Supplementary information

**Key groups of fishes**

There are several reasons why certain groups of fishes have received relatively more attention from researchers, including accessibility, viability in a laboratory setting, short generation time, size, degree of phenotypic variation, or simply the interesting questions that can be addressed with the specific group. To investigate the role of biomechanics in speciation, we focus on several groups of fishes in this review that have received considerable attention with respect to evolutionary ecology [1, 2], genetics [3, 4], biomechanics [5, 6], hydrodynamics [7, 8], functional morphology [9, 10], neuromechanics [11], and reproductive isolation [12, 13]. We fully acknowledge that not every potential group is covered by our study, but our aim is to highlight a range of species and groups that have been studied thoroughly and that will provide a foundation for future research. For each group, we will focus on WHY it is important and what it can offer toward understanding speciation through the lens of biomechanics. By integrating the information across the groups, we can also identify the gaps and shortfalls that exist. Topics will include adaptive trait variation, ecology, morphology, biomechanics, and neuromechanics.

***Zebrafish***

Zebrafish, *Danio rerio*, are now a valuable model system in several fields of biology, including biomedicine, developmental biology, genetics, neurophysiology, and behavior, because they are small, tractable, optically transparent as larvae, and relatively easy to keep and breed in the lab. Zebrafish have emerged as a model for understanding predator-prey interactions because their behavior as both predator and prey are quite typical of many other fishes. Zebrafish naturally inhabit slow-moving and still bodies of shallow freshwater in Southeast Asia [14]. They are small in size (body length < 4 cm), exhibit a fusiform body that is slightly compressed laterally, and face predation from larger fish and birds. Zebrafish are omnivorous and mainly feed within the water column [15] on a variety of plankton, such as small aquatic insects, insect larvae, zooplankton, algae, plant material [16], and even zebrafish larvae [14]. To catch prey, zebrafish swim at a moderate speed [11] before protruding their jaws [17] and executing a rapid suction-feeding strike in less than 20 ms [11], which drives nearby prey into the mouth.

Work on zebrafish has helped us understand how fish detect and evade predators. Zebrafish adults are startled by the visual stimulus produced by an approaching predator, and the timing of the fish’s response depends on the perceived speed of the predator [18]. In addition to the visual system, the flow-sensitive lateral line system is crucial for prey. Disabling the lateral line system in zebrafish larvae prevents them from detecting suction, like that produced by a predator [19], and reduces their chances of evading a predator’s attack by 80% [11]. A study employing a robotic predator and larval zebrafish revealed that prey detect the subtle disturbance of flow ahead of an approaching predator [20]. Once startled, prey are most successful when they initiate the c-start at an intermediate distance from the predator, [11], and orient their swimming in an optimal direction that depends on the predator’s speed [21].

Studying zebrafish as predators has advanced our understanding of how fish feed effectively. Zebrafish larvae employ both vision and flow sensing when foraging, but in order to successfully capture prey in the dark, larval zebrafish must learn how to sense water flow over the first few weeks of life [22]. Adult zebrafish have also revealed cryptic hunting strategies, whereby they disguise the bow wave by slowly pulling water into the mouth when approaching prey [23], which decreases the chances of startling invertebrates. Work on zebrafish has helped us understand the evolution of complex traits, as zebrafish have evolved a unique method for protruding their jaws using a novel bone called the kinethmoid [24].

Leveraging the genetic and neurophysiological advantages of the zebrafish model system will be instrumental for future investigations on prey fish. Studies that investigate how zebrafish larvae encode sensory stimuli at the cellular level [25] are now increasing our understanding of how prey detect flow stimuli. Transgenic lines of zebrafish that express calcium-indicators in the hair cells and afferent neurons of the lateral line system now permit the visualization of nervous signals *in vivo* [26], which will allow future investigations of how fish integrate and translate sensory information from different parts of the body. Developing future lines of zebrafish in which some sensory pathways are genetically disabled (e.g., the efferent system of the lateral line) will be invaluable for determining how different components of the nervous system affect behavior.

***Trinidadian guppies***

Guppies that live in streams that drain the Northern Range Mountains of Trinidad co-occur with a diversity of predators in the higher order streams. Waterfalls exclude predators, but not guppies and a few less predatory species of fish from the upper portions of these streams [27, 28]. The presence of guppies in high versus low predation communities is repeated in multiple streams and provides the equivalent of a naturally replicated experiment.

