactions and offer the best opportunities for future studies that link genetic architecture to biomechanics and reproductive isolation (RI). In addition to emphasizing the key biomechanical techniques that will be instrumental, we also propose that the movement towards linking biomechanics and speciation will include (i) establishing the genetic basis of biomechanical traits, (ii) testing whether similar and divergent selection lead to biomechanical divergence, and (iii) testing whether/how biomechanical traits affect RI. Future investigations that examine speciation through the lens of biomechanics will propel our understanding of this key process.

1. Introduction

The quest to understand the origin of species requires integration across all facets of the biological sciences. Biochemical, molecular, behavioural, physiological and morphological levels of variation routinely contribute to the process of speciation. Although not all species evolve from natural selection, most do, even in the face of gene flow. The evolution of complex genetic architectures (numbers, location and effects of genes) contributing to reproductive barriers can be rapid, and involve similar or different solutions to the same problem [1]. Ecology, therefore, plays a critical role in speciation [2–4].

Selection is often multifaceted, from abiotic habitat characteristics to biotic interactions. Yet, when looking to the fossil record and across extant taxa, substantial evidence suggests that predator–prey interactions have repeatedly and consistently produced long-term behavioural and morphological (e.g. locomotion and feeding) trends in various clades (e.g. [5,6]). Evolutionary branching has been commonly induced by ecological interactions between predators and their prey [7,8]. Alternatively, predator culls of prey can reduce interspecific competition and stifle speciation under some circumstances

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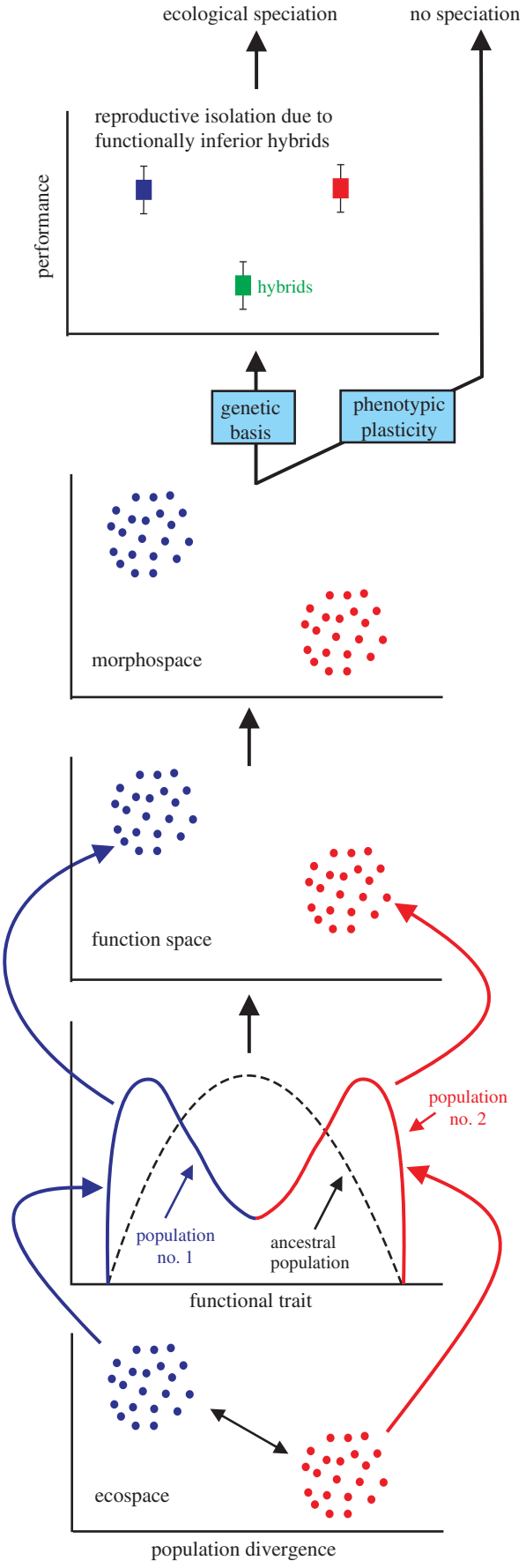

Figure 1. (*Caption opposite.*)

(e.g. [9]). Understanding the mechanistic nature of these interactions and their evolutionary consequences requires a multidisciplinary approach that integrates structure, function and performance—that is, a biomechanical approach.

