ORIGINAL ARTICLE

Adaptive radiation in labrid fishes: A central role for functional innovations during 65 My of relentless diversification

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Early burst patterns of diversification have become closely linked with concepts of adaptive radiation, reflecting interest in the role of ecological opportunity in modulating diversification. But, this model has not been widely explored on coral reefs, where biodiversity is exceptional, but many lineages have high dispersal capabilities and a pan-tropical distribution. We analyze adaptive radiation in labrid fishes, arguably the most ecologically dominant and diverse radiation of fishes on coral reefs. We test for time-dependent speciation, trophic diversification, and origination of 15 functional innovations, and early bursts in a series of functional morphological traits associated with feeding and locomotion. We find no evidence of time-dependent or early burst evolution. Instead, the pace of speciation, ecological diversification, and trait evolution has been relatively constant. The origination of functional innovations has slowed over time, although few arose early. The labrid radiation seems to have occurred in response to extensive and still increasing ecological opportunity, but within a rich community of antagonists that may have prevented abrupt diversification. Labrid diversification is closely tied to a series of substantial functional innovations that individually broadened ecological diversity, ultimately allowing them to invade virtually every trophic niche held by fishes on coral reefs.

KEY WORDS: Early burst, ecological opportunity, functional innovation, rates of evolution, trophic diversity.

Adaptive radiation–the rapid diversification of a lineage into novel distinct adaptive zones (Simpson 1953)–holds a special position in our understanding of the origins of biological diversity. Adaptive radiation links population dynamics, competition, ecological opportunity, and the fitness landscape with speciation and interesting macroevolutionary outcomes (Schluter 2000; Mayr 2001). Although not universally agreed to be a necessary component, theory (Simpson 1953; Schluter 2000; Gavrilets and Losos 2009) and empirical work (Losos et al. 2001; Rabosky 2009; Martin and Wainwright 2013) have led to the realization that adaptive radiation is often characterized by an early period of rapid speciation and ecological diversification that slows as ecological opportunity is exploited and niches are filled (often referred to as an "early burst"). Thus, for many authors adaptive radiation requires the rapid diversification of a single lineage into many, ecologically diverse species (Schluter 2000; Simpson 1953), a view that places heavy weight on the importance of changes in ecological opportunity in modulating the pace

of diversification (Glor 2010; Yoder et al. 2010; Stroud and Losos 2016).

In recent years, the so-called "early burst" has flirted with becoming synonymous with adaptive radiation. Many studies now "test for adaptive radiation" by looking for evidence of an early burst of phenotypic diversification or speciation in their study group. Indeed, some well-known examples of adaptive radiation exhibit high rates of morphological or ecological differentiation early in the radiation (Harmon et al. 2003, 2008; Freckelton and Harvey 2006; Agrawal et al. 2009; Mahler et al. 2010). Similarly, a declining rate of lineage diversification from the earliest stages of the radiation toward the present has been interpreted as evidence of parallel reductions in ecological opportunity in the context of adaptive radiation (Rabosky and Lovette 2008; Rabosky 2009; Glor 2010). But, whether diversity-dependent species diversification and early bursts of trait evolution should be equated with adaptive radiation is challenged by the many radiations that do not show such patterns (Harmon et al. 2010; Derryberry et al. 2011;

Puttick 2018), highlighting a need for a nuanced concept of adaptive radiation that considers the diversity of circumstances and mechanisms under which adaptive radiation takes place (Gavrilets and Losos 2009).