Guppies that live with predators experience significantly higher mortality rates [29] and display a diversity of traits that represent adaptations to life with predators that have evolved independently in different rivers. These adaptations include behavior [30], life histories [31, 32], neuromuscular performance [33], survivorship in the presence of predators [34], and diet [35, 36].

Ghalambor et al. (2004) quantified c-start (reflexive alarm response) performance in second generation, lab reared guppies [37]. The use of lab reared, as opposed to wild-caught, guppies means that differences between populations in performance are likely to have a genetic basis. Ghalambor et al. evaluated high (HP) versus low (LP) predation guppies from two different rivers (Yarra and Oropuche) and hence performed two paired comparisons that represent independent instances in which guppies adapted to life with and without predators. HP guppies had faster acceleration and higher maximum swimming velocities. However, there was also evidence of a tradeoff with reproduction. The volume of developing embryos increases as they progress through development, causing a decline in all aspects of C-start performance. HP guppies produce more offspring and have a correspondingly higher rate of decline in performance as their offspring develop. The net result is that they are significantly faster when not pregnant and when their offspring are early in development, but lose this advantage as development proceeds. Walker et al. [38] show that the magnitude of the differences in performance of HP and LP guppies is sufficient to make the difference between life and death in an encounter with a real predator.

Zandona et al. [36] compared the diets of wild-caught HP and LP guppies from two rivers (Aripo and Guanapo). HP guppies consumed a more invertebrates and less diatoms and detritus than LP guppies. HP guppies prey selectively on higher quality prey (ones with lower carbon/nitrogen body ratios) while LP guppies consumed invertebrates in proportion to their abundance. Bassar et al. [35] compared the diets of wild-caught from the same four localities in an experiment performed in replicate, artificial streams and obtained the same results. The important distinction between the two studies is that Zandona et al. evaluated fish collected from their natural environment, where there were confounding differences in food availability. Bassar et al. compared fish in artificial streams that had comparable resource bases, yet they obtained the same result.

O’Steen et al. [34] quantified the survivorship of HP and LP guppies housed in a 1.8 m diameter wading pool with an adult pike cichlid (*Crenicichla alta*). Each experiment was run until the predator had consumed half of the prey; the duration ranged from 15 to 240 minutes. They compared HP and LP guppies from three rivers (Yarra, El Cedro, Aripo). In addition, they included guppies three introduction experiments in their comparisons – two were populations of guppies that had been transplanted from HP communities to previously guppy-free low predation sites above barrier waterfall 16 to 22 years earlier (Aripo and El Cedro Rivers). These fish were compared to representatives from the HP locality from which the introduced ancestors were derived. The third experiment was the introduction of a predator into a low predation site on the Aripo River. These fish were compared to a population found further upstream, above a barrier waterfall that excluded the introduced predators. O’Steen et al. repeated this experiment on the second generation of laboratory reared guppies from the HP and LP sites and two introduction experiments on the Aripo River.

HP guppies had higher survival than LP guppies in all three paired comparisons among wild-caught fish. Likewise, guppies from the two guppy introduction experiments had lower survival than those from the ancestral HP site. Guppies from the predator introduction site had higher survival than those from the control site upstream. The results for the second generation lab reared guppies were the same, although the magnitude of the differences was smaller. Together, these results show that there are genetic differences among populations in their ability to escape predators. There is some environmental component to escape ability because the lab reared fish from HP environments had a smaller advantage than the wild-caught fish from the same localities. Finally, the ability to escape predation evolved since guppies were transplanted from a HP to LP environment (22 years in the Aripo introduction and 16 years in the El Cedro Introduction) or when predators were introduced to a low predation environment (16 years).

These experiments do not tell us is why HP guppies are better at escaping predators than LP guppies. In addition to neuromuscular performance, HP and LP guppies also differ in behavior. For example, Seghers and Magurran [39] show that HP guppies are genetically predisposed to aggregate more than LP guppies. Aggregation behavior is known to increase a fish’s ability to escape predators, so performance and behavior contribute to susceptibility, but we do not know their relative importance. The combination of these attributes, and all of the other aspects of guppy biology that differ among HP and LP environments, is a testament to the profound and pervasive ways in which predators shape the evolution of their prey.