Figure 1. (*Opposite.*) The theoretical framework for ecological speciation. A species will be divided by an abiotic or biotic isolating mechanism (bottom panel). This will result in the occupation of different regions of ecospace (e.g. two lakes with completely different structural and biotic attributes), followed by divergence of the two populations away from the ancestral population, resulting in the occupation of two distinct regions of function space. The differential functional demands will ultimately drive the alteration of underlying physiological (not shown) and morphological traits. If this is a result of phenotypic plasticity, no speciation will likely occur. With a genetic basis, and assuming reduced fitness of hybrids, speciation will likely occur. However, variation in morphology and biomechanics will likely exhibit a combination of plasticity and genetic-basis. In addition, we are not implying that some plasticity will hinder speciation.

Biomechanics represents the study of biological structure and function using physical principles. Organismal performance represents the primary substrate upon which selection acts [10–12], and variation in performance often arises via variation in biomechanics. For instance, changes in organismal performance are often reflected in morphological shifts, such as muscle and bone size, shape, and arrangement, ultimately leading to an alteration of the forces acting within an animal, or between an animal and its environment. Such changes can occur during adaptation to new ecological conditions [13]. For example, consider a single fish population that is split into two new habitats (figure 1). One habitat is a low-flow environment, much like the ancestral condition. The other is a high-flow environment, imparting new selective pressures. The biomechanical demands in a high-flow environment favour a more streamlined and slender body to minimize drag, and higher aspect-ratio caudal fins to maximize thrust [14–16]. Drag is a force that resists the forward motion of an animal, and thrust is a force that propels an animal forward. Thus, the response to changes in selective pressures is directly related to the resistance and/or production of force. As these two populations diverge over time, they may become reproductively isolated for several reasons, including decreased fitness of immigrants and hybrids if these individuals show maladaptive functional traits compared with residents. This simple illustration of the biomechanical basis of reproductive isolation (RI) highlights the potential for biomechanical approaches to enlighten our understanding of the *mechanisms* of speciation.

The tight fits between form and function suggest the influence of adaptive evolution; however, the prevalence of adaptive traits, the mechanisms by which they arise and the corresponding phenotypic and molecular responses to selection are subjects of extensive debate. Here, we present a unique multidimensional approach to studying how natural selection influences speciation, with the ultimate goal of building an understanding of the origin of species through the study of the adaptive evolution of biomechanical traits and their effects on RI. The lens of biomechanics can open up new predictions about the evolution of whole-organism performance in particular ecological environments. Moreover, biomechanical consequences of phenotypic variation are not always straightforward, sometimes leading to mismatches between morphological changes and functional changes [17]. Thus, assumptions of functional inferiority based on morphology alone are not adequate for predictions about speciation.

We highlight a quantitative framework for understanding population divergence and speciation built on a biomechanical foundation—i.e. study the evolution of organismal

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function to uncover insights into the evolution of RI. As function diverges, as a result of altered or similar selective pressures, lower-level morphological and physiological traits also diverge (figure 1). Population divergence can lead to reproductive incompatibility, either in the presence or absence of gene flow, and can occur during the expansion of populations into new habitats [18,19] or as habitats are fragmented or modified [20,21]. Although genetic drift and intrinsic incompatibilities may contribute to RI in these circumstances, here we focus on extrinsic forms of isolation resulting from functional mismatches (e.g. functional inferiority of migrants and hybrids in foraging, feeding, avoiding predation, attracting mates and mating). That is, functional divergence begets lineage splitting via functional incompatibility of the diverging populations, although additional (non-biomechanical) mechanisms also could hasten or restrain the evolution of RI. Of course, not all hybrids or migrants will be functionally inviable or even inferior, as in hybrid vigour [22], highlighting the need for empirical investigation of organismal function in the context of speciation.

Our thesis that the 'lens of biomechanics' provides insight into the speciation process relies on the following well-supported assumptions: (i) changes in ecological factors will result in differential selective pressures on one or more functional systems [23]. (ii) Multiple solutions to a functional problem are probably common [24], and can lead to functional divergence between populations experiencing similar selective pressures. (iii) Functional capabilities of animals emerge from the combination of underlying physiological and morphological traits [25]. (iv) Functional and morpho-physiological traits are commonly genetically based (e.g. [26]). (v) As function diverges between populations, immigrant and intermediate forms may be functionally inferior to resident forms [27], and thus speciation can occur by reducing migration and excluding any hybrids that might form between populations, resulting in RI.