Coral reefs harbor exceptional biodiversity, including about 20% of all fish species (Kulbicki et al. 2013). Among more than 70 families of coral reef fishes, Labridae (wrasses and parrot-fishes) stands out as consistently ranking among the most species-rich, locally abundant, ecologically diverse, and central to ecosystem processes (Bellwood 1996; Robertson 1998; Bellwood and Wainwright 2002). Over 510 labrid species occur on coral reefs throughout the tropics, making them the most species-rich fish family found on coral reefs, with another 100 species found in temperate rocky habitats around the world (Cowman 2014). Species range in body size from the tiny 5 cm *Wetmorella tanakai* to the giant 230 cm, 190 kg *Cheilinus undulatus*. Their trophic diversity covers nearly the entire range of feeding habits found among fishes on coral reefs, including myriad crustaceans, molluscs, echinoderms, zooplankton, fishes, polychaetes, bryozoans and in some of the more specialized taxa, algae, detritus, autotrophic microbes, foraminifera, coral mucus, and ectoparasites of other fishes. Their feeding activities can have profound effects on benthic communities, especially parrotfishes, which constantly graze hard surfaces, shaping recruitment of algae, clearing space for other settlers (Burkepile and Hay 2008; Bonaldo et al. 2014), and acting as the most potent bioeroders of carbonate reef structures (Bellwood 1995; Bruggemann et al. 1996). Labrid diversity extends along other dimensions as well, including depth (Wainwright et al. 2018), microhabitat (Bellwood and Wainwright 2001; Fulton et al. 2005), a wide range of mating systems (Robertson and Choat 1974; Warner 1984), and variation in patterns of sexual ontogeny (Warner and Robertson 1978) that have led to extensive color diversity. With their high species richness, local abundance, and ecological exuberance, labrids are the quintessential adaptive radiation of fishes on coral reefs. But are they?

In the present study, we evaluate the tempo of the labrid adaptive radiation, specifically asking whether they exhibit early bursts of speciation, trait evolution and ecology, consistent with an abrupt response to ecological opportunity. Using a time-calibrated molecular phylogeny, we test for changes in net diversification rate through the 65 My history of the group. We reconstruct the history of feeding habits in labrids, asking whether we see evidence of diversity-dependent dietary diversification. We also test for an early burst in the evolution of several continuous functional traits that characterize the complex labrid feeding apparatus and are known to be associated with the ability of labrids to capture and process various types of prey. Similarly, we test for an early burst of evolution in pectoral fin shape, a strong correlate of swimming performance in labrids, which is known to underlie some of their microhabitat diversity. Finally, we estimate the origination rate of

15 functional innovations associated with niche-shifts in feeding habits and habitat use. Cumulatively, these tests are used to determine whether labrid fishes fit the classic notion of an adaptive radiation in which diversification slows over time as the clade becomes more diverse and fills available niches (Simpson 1953; Schluter 2000; Stroud and Losos 2016).

Methods

PHYLOGENETIC INFERENCE

We used a previously published phylogeny of 320 labrid species (Baliga and Law 2016), representing slightly more than half of the nominal species (Froese and Pauly 2015). Briefly, their dataset included four mitochondrial (12S, 16S, COI, and Cyt b) and three nuclear gene regions (RAG2, TMO4c4, and S7), with 5462 total base pairs obtained from GenBank. Sequences were aligned in Geneious 4.8.5 (Kearse et al. 2012), the best-fitting model of nucleotide substitution was identified using jModelTest 2.0 (Darriba et al. 2012), and sequences were concatenated into a supermatrix using SequenceMatrix 1.7.8 (Vaidya et al. 2011). Then, the authors estimated phylogenetic trees using a relaxed log normal clock model with BEAST 2.2.1 (Bouckaert et al. 2014) under a GTR + Γ model. Seven informative parametric priors based on fossil and biogeographic information were set during this procedure (Baliga and Law 2016). The authors ran five separate MCMC runs and after discarding burn-in (15–20%), the combined set of runs included 41,323 trees, which were used to estimate the maximum clade credibility (MCC) tree in TreeAnnotator 2.2.1 (Bouckaert et al. 2014; Fig. S1). In this study, to account for uncertainty in phylogenetic tree topology and divergence times, we repeated most analyses across 1000 trees sampled randomly from the posterior distribution (see below for analysis-specific details).