***Gambusia***(mosquitofishes)

*Gambusia* fishes are small, livebearing fish in the family Poeciliidae (typically < 60 mm standard length), commonly referred to as mosquitofishes. *Gambusia* is the most speciose poeciliid genus, and species are distributed in the New World from northern Colombia to the central and south-eastern U.S.A., and across numerous Caribbean Islands [40]. These fish inhabit many diverse types of aquatic habitats, including nearshore marine environments, estuaries, lakes, hypersaline lakes, marshes, ponds, temporary ponds, rivers, springs, and even waters with high levels of toxic hydrogen sulfide. Indeed, *Gambusia* are well known for their successful colonization of a wide range of aquatic environments, and two species are notorious as some of the most highly invasive species on earth (IUCN 100 worst list).

Importantly, variation in these environmental variables exists at multiple timescales: across species separated by millions of years of evolution, across populations / incipient species with thousands of years of divergence, and across populations experiencing environmental change over decades to centuries. This situation has led to research addressing the ecological causes and predictability of phenotypic evolution and speciation in this group. Combined with their amenability for laboratory and field work, and the ecological and biomechanical knowledge about the group, they represent a remarkable model system for studying evolution, and using functional approaches to understand the causes of speciation.

Although numerous environmental factors have been implicated in some aspect of *Gambusia* evolution, existing evidence clearly points to predation as being the most important driver of diversification in the group. Similar to guppies, *Gambusia* populations/species show a wide range of adaptations to divergent predation regimes (living either with or without major piscivorous fish; e.g. [2]). This includes diversification in male coloration [41], a variety of behaviors [42], life histories [43], body and fin morphology [12, 44], trophic morphology [45], male genital morphology [42], female genital morphology [46], steady and unsteady locomotor performance [12, 47], survivorship in the presence of predators [47], and diet [48]. The majority of these traits have been shown to have a genetic basis, although plasticity in some traits occurs as well.

One particular study system that offers a striking opportunity for studying the role of predator-prey interactions in trait diversification and speciation is the adaptive radiation of Bahamas mosquitofish (*G. hubbsi*) in blue holes. Bahamas mosquitofish colonized inland blue holes of Andros Island during the past ~15,000 years, and repeatedly evolved different adaptive traits in either the presence (high-predation) or absence (low-predation) of the predatory fish, bigmouth sleeper (*Gobiomorus dormitor*). Molecular genetic evidence indicates that similar phenotypes independently evolved in similar environments multiple times [12, 42, 43]. These populations are further undergoing speciation, with significant reproductive isolation among many populations, especially populations that differ in the presence of predatory fish [12, 49]. Variation in the presence of piscivorous fish represents the primary source of environmental variation in these populations, with no known environmental factor co-varying with the presence of predatory fish (e.g., productivity, salinity, turbidity, water transparency, depth, dissolved oxygen, temperature, pH; [12, 42]. This system thus permits the more-or-less exclusive investigation of the effects of predation regime in driving trait divergence and speciation in the wild. Combined with biomechanical knowledge, this could prove especially insightful regarding the biomechanics of speciation.

Considerable biomechanical work has been conducted in this group, and continues to grow. Functional research in *Gambusia* has investigated steady swimming capacities, c-start escape performance, mating, feeding, and terrestrial jumping (e.g. [47, 50, 51]. Because variation in predation risk has repeatedly driven parallel changes in body morphology and steady and unsteady swimming abilities, a major line of inquiry is understanding how this divergence influences the evolution of reproductive isolation. Work has already demonstrated fitness consequences of locomotor performance and their morphological underpinnings, showing the effects of functional morphology and whole-organism performance on reproductive isolation due to immigrant inviability, behavioral isolation (mating preferences partially based on body morphology), and has led to clear predictions of reduced hybrid fitness [12, 47, 49]. Moreover, evidence for an important role of body morphology in speciation comes from multiple timescales of analysis [12]. Work in this genus is poised to shed new light on speciation through the lens of biomechanics, with the one clear limitation in this system being the relative paucity of work on the genomics of adaptation and speciation in *Gambusia*.