Unlike other studies that have discussed biomechanics and speciation [13], we leverage the strong foundation of knowledge in fishes to describe approaches that directly link biomechanics and speciation, detailing multiple modes of selection, multiple isolating barriers and modern biomechanical techniques that are critical for quantifying function. While applicable to a wide range of animal systems, we focus on fishes because of their extensive ecological, phylogenetic and phenotypic diversity, as well as their prevalence as model systems for studying speciation, many-to-one mapping, and biomechanics. Predator–prey interactions in fishes have been a major focus of research over the past several decades [28,29], where survival depends on both the ability to escape from predators and to catch prey [30]. Locomotor and feeding traits underlie predator–prey interactions, and both respond to selection and contribute to RI [31,32], making predator–prey interactions central to the study of speciation. Despite the incredible diversity among fishes, common biomechanical links between form and function persist in the evolution of feeding and locomotion across broad phylogenetic groupings [33,34]. The groups that we propose as model systems are outlined in the electronic supplementary material and highlighted in figure 2. We illustrate a framework that identifies the key ecological variables shaping predator–prey interactions, links genetic architecture to phenotype, biomechanics and performance, determines the fitness consequences of functional variation and quantifies its effects on RI (figure 3).

2. Predator–prey interactions

(a) Prey capture

Suction feeding, the primary mode of prey capture among fishes, involves the rapid expansion of the mouth cavity that causes a sharp drop in pressure [55], driving nearby water and prey towards the mouth. Suction affects only a small area near the jaws [56], meaning that the fish must use locomotion to accurately position the mouth close to the prey for successful capture [57]. Thus, prey capture involves the tight functional integration of locomotion and feeding [58–61]. Key locomotor factors include approach speed, acceleration/deceleration, trajectory, stability and timing [59]. The functional divergence in response to selection for enhanced feeding performance on different prey can lead to a wide array of multivariate phenotypic changes. For example, *Gobiomorus dormitor* populations that have colonized inland blue holes in the Bahamas experience shifts in the available prey, driving changes in body shape, mouth morphology, suction generation capacity, strike kinematics and feeding performance on different prey types [62].

(b) Predator evasion

Fishes evade predation attempts using rapid escape behaviours. An example is the C-start, whereby powerful muscle contractions bend the fish into a C-shape and rapidly accelerate the animal [63]. Much research has focused on describing escape behaviours induced by controlled stimuli, yet in reality, changes in ecological and predatory parameters can significantly alter these patterns. The sensory signals that mediate the prey's response and the motor behaviours leading to escape have been investigated for decades. Research on zebrafish found that prey are startled by the visual cues produced by an approaching predator. Specifically, fish initiate a C-start when the appearance of the predator, from the perspective of the prey, increases in size above a critical rate (apparent looming threshold) [28], meaning that fish will most probably respond to a close and fast-moving predator. The flow-sensitive lateral line system is also crucial for detecting a predator's attack [64–66]. Zebrafish larvae use the lateral line to detect the subtle disturbance of water ahead of a swimming predator [65], and larvae without the lateral line are over three times more likely to be captured [64]. Ecologically divergent populations of three spine stickleback exhibit considerable differences in lateral line morphology [67] that are related to their ecological conditions (e.g. vegetation, amount of visual cues, habitat complexity), potentially impacting the fitness of migrants or hybrids.

3. Key ecological variables

Many environmental factors can affect whole-organism performance capabilities, and can influence selection on functional traits (figure 3). Here, we focus on the set of factors that represent the most widespread importance for speciation in fishes. Substantial evidence points to predator–prey interactions as major drivers of diversification in fishes, strongly influencing the evolution of locomotion and feeding [4,29,68]. Important factors that can affect predator–prey interactions in fishes include abiotic variables such as temperature, flow conditions, dissolved oxygen, salinity and pH, as well as biotic variables such as predator density and type, interspecific competitors, population density and prey resource quality and type (figure 3).