LINEAGE DIVERSIFICATION

We employed the γ test using the R package PHYTOOLS (Revell 2012) to evaluate the pace of diversification through time. We estimated γ for each of the 1000 randomly sampled trees from the posterior distribution, then employed the Monte Carlo Constant rates test (MCCR) implemented in LASER (Rabosky 2006a) to conduct γ-statistic analysis for incompletely sampled phylogenies (Pybus and Harvey 2000). Complete phylogenies (i.e., with 638 tips) were simulated under the null hypothesis of a constant pure birth diversification process and taxa were randomly pruned to mimic the degree of incomplete taxon sampling in the empirical trees (i.e., 50%). This procedure was conducted across 5000 Monte Carlo simulations. We then compared the mean γ of the 1000 empirical trees to the null distribution of γ statistics. Secondly, we fitted models of diversification using the R package LASER version 2.4-1 (Rabosky 2006a). To test whether the diversification rate has slowed over time (Rabosky 2006b; Rabosky

and Lovette 2008), we compared the fit of a pure birth model (PB) in which the number of lineages accrues log-linearly with time, a birth-death model (BD) in which the probability of speciation and extinction are constant, and two diversity-dependent models in which diversification slows exponentially (DDX) or linearly (DDL) using Akaike Information Criterion (AIC). To account for phylogenetic uncertainty, models were fit to the 1000 randomly sampled trees from the posterior distribution. Lastly, we estimated net diversification over time under an episodic birth-death process and the number and magnitude of rate shifts using a reversible-jump MCMC algorithm with the R package TESS (Höhna et al. 2015; May et al. 2016). We did not have an expectation of rate shifts or mass extinction events during the evolutionary history of Labridae; therefore, we set priors to 1 rate shift and 1 mass extinction event. We designated the sampling probability based on the proportion of valid species included in our tree (i.e., 0.5). The analysis was run for 1 million iterations, thinning every 1000, and 10% burn in. We assessed the probability of rate shifts using Bayes factors (BFs), which compare the marginal likelihood of a shift to the marginal likelihood of zero shifts (Kass and Raftery 1995). Net diversification and rate shifts were estimated using the MCC tree. We assessed sensitivity to the prior by performing two additional runs with a prior of 5 and 10 rate shifts (Fig. S2).

ECOLOGICAL DIVERSIFICATION

We classified species into 10 trophic guilds based on their primary prey items: shelled invertebrates, soft-bodied invertebrates, mollusk, fish, herbivore, zooplankton, coral, foraminifera, cleaners (ectoparasites), and omnivores (Supplementary File 1). We then estimated the evolutionary histories of these guilds with stochastic character mapping using the make.simmap function implemented in PHYTOOLS (Revell 2012). The histories of each diet were estimated across 1000 simmap reconstructions on the MCC tree using an equal rates model (i.e., "ER"; favored over a model in which all rates were different across the majority of trees based on AICc) and fitting a continuous-time reversible Markov model for the evolution of trophic guild, then simulating stochastic character histories using the tip states on the tree (i.e., "empirical"). These simmaps were used to identify the origin (i.e., ancestral node) of each guild. To account for uncertainty in the origin of each novelty, we created age distributions for each guild based on the ages of their node of origin across 1000 randomly sampled trees from the posterior distribution.

Additionally, we determined whether transitions in trophic guilds varied through time by fitting time-dependent evolutionary models using the fitDiscrete function implemented in GEIGER (Harmon et al. 2007). We fit a constant rate model in which no tree transformation was used and a model in which a delta transformation was used to determine if transitions occurred constantly or increased/slowed through time, respectively. Models were fit

to 1000 randomly sampled trees from the posterior distribution. To visualize transition rates through time, we calculated the average transition times from 1000 randomly sampled trees and partitioned those into seven age bins (e.g., 0–10 Mya) and then calculated the total branch lengths for each bin. Then, we divided the number of transitions by the total branch length for each bin and regressed these transition rates against time (Mya).