***Threespine stickleback***

Threespine stickleback (*Gasterosteus aculeatus*) are euryhaline fish circumpolar in their distribution and occupying many coastal marine environments and recently formed freshwater lakes and streams following the last glacial recession (10 – 15 000 years ago). Populations are derived from two distinct marine lineages (Euro North American Clade and the Trans North Pacific Clade) that diverged during a period of allopatry ~1 mya [52]. In general, they are a small streamlined fish (up to ~75 mm in length) with a body form similar to most teleosts, albeit with unique body armour. They have modified dorsal fins in the form of three dorsal stickles (spines), modified pelvic fins in the form of pelvic spines and modified scales in the form of bony lateral plates running dorsoventrally along the abdomen [53]. All of these traits are heritable but may vary with the environment, and indeed stickleback have undergone a multitude of phenotypic transitions in association with freshwater environments, in many cases evolving parallel changes with respect to behavior [54], physiology and morphology [3, 53, 55]. They eat a variety of insect larvae, amphipods, ostracods, and copepods [56], with the latter being capable of escape maneuvers [57].

Threespine stickleback have emerged as an excellent vertebrate organism for the study of evolution for a number of reasons. Females are highly fecund and husbandry techniques for breeding and maintaining crosses in the lab, including hybrid marine-freshwater forms, have been well developed. They have a relatively short generation time (nine months from hatching to maturity). In addition, the genome has been sequenced and partly annotated [58].

Adaptive peak shifts upon colonization of fresh water environments, at least with respect to morphology, are predictable and leave a genetic signature in the genomes of stickleback evolving in these environments [3]. In addition, many studies have emerged that have characterized striking population divergence among and between freshwater and marine environments (e.g. [58-60]). Phenotypic divergence in tight association with distinct freshwater environments has resulted in speciation within a lake (e.g., benthic and limnetic species pairs), often closely linked with specific ecological conditions [56]. For example, open water stickleback tend to consume water column plankton, whereas benthic stickleback tend to consume benthic macroinvertebrates [61].

What are the functional consequences of feeding on zooplankton *versus* benthic macroinvertebrates? Among the open water plankton are calanoid copepods, which have the ability to evade predatory attacks from stickleback [62]. Suction performance is likely elevated when feeding on benthic prey given that the prey are often embedded in, or attached to, the substrate [63]. A recent morphological investigation confirmed this by quantifying suction index, a reliable proxy for suction performance [9], for benthic and anadromous stickleback populations [64]. Conversely, those fishes that feed on zooplankton in the water column should exhibit a streamlined body (dorso-ventrally compressed), elongated jaws, and a terminal mouth [65]. These characteristics enable faster swimming during prey capture and a mouth adapted for capturing prey in front of the fish. Stickleback have been found to be more pelagic in the presence of a predator and competitor, the prickly sculpin (*Cottus asper*), which also inhabit a number of the same lakes that were isolated following the recession of the Cordilleran Ice Sheet [66-69]. Prickly sculpin not only feed on stickleback, they also compete with them for invertebrate prey [69-71]. Interestingly, not all lakes with stickleback contain sculpin predators [67], which has resulted in both phenotypic and genetic shifts in accordance with predation by sculpin [3]. Recent work has also noted the behavioral shifts that occur when stickleback are in the presence of different predators [72]. Open-water stickleback morphotypes exhibit greater capture success than benthic morphotypes in open-water feeding trials [61]. Additionally, morphological analyses have confirmed that pelagic populations that are sympatric with sculpin exhibit decreased body depth, a narrower caudal peduncle, larger eye diameter, and a longer jaw [69]. Collectively, these observations reinforce the extent to which investigation of biomechanic phenotypes in stickleback can elucidate the genetics of adaptive divergence and potentially speciation.

***Centrarchids***

Centrarchidae is a clade of North American perch-like freshwater fishes with 34 extant species [73]. They are often top predators in the freshwater habitats in which they live, and they have been the subjects of numerous fields of research including biomechanics [9, 74-78], ecomorphology (reviewed in [79]), evolution [80, 81], and ecology [82-85].