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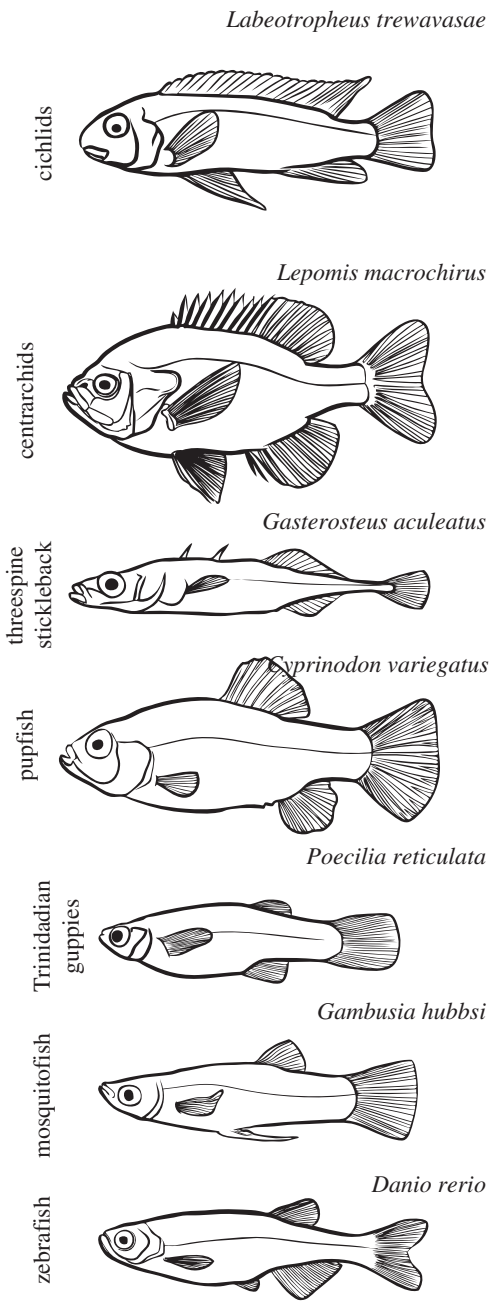

	interspecific ecological divergence	intraspecific ecological divergence	morphological divergence	biomechanics associated with ecological divergence	genetic basis of biomechanical trait divergence	reproductive isolation linked to biomechanics
cichlids	A, B [36]		C, PC [35–37]	L, F [35,37,38]	Q [38]	R [36]
centrarchids	A, B [96]	A, B [39]	C, PC [39,41]	L, F [40,57]	CG [39]	—
threespine stickleback		A, B [4]	C, PC [43–45]	L, F [43,45]	Q, CG [42–44]	R [42]
pupfish	A, B [46]	A, B [49]	C, PC [47,50]	F [47,48]	RAD [48,49]	R [49]
Trinidadian guppies		A, B [51]	PC [51]	L [51,97]	CG [97]	—
mosquitofish	A, B [14,31]	A, B [31]	C, PC [31]	L, F [68,69]	CG [31,69]	R [31,69]
zebrafish		A, B [52]	—	—	AS [53]	—

Figure 2. Representative line drawings of the seven species/groups of fishes highlighted as model systems for locomotion and feeding. Species names are listed by each drawing. Tabular information indicates whether the group has been examined in each of the categories. The citations are merely examples [35–53]. A, abiotic; B, biotic; C, cranial; PC, post-cranial; L, locomotion; F, feeding, Q, quantitative trait loci; CG, common garden; RAD, RADseq; AS, artificial selection; R, reproductive isolation confirmed.

4. How to obtain and quantify phenotypic variation?

Understanding phenotypic variation is critical for assessing which forms provide an advantage in a given set of conditions. To obtain this information, we can (i) directly assess existing phenotypic variation in natural populations and test how this translates into differences in performance and fitness [69], (ii) manipulate animals by altering their morphology (including sensory systems) [64], (iii) use robotics/physical models [70], theoretical models and computational fluid dynamics to explore phenotypic space [71], and (iv) segregate phenotypic differences using experimental crosses between genetically and phenotypically distinct populations (e.g. [72]) (figure 3).