MORPHOLOGICAL EVOLUTION

Traits

We used 10 traits related to swimming and feeding performance in labrids: the aspect ratio of the pectoral fins, premaxillary protrusion, mouth gape, masses of the adductor mandibulae, levator posterior, and sternohyoideus muscles, mouth-opening and -closing lever ratios, and kinematic transmission coefficients of the oral jaw and hyoid four-bar linkage systems. During swimming at most speeds, labrids rely on the pectoral fins to generate thrust. Pectoral fin shape is correlated with typical swimming speeds in labrids (Wainwright et al. 2002) and is known to have substantial consequences for microhabitat use across the group (Bellwood and Wainwright 2001; Fulton et al. 2005; 2017). We used previously published data on the aspect ratio of the pectoral fin from 829 individuals representing 127 species (Wainwright et al. 2002). Fin aspect ratio was calculated as the square of the leading edge length divided by the area of the fin and multiplied by two such that the values represent both fins. Additionally, we used species averages for nine traits based on three specimens each of 128 species (Wainwright et al. 2004; Price et al. 2011). The traits characterize functional morphological diversity in relation to prey capture and processing (Wainwright et al. 2004; Collar et al. 2007). These traits included two linear distances: premaxillary protrusion and mouth gape, which contribute to suction feeding performance and prey size restrictions; three muscle masses: adductor mandibulae, levator posterior, and sternohyoideus muscles, which are dominant actuators in the biting mechanism of the oral jaws, the pharyngeal jaws, and buccal expansion during suction feeding, respectively; mouth-opening and -closing lever ratios, which capture mechanical advantage of jaw adductors and abductors; and lastly kinematic transmission coefficients of the oral jaw and hyoid four-bar linkage systems, which transmit force and movement during oral jaw function and expansion of the buccal cavity, respectively. Species means of all traits were log-transformed. Additionally, we employed phylogenetic size-correction to traits that scaled with body size (i.e., lengths and masses; Fig. S3) using the phyl.resid function implemented in PHYTOOLS (Revell 2012).

Comparative phylogenetic methods

We employed three approaches to evaluate the mode and rates of morphological evolution. First, we calculated disparity through

time using the dtt function implemented in GEIGER (Harmon et al. 2007). Disparity was calculated using average squared Euclidean distance. The null distribution of disparity through time for each tree was based on 1000 simulations. Incomplete taxon sampling was addressed by excluding the most recent 30% of the tree while calculating the MDI statistic (Harmon et al. 2003). The MDI statistic can be prone to high type-2 error; therefore, we also compared the empirical DTT curve to those of the null model using the Rank Envelope Test (Murrell 2018). Second, we fit time-dependent evolutionary models to each morphological trait using the fitContinuous function implemented in GEIGER (Harmon et al. 2007). Fitted models include Brownian motion (BM; Felsenstein 1985), which assumes that trait variance accumulates proportional to time, an Early-burst model (EB; Blomberg et al. 2003; Harmon et al. 2010), where the rate of evolution decreases exponentially through time, and the delta model (Pagel 1999), which fits the relative contributions of early versus late evolution, where a delta (δ) greater than 1 indicates recent evolution was relatively fast and δ less than 1 indicates recent evolution has been comparatively slow. Speed-ups in morphological evolution may be consistent with and statistically indistinguishable from selection (Cooper et al. 2016). Therefore, we also fit Ornstein-Uhlenbeck (OU) models (Butler and King 2004). We also simulated datasets with BM across each of the 1000 trees using the fastBM function in PHYTOOLS (Revell 2012) and subsequently fit BM, EB, delta, and OU models to these null datasets to evaluate if our phylogenetic trees were biased toward detecting non-Brownian models (Cooper et al. 2016). Lastly, to further assess rates of morphological evolution through time, we performed node-height tests in which the absolute values of standardized contrasts were regressed against the heights (i.e., time since root) of the nodes at which they were calculated (Freckleton and Harvey 2006). Standardized contrasts are point estimates of the Brownian rate parameter (Felsenstein 1985); therefore, negative and positive correlations between absolute contrasts and node heights would depict rates that have slowed and increased through time, respectively. We assessed the statistical significance of these relationships using robust regression, which weights data points according to their residual such that outliers are downweighted and has been shown to provide greater power to detect early bursts (Slater and Pennell 2013). To estimate the evolutionary rates of overall feeding morphology, we performed the node-height test using multivariate contrasts (McPeek et al. 2008) calculated from the nine feeding traits. Phylogenetically independent contrasts were calculated using the pic function implemented in APE (Paradis et al. 2004). To account for phylogenetic uncertainty, disparity through time, evolutionary model fitting, and node-height tests were repeated across 1000 randomly sampled trees from the posterior distribution.