Given that centrarchid fishes are relatively large and top predators, they are not as amenable to laboratory studies aiming to develop hybrids and rear multiple generations. That said, there are countless cases of hybridization between species in natural populations of centrarchids [86]. Although they often make up a small percentage, there are locations where hybrids can make up over 75% of the population. Interestingly, hybrid viability declines with the age of the node separating parental species, supporting the "speciation clock" idea [87]

Trophic polymorphisms have been identified and studied in various populations of pumpkinseed sunfish, *Lepomis gibbosus* [88-90]. In Ontario lakes, for example, littoral pumpkinseed populations are more generalist feeders, consistently feeding on benthic prey. Pelagic pumpkinseeds were highly specialized on zooplankton [88]. These differences in ecology could be exploited in future laboratory studies of biomechanics and performance, especially in light of the large amount of data that already exists for centrarchids. Several studies have assessed whether the differences between populations are a result of phenotypic plasticity or evolution, and the results are mixed [90-93]. That said, aspects of both feeding and locomotion vary substantially between populations, between regions of a single habitat, and between species. These differences are often associated with biotic and abiotic environmental factors, including water flow, competition, prey type, and other factors.

In terms of biomechanics, centrarchids are the predominant model system among fishes, and this includes both feeding and locomotion. This role likely stems from their predominance in North American freshwater systems and their relatively large size. Suction feeding performance in bluegill sunfish and largemouth bass has been explored for decades, and techniques have included kinematics [94], DPIV [95-98], sonomicrometry [99] and *in vivo* pressure recordings [77, 100, 101]. Centrarchids are a very profitable system in terms of interspecific variation in feeding performance given that they include a range of functional types. Largemouth bass, *Micropterus salmoides*, occupy one end of the spectrum in which ram speed dominates and suction-induced fluid speeds are relatively low [98, 102]. They exhibit a large mouth that aids in the capture of evasive fish prey by ingesting a lot of water during suction [98]. This alleviates the constraints involved with accurately positioning the prey item relative to the mouth. Recent work with largemouth bass has explored muscle function during feeding using XROMM [103], sonomicrometry, and electromyography [104-107]. In contrast with largemouth bass, bluegill, *Lepomis macrochirus*,fall on the other end of the spectrum with low ram speeds and higher suction-induced fluid speeds [98]. This leads to the need for high accuracy during feeding in order to entrain the prey within a very small ingested volume of water.

Locomotor hydrodynamics have been studied extensively among centrarchids [5, 7, 74, 108]. Most centrarchids, especially sunfish, have relatively large median and pectoral fins that are used for swimming at low speeds, although the body and caudal fin are employed during faster bursts of locomotion. Thus, much of the work on centrachids has focused on the function of the fins. A gait transition in smallmouth bass (*Micropterus dolomieu*) is observed at intermediate speeds, and this gait is thought to involve the recruitment of fast-glycolytic white muscle [109].

The integration of locomotion and feeding during prey capture is critical for centrarchids [76, 98, 110-113]. Selective pressures acting on one system will, therefore, undoubtedly impact the other. Divergence between populations of centrarchids is commonly associated with trophic shifts, and biomechanics is very likely to play a major role in this divergence and ultimate speciation. Only recently are studies teasing apart the functional changes that accompany divergence in microhabitat use among populations [114]. Future studies will be very fruitful in this area.

***African cichlids***

Cichlidae are the most functionally and ecologically diverse group of freshwater fishes, including more than 3,000 species throughout the Neotropics, Africa, Madagascar, the Middle East, India, and Sri Lanka with a crown age of 57-65 Ma [115-117]. They are best known for their spectacular adaptive radiations in the East African Great Lakes of Malawi, Tanganyika, and Victoria, rapidly filling nearly all ecological niches in these lakes from one or a few common ancestors [115, 118, 119], but have also diversified in hundreds of smaller lakes [4, 120], paleolakes [121], alkali flats [122], rivers [123], rapids [124], and estuaries [125], and have crossed oceans [117]. Their physiological tolerances span the extremes of salinity (0 – 180% seawater) and pH (4.5 – 12) known in any fish group [126], but they are limited to tropical and subtropical environments, reaching as far north as Texas and Israel [115].