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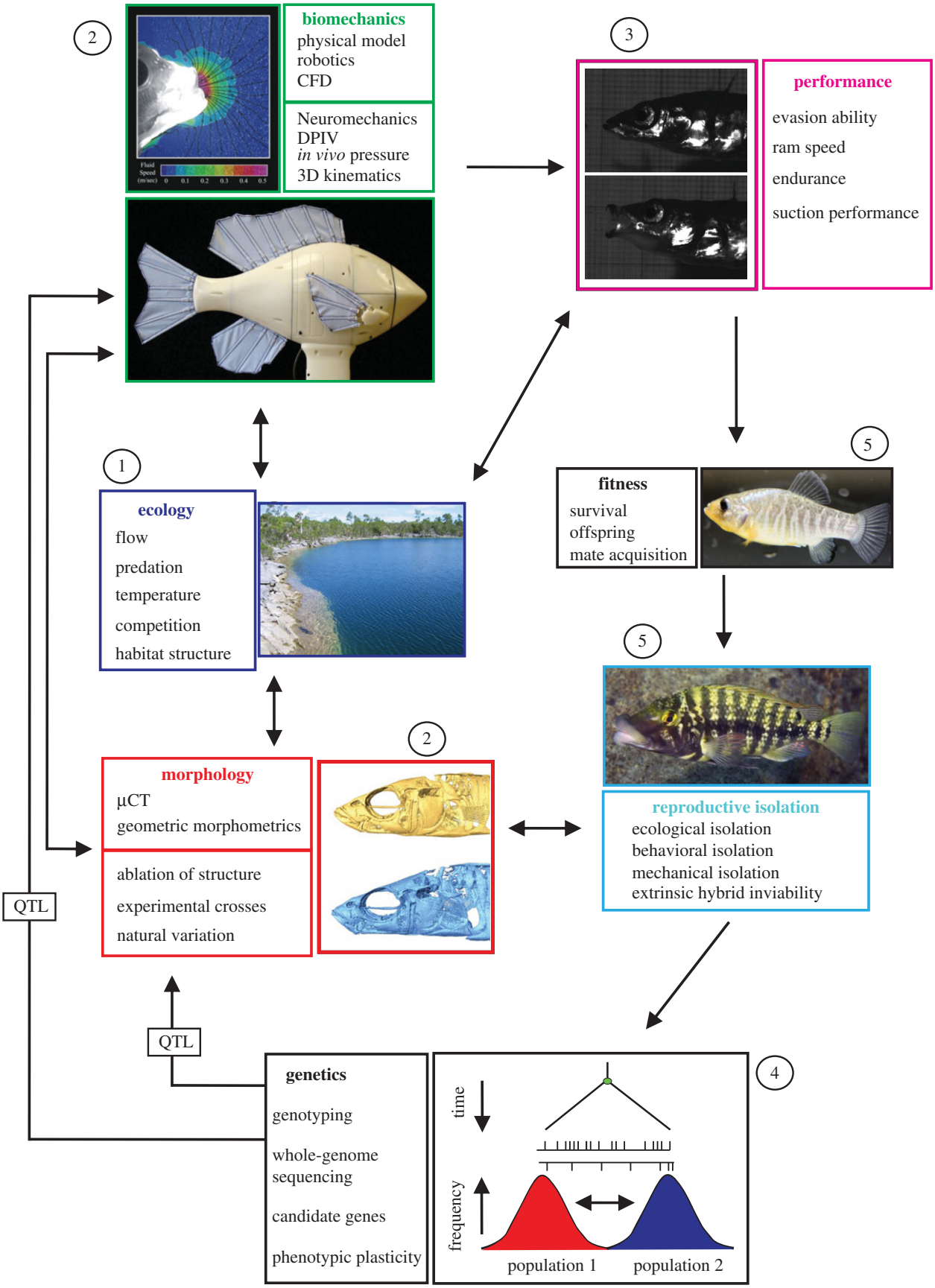

Figure 3. Our proposed methodological framework. The general flow is genetics—morphology—ecology—biomechanics—performance—fitness—reproductive isolation. However, multiple categories interact along the path. For each category, we highlight some of the factors that should or could be quantified. For morphology, the top box represents ways to quantify the phenotype, and the lower box represents ways to alter morphology. For biomechanics, the top box represents ways to mimic the biomechanics of the species or population of interest, and the lower box represents ways to quantify biomechanics in fishes. The robotic fish in this section is from [54]. The circled numbers represent the order in which particular components may be quantified when seeking to understand the biomechanics of speciation, and this is described in more detail in the text. (Online version in colour.)