ORIGINS OF INNOVATIONS

We coded 320 labrid species based on the presence/absence of 15 functional innovations–features, either morphological, behavioral, or physiological, that allow a lineage to interact with the environment in a novel way and may provide access to previously unavailable resources (as distinct from "key innovations" – traits that promote diversification; Hunter 1998; Galis 2001; Rabosky 2014): pharyngognathy, phyllodont dentition, parrotfish pharyngeal jaw apparatus, coalesced premaxillary teeth, intramandibular joint, rotating quadrate, folded lip, split lip, singular large pharyngeal tooth, incisiform teeth, antifreeze proteins, recurved oral teeth, elongate mandible, fin waving, and ultra-elongate body (see Supplementary File 1 for detailed explanations of each trait). Elongate mandible and ultra-elongate body are based on continuous traits that we recoded as discrete based on the presence of extreme values (Fig. S4). We then estimated the evolutionary histories of these innovations using SIMMAP following the methods described above for trophic guilds (see *Ecological diversification*). Lastly, we determined whether the origination rate of functional innovations varied through time using the same methods as described for trophic guilds (see *Ecological diversification*). The time of origination of each innovation was identified using its evolutionary history based on stochastic maps (Bollback 2006). In the cases of three innovations that were represented by a single species, we used the entire length of the branch to represent its age of origin, resulting in estimates likely biased towards ages older than the true origin. Because pharyngognathy is believed to be a synapomorphy for Labridae (Wainwright et al. 2012), we used the crown age of labrids to represent the origin of pharyngognathy.