Cichlids are unrivaled in their morphological, ecological, and behavioral diversity, occupying nearly every ecological niche and body shape known in freshwater fishes, from elongated rapids specialists, algae-scrapers, piscivores, and open-water planktivores to more specialized niches such as scale-eaters, paedophages, and sponge-eaters [124]. More fine-scale partitioning may also exist. For example, three different sympatric species of paedophage specialize on ramming mouth-brooding females from different ventral or dorsal angles [127]. These specialized niches are all the more striking due to the large amount of convergent evolution. For example, scale-eating has evolved at least four different times in cichlids [128] and hypertrophic lips at least eight times on three continents [128]. Cichlids also exhibit a diverse array of parental care behaviors, from biparental mucus-feeding to mouthbrooding [129, 130], complex social signaling [131], and male courtship displays, including over 200 species that build display platforms out of sand and rock, analogous to bowerbirds [132, 133].

A sister clade to the monotypic engineer ‘goby’ (Pholidichthyidae), cichlids are defined by pharyngognathy: pharyngeal jaws composed of fused left and right fifth ceratobranchial bones encased in a muscular sling articulating with the neurocranium [134]. This key innovation freed up the cichlid oral jaws to specialize on prey capture [135]. Accordingly, most studies of cichlid functional morphology focus on the pharyngeal jaw, including its biomechanics [136], plasticity [137] and strength [138]. However, this innovation is not sufficient to explain the highly variable rates of *in situ* diversification across cichlid lineages [139]. Recent work also suggests pharyngognathy may slow prey processing by piscivores, facilitating the invasion of the Nile Perch and the largest human-induced vertebrate extinction of over 300 cichlid species in Lake Victoria ([140] ; also see [141]. Additional functional studies have focused on crevice-feeding [142], jaw protrusion [143], scale-eating [144], and locomotion [145], but surprisingly little is known about cichlid performance given their diversity.

Most cichlid research centers on explanations for their extraordinary diversification. Many cichlid lineages have failed to diversify, while others do so repeatedly and ‘explosively’, even within the same environments [139]. Numerous hypotheses have been proposed for this pattern, including egg spots on the anal fins [146], hybridization [147], and repeated sweeps of sex determination loci [148], but a recent comparative analysis found that lake depth and sexual dichromatism best predicted the occurrence of sympatric cichlid radiations [149]. However, there are notable exceptions to this pattern, such as the sympatric diversification of two different monochromatic cichlid lineages within a tiny, shallow lake [150], and future work will need to address these alternative routes to diversification.

The evolution of reproductive isolation in sympatry may also contribute to the prevalence of cichlid radiations. Cameroon and Nicaraguan crater lake cichlids are the most widely celebrated examples of sympatric speciation due to replicated speciose radiations within uniform crater basins [151]. However, recent work indicates repeated colonization of these craters by riverine cichlids [152] and suggests that assortative mating by habitat may be necessary to complete speciation in sympatry [152]. Indeed, the only solid remaining examples of sympatric speciation in cichlids involve steep depth gradients [4] while sympatric shallow-water species pairs exhibit incomplete genetic and phenotypic divergence, suggestive of stalled speciation [150].

Considerable recent progress has been made in characterizing the genomic basis of species differences and the genetic architecture of ecologically relevant traits in African cichlids [4, 153], yet it is still unclear if hybridization has played a driving role in their diversification or is simply pervasive in all young taxa [154]. Similarly, the substantial behavioral complexity of cichlids affects speciation through mechanisms such as male-male competition [155], phenotype-matching [156], multimodal displays [157], and deceptive signaling [132], yet more work is needed to connect these findings to patterns of diversification across the group.

There is still surprisingly little knowledge of the ecology of cichlids, which mostly comes from a few large-scale studies [128]. For example, in addition to their celebrated ecological diversity, many sympatric species appear to be ecologically equivalent [158], inspiring Liem’s paradox: highly specialized morphologies may only be useful during times of scarcity [159]. However, a year-long study found that sympatric cichlid specialists did not partition resources during periods of scarcity and still managed to invade new habitats [158]. Much remains unknown about the stages of ecological and sexual divergence across cichlid radiations which exhibit complex dynamics (contra [160]). Indeed, existing knowledge of selection on cichlid morphology comes almost entirely from its genetic architecture [161]. Much more work is needed to connect emerging cichlid genomic and behavioral insights with functional morphology, performance, fitness landscapes, and ecology across diverse radiations and non-radiations in nature.