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Determining the phenotypic changes that produce biomechanical differences affecting performance, as well as the genetic underpinnings of these changes, requires quantification of morphology in different regions of morphospace, which is a multivariate representation of shape and structure of a species or multiple species. Photography, microscopy and radiography are commonly employed for quantifying morphology. More recently, techniques such as microcomputed tomography (μCT) allow three-dimensional modelling and visualization of hard and soft tissue components.

Measuring phenotypic covariation patterns is key to capturing the nature and extent of variation present in a system, and in understanding evolutionary responses of multiple traits to selection. The action of selection on the developmental-genetic architecture underlying functionally correlated traits relatively stronger covariation between such traits as a unit, in comparison to the rest of the phenotype [73,74]. Covariation is also influenced by drift and gene flow [75,76], and can constrain the range of possible phenotypes available for selection [77,78] and bias the direction of evolution [79]. Alternatively, patterns of phenotypic covariation can facilitate adaptive change without compromising function [74,80–82].

5. Quantifying functional consequences of phenotypic variation among fishes

Two important steps in understanding how different phenotypes differ in function or performance are first, to quantify organismal function and any differences among populations or species, and second, to generate testable hypotheses about both the consequences and causes of these functional differences. This process is often quite challenging, but in recent years a number of techniques (below) have become available that permit a much better understanding of organismal function and enable testing of the causes of differences among species.

(a) Three-dimensional kinematics

High-speed videography can be used to capture extremely small or rapid motions to quantify kinematics and ultimately performance. When coupled with approaches explained below, this can provide a powerful tool for understanding the biomechanics of fish locomotion and prey capture [57].

(b) Hydrodynamics

Fishes exert forces on the surrounding fluid using multiple control surfaces (locomotion) or by the rapid expansion of the mouth (feeding). Force production in fluids involves the transfer of momentum from the animal to the fluid, leading to the shedding of vorticity [83]. Quantifying the motions of fluid around moving structures can be achieved with engineering techniques such as digital particle image velocimetry (DPIV). With DPIV, water surrounding the fish is seeded with neutrally buoyant particles, a laser sheet illuminates those particles, and the movement of the particles can then be imaged with high-speed video. The two-dimensional and three-dimensional global flow fields can be calculated from spatial cross-correlation techniques to help reveal the fluid basis of fish function and behaviour [84]. For example, three-dimensional suction accuracy in centrarchid fishes was recently modelled and related to capture success [85].

(c) Robotics

One of the most challenging aspects of organismal biomechanics is separating cause from effect, and identifying the specific functional consequences of phenotypic traits in live animals. It is difficult to fully and accurately understand functional observations given the inability to control all relevant variables: individuals and species always differ in numerous traits other than the one of interest. One avenue of research that minimizes such confounding factors is the use of a robotic system to alter only the parameters of interest. Robotic systems offer the advantage of facilitating force measurement, the ability to explore a large parameter space of possible parameters, and greater control over flow visualization measurements. We believe that there will be increasing use of robotic systems in comparative biology to allow more precise understanding of the relationship between the phenotype and performance [86,87], especially where interspecific comparisons involve such distantly related species that one cannot have confidence in comparisons of biological systems or can serve as 'surrogate organisms' in cases where animal function cannot be directly observed. The design of robotic models that capture key phenotypic features of these hard-to-get species may be of use in testing the performance consequences of interspecific phenotypic differences that arise during the process of speciation.

(d) Computational fluid dynamics

Computational approaches share some of the same advantages that robotic systems have in serving as an abstracted version of biological reality that can be manipulated with relative ease to explore a large parameter space. Computational fluid dynamics mathematically simulates how fluids interact with surfaces using the Navier–Stokes equations. The main challenge associated with computational models of swimming and feeding in fishes is the rapidly developing and unsteady nature of the flow patterns that are produced (e.g. [88]). And the phenotypic features of fishes involved in feeding and swimming are flexible and complex biomechanically, making development of an accurate three-dimensional structural model challenging and the analysis of structure–fluid interactions difficult. Centrarchid fishes have served as the basis for computational models of both feeding [89] and locomotion [90], and these have provided considerable insight into the link between structure and function. For example, sunfish (*Lepomis*) pectoral fins deform in a complex way during slow speed labriform swimming and computational fluid dynamic analysis showed, unexpectedly, that this deformation pattern results in thrust generation on both the outstroke and instroke of the fin beat cycle.