Results

LINEAGE DIVERSIFICATION

The mean (range) γ statistic across 1000 randomly sampled trees from the posterior distribution was –0.984 (–2.29–0.434); however, these estimates fell well within the null distribution of γ statistics simulated with the MCCR test (Fig. 1A). This result indicates that lineage accumulation is consistent with that of a constant pure birth diversification process and that the observed negative γ statistic is likely a result of incomplete taxon sampling rather than diversification having slowed over time (Pybus and Harvey 2000). Likewise, a pure birth diversification model best fit 963 of the 1000 trees (Table 1). In the remaining 37 trees, both diversity-dependent models fit better than the constant rate models, with the diversity-dependent exponential model best fitting those trees (Table 1). Based on Bayesian analyses using TESS, net diversification rates gradually increased through time (Fig. 1B). Bayes Factors suggest that there were no rate shifts through time
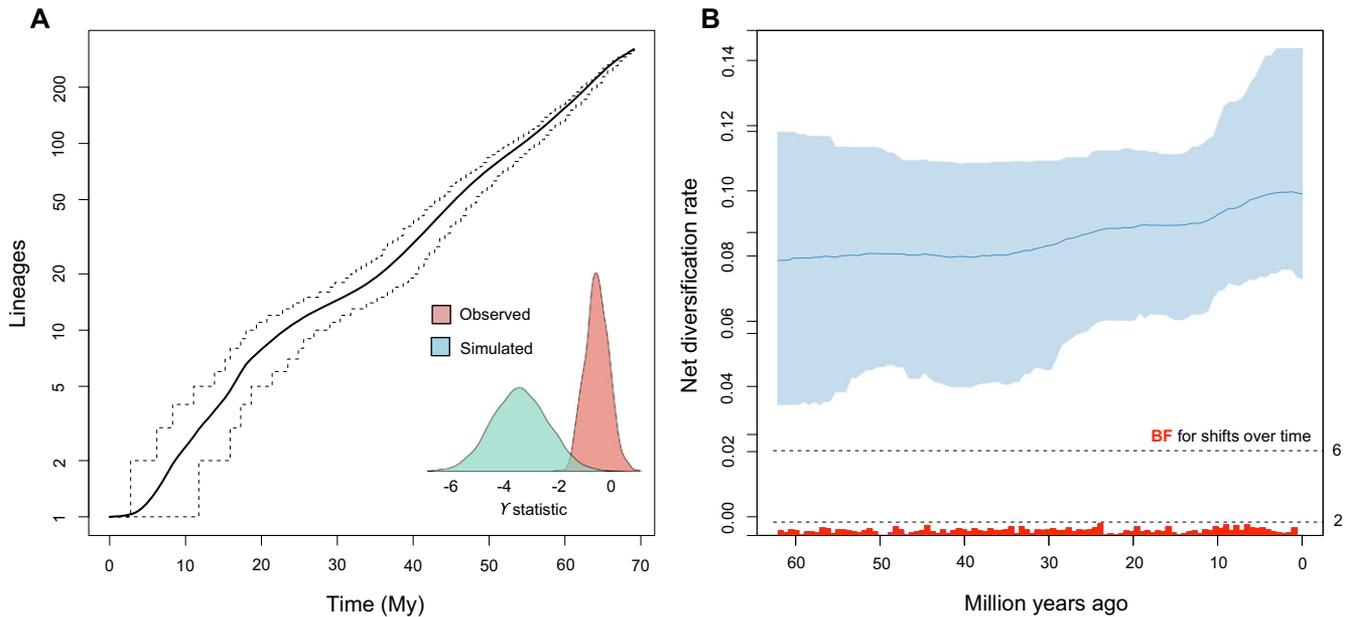
Figure 1. The accumulation of lineages through time in labrid fishes (A). Solid and dashed lines depict the mean and 95% confidence interval, respectively, summarized from 1000 randomly sampled trees from the posterior distribution. The inset density plot shows the distribution of observed γ-statistics from the 1000 trees and null distribution based on 5000 trees simulated under a constant rate pure birth diversification process. Net diversification through time (B). The shaded area depicts the 95% confidence interval. Red columns depict the Bayes Factors (BF) for rate shifts at the corresponding point in time, from analyses with TESS. None reach the value of six expected for a significant rate shift.

Table 1. Diversification-process model fitting to 1000 randomly sampled trees from the posterior distribution of labrid trees.

Model	ln L	AIC	ΔAIC	Prop.
Pure birth (Yule)	397.03 (351.36–447.57)	−792.07 (−893.13 to −700.72)	0.00	0.963
DDX	397.35 (352.37–447.57)	−790.70 (−891.14 to −700.73)	1.36	0.000
Birth death	397.03 (351.36–447.57)	−790.07 (−891.13 to −698.72)	2.00	0.000
DDL	395.36 (350.43–447.93)	−786.72 (−891.86 to −696.86)	5.35	0.037

Models are ranked from best to worst fit according to the log-likelihood (ln L), Akaike Information Criterion (AIC), and the proportion of the 1000 trees in which the model was the best fit (Prop.). Values depict the mean across 1000 trees. Values depict the mean (range) across 1000 trees.
DDX, diversity-dependent exponential; DDL, diversity-dependent linear.

(Fig. 2B). Inflating the prior number of shifts increased the variability of net diversification through time; however, there was still no support for rate shifts using BFs (Fig. S2).

ECOLOGICAL DIVERSIFICATION

Transitions in trophic guild were well distributed across the labrid phylogeny (Fig. 2A) and through time (Fig. 2B). Trophic guild evolution best fit a constant rate model on 757 of the 1000 trees (Table 2; Fig. 2C). Estimates of the δ parameter were positive across all trees, ranging from 1.3 to 2.1, indicating a general increase in transition rate over time (Pagel 1999). Specifically, trophic guild diversity began accumulating approximately 38 Mya (Fig. 2D).