***Pupfish***

In contrast to cichlids, *Cyprinodon* pupfishes (family Cyprinodontidae) comprise a very recent radiation (crown age: 25 kya) which rarely diversified in sympatry despite their wide distribution across the western Atlantic, Caribbean, and Mojave and Sonoran deserts [10, 162]. Only two sympatric *Cyprinodon* radiations are known from hypersaline lakes on San Salvador Island, Bahamas and a brackish lake in the Yucatan, Laguna Chichancanab [10]. These two independent radiations of generalist and specialist pupfishes occur in remarkably similar habitats with abundant ecological opportunity due to lack of predatory fishes and only 1-2 co-occurring fish species. However, the paradox in this system is that generalist pupfish species have also colonized thousands of similar lakes throughout the Caribbean with identical depauperate fish communities and comparable levels of resource diversity, genetic diversity, population size, lake area, and island size, and yet have failed to diversify in all these environments (Martin in revision). Thus, in contrast to classic adaptive radiations found in unique environments (e.g. African rift lakes) and incipient speciation replicated across many similar environments, pupfish adaptive radiations pose a different problem: why are sympatric radiations of ecological specialists so localized, despite so many ecologically and genetically similar generalist populations on neighboring islands? Answering this question is key to understanding the origins of adaptive radiation.

Despite their young age, pupfish radiations exhibit striking divergence in trophic morphology and niche specialization. One species on San Salvador Island is a specialized scale-eater and has evolved much larger jaws, larger adductor mandibulae muscle mass, and an elongated body, driving rates of jaw diversification 50 – 1,000 times faster than other pupfish clades (Martin in revision; [10, 163]). To quantify the novelty of this trophic niche, we note that the most closely related scale-eating specialists are found within the African cichlids, separated by thousands of species and 168 million years of evolution from the scale-eating pupfish [164]. A second hard-shelled prey specialist on San Salvador exhibits an enlarged nasal skeletal protrusion, convergent with the anatomy of a unique reef fish, the black musselcracker *Cymatoceps nasutus*, which may stabilize its oral jaws for shell-crushing [165]. Laguna Chichancanab species have specialized on a different set of resources, including zooplankton and other fish [166], but their extinction in the wild has constrained laboratory studies of these endangered species [10]. Although there is some work on the functional morphology of scale-eating [167, 168], which may be facilitated by the decoupled jaw protrusion mechanics of Cyprinodontiform fishes [169, 170], future work is needed to connect divergent pupfish morphology to performance.

Field measurements of the fitness landscape for the San Salvador pupfish radiation provide a central focus for research on this system and offer an unexpected explanation for their ecological, behavioral, and genetic divergence. Pupfishes are nearly ideal for fitness experiments due to their hardiness, fecundity, high densities, and short generation time (four months). Furthermore, most species can be hybridized in the lab and produce viable and fertile hybrids [171], enabling manipulation of the phenotype using laboratory crosses among divergent species. Field experiments measuring the growth and survival of F2 hybrids among all three species in the San Salvador radiation demonstrated a complex landscape with two fitness peaks corresponding to the phenotypes of the generalist and molluscivore species. A small fitness valley separated the intermediate generalist phenotypes from a higher fitness peak corresponding to mollusk-eating hybrids with nasal protrusion, whereas a large fitness valley isolated the scale-eating large-jawed phenotypes from the other two species [172]. This fitness valley asymmetry makes biomechanical sense given the divergent performance demands of non-evasive (molluscs) versus evasive prey (biting scales) and high efficiency necessary for scale-eating [173]. The topography of the fitness landscape thus suggests an explanation for the rarity of scale-eating. Different-sized fitness valleys separating the two specialist species from the ancestral generalist phenotype also predict reduced gene flow between the scale-eater and other species in sympatry (supported by [165]), reinforcement of scale-eater pre-mating isolation (supported by [174]), rapid trait diversification of specialist phenotypes ([10]; Martin in revision) and a greater number of large-effect alleles underlying the scale-eater phenotype (Martin et al. in prep). Interestingly, hybrid fitness appears to reflect the foraging performance of different phenotypes, rather than the frequency of similar competitors, and varies in complex ways across different trait subsets, even within the oral jaws (Martin in press). In summary, measurement of the complex fitness landscape spanning an incipient adaptive radiation can inform patterns of speciation, gene flow, and divergence in ecology and performance.

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