(e) Neuromechanics

Our understanding of how fish trigger escape responses has been advanced by a wide variety of techniques, including electrophysiological recordings of the Mauthner cells [91], laser ablations of the Mauthner cells [92], and the addition of extra neurons during development [93]. Work on fish as predators has helped us understand how visual information is processed for hunting [94]. Work on the lateral line system is revealing how information encoded by a single mechanoreceptor elicits behaviour [95]. Further investigation of the neuromechanics of predator–prey encounters promises to yield insight into the unique demands of different habitats. For example, using calcium imaging or electrophysiology to

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measure the differential activity of nerves in different environmental conditions (e.g. still versus turbulent water) will help us understand the basis of how habitat affects performance.

6. Biomechanics of locomotion and feeding in fishes

Fish typically respond to two ecological shifts related to predator–prey interactions: (i) changes in trophic niche and (ii) changes in predation pressure. For example, rapid jaw evolution is observed in pupfish as they specialize on different types of prey (e.g. hard prey or scales). Comparable patterns are observed in African cichlids. In stickleback, divergence within a lake due to competition or among lakes due to predation pressure has led to shifts and divergence in the type of prey consumed. Across most groups, fish that become more pelagic will tend to eat zooplankton whereas benthic ecotypes tend to focus on benthic macroinvertebrates. Although shifts in trophic niche can occur as a result of competition [96], sometimes leading to sympatric divergence in feeding structures (e.g. stickleback, centrarchids), predation pressure can induce a trophic shift in prey by driving a change in habitat use. The latter is common in a number of the groups outlined in the electronic supplementary material. And in guppies and mosquitofish, variation in predation risk also leads to evolution of functional divergence independent of trophic niche (e.g. predator evasion, [69,97]).

A major question in evolutionary biology concerns the predictability and repeatability of evolutionary change and its role in the origin of species. With divergent fish lineages repeatedly experiencing similar environmental/ecological gradients, this provides an opportunity to gain insight into the predictability of functional divergence at multiple scales (e.g. genetics, morphology, kinematics, performance, RI). The bright future in this area is exemplified by the fact that we were able to highlight seven model systems in this paper (figure 2). Thus, there is great promise for shedding light on the extent of parallelism in functional evolutionary patterns at different scales among disparate groups.

7. Framework for the biomechanics of speciation: the functional link from genetics to reproductive isolation

Selection is a common driver of speciation [2,3], but the functional mechanisms linking adaptive changes in genotype and phenotype to the evolution of RI are still largely unknown [1]. Relatively recently, a framework for linking morphology, performance and fitness was solidified [10,11]. But little work has extended this framework to speciation. We propose that biomechanics provides a necessary piece as it bridges morphology and performance (figure 3), and generates testable predictions for evolutionary divergence and RI [13,14,68]. Biomechanics is critical for defining the limits (constraints) to performance, and morphology is defined, at least in part, by genetics. Using an integrative framework that recognizes connections from genetics to RI, we can identify functional mechanisms of speciation: e.g. using model fish groups to predict the evolution of divergent morphologies and post-zygotic isolation based on biomechanical and ecological knowledge, and test the genetic basis of the reproductive isolating barriers [98]. The primary impediment to such an integrative analysis is the lack of study system for which all of the variables can be studied, but locomotion and feeding in fishes represents a promising avenue as they represent a suite of integrated characters that routinely exhibit convergent evolution in association with adaptations to similar environments or ecological niches. Thus, our suggestion to focus on fish predator–prey interactions is based on the vast amount of existing information and the utility of the system. Insights gleaned from fish into the biomechanical basis of speciation will be applicable for almost all animals that capture prey or get eaten by a predator.

The primary reasoning for including genetics in this framework is not necessarily to pinpoint the genes for particular traits *per se*, but rather to uncover the nature of multi-trait divergence (e.g. genetic correlations versus independent evolution) and establish the extent to which population divergence reflects genetic differentiation, phenotypic plasticity or both (e.g. common-garden experiments). If performance exhibits adaptive plasticity, this could minimize genetic divergence and slow speciation. By contrast, identifying a genetic basis for a critical biomechanical trait will potentially reveal the functional basis of speciation. Once the extent of the genetic basis has been characterized, testing the outcomes of hybridization or migration will be more productive with biomechanical approaches, because these traits have definitive links to function in association with the environment and, as a consequence, more probably represent targets of selection.

Adaptive divergence in biomechanical traits can facilitate speciation under two primary scenarios: (i) divergent selection favours different aspects of performance in different ecological environments, and divergence in traits increases RI among populations (i.e. ecological speciation), and (ii) populations respond to similar selection on performance by evolving different adaptive solutions that enhance RI among populations (i.e. mutation-order speciation). Under both scenarios, populations must persist following adaptive peak shift [26] (figure 1) and the biomechanical traits involved in adaptive divergence must directly or indirectly cause RI (e.g. immigrant inviability, extrinsic hybrid inviability, behavioural isolation via mate choice (reject individuals with 'wrong' form or performance), mechanical isolation). Prior work has so far centred on the first scenario, revealing that divergent selection appears to drive functional divergence, with some studies linking biomechanical traits to RI—e.g. Bahamas mosquitofish that have evolved different body forms to accommodate different swimming abilities in different predatory environments have consequently evolved enhanced RI due to immigrant inviability and assortative mating for body shape [31,69,99]. Little research to date has addressed the second scenario, although given the ubiquity of non-parallel phenotypic responses to similar environmental gradients [1], combined with the potentially widespread phenomenon of many-to-one mapping of form to function [100], this could prove quite important. That is, the selection surface for biomechanical traits might often be quite complex, with multiple adaptive peaks of similarly high fitness levels—and different populations could traverse different peaks. This is because performance reflects how good an animal is at executing an ecologically relevant task [101], and this execution emerges from the integration of multiple underlying traits that could be combined in various ways to create similar levels of performance.

To determine the biomechanical basis of RI, we must do the following things: (i) identify ecological divergence (e.g. lake

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versus stream), (ii) identify divergent morphological and biomechanical traits across populations/species inhabiting similar/different environments (population divergence), (iii) quantify the performance outcomes, (iv) determine the genetic basis or plasticity of these traits and (v) uncover the role of these traits in speciation by linking them to fitness, RI or lineage diversification rates. Several of these steps will necessarily exhibit complex interactions, such as performance driving ecological differences and ecology driving performance differences. Figure 3 illustrates and expands on this framework.

Studies of recent divergence are best suited to test hypotheses of the effects of adaptive biomechanical variation on RI. This is because the observed phenotypes and genotypes involved are more likely to reflect RI that evolved in association with divergence rather than variation that evolved following the evolution of RI and speciation. Recent studies of adaptive traits provide frameworks for testing RI in fishes, such as immigrant inviability [102,103], extrinsic hybrid inviability [98], behavioural isolation via mate choice [99] and mating incompatibility (mechanical isolation) [104]. Examining the role of physiological and biomechanical divergence among nascent populations will be important for examining mechanistic underpinnings of RI [105]. Studies of older divergence can use phylogenetic comparative methods to test for associations between evolution of biomechanical traits and lineage diversification.

8. Conclusion

From bee pollination to the function of the heart, biomechanics is crucial for understanding evolution. We provide a specific framework for incorporating biomechanics into the study of ecological and mutation-order speciation. Considering speciation through the lens of biomechanics, specifically through measuring biomechanical traits associated with locomotion and prey capture, offers a holistic way of measuring traits that are often the targets of selection in fishes, and indeed across taxa. Although the groups of fishes presented here represent the best targets for understanding speciation through the lens of biomechanics, it should by no means exclude other fishes that clearly contribute to these questions (e.g. salmonids [106]). We propose that the low-hanging fruit in the movement towards linking biomechanics and speciation will include (i) establishing the genetic basis of biomechanical traits, (ii) testing whether similar and divergent selection lead to biomechanical divergence, and (iii) testing whether/how biomechanical traits affect RI. The next steps could be experimental tests that directly demonstrate links with RI. For example, using controlled crosses under a common-garden design, the genetic basis of biomechanical traits could be established while performance trials could test the prediction that hybrids are functionally mismatched for these traits. Because of the strong link of biomechanical traits with function in association with the environment, the opportunities to test the alternative consequences of hybridization and migration with these approaches will contribute to the quest for the origin of species.

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