FUNCTIONAL MORPHOLOGICAL EVOLUTION

Morphological disparity evolved consistent with BM for all ten traits (Fig. 3 and S5; Table 3). Early burst models were universally worst fit (Table S1). The aspect ratio of the pectoral fin and mass of the levator posterior best fit BM and delta models, respectively, whereas the evolution of all other traits best fit by the OU model (Table 4 and S1). These results were consistent across 1000 trees (Table S1). Mean estimates of the δ parameter were positive for all traits, ranging from 1.39 (aspect ratio) to 2.90 (jaw opening lever), indicating that recent evolution has been comparatively fast (Pagel 1999); however, we interpret this pattern with caution as delta and OU models often fit similarly because increasing rates of evolution over time may be consistent with and statistically indistinguishable from selection (Cooper et al. 2016). Likewise,
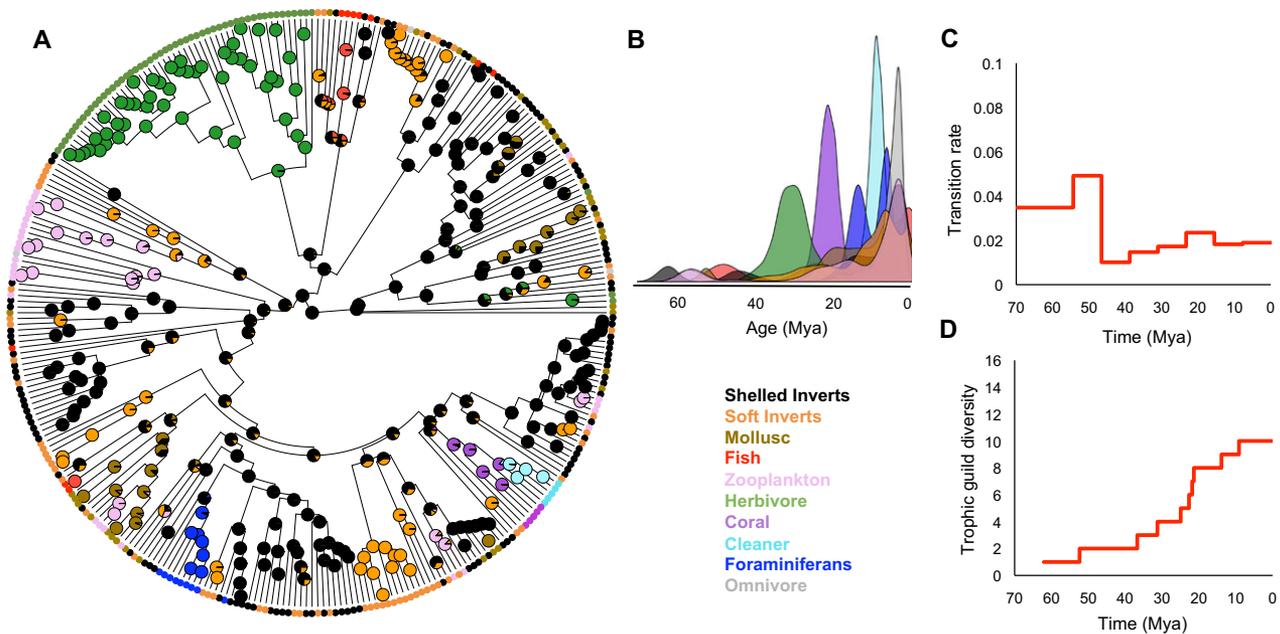
Figure 2. The evolutionary history of trophic guilds in labrid fishes (A), through time (B), and their transition rates (C) and accumulation (D) through time. Internal nodes are colored based on summaries of 1000 stochastic character mappings on the MCC tree. Circles around the edge of the tree indicate the guild of each species. The distributions in B correspond to the ancestral node for each guild across 1000 trees randomly sampled from the posterior distribution. Note that D shows the accumulation of unique trophic guilds, whereas because most diets evolve several times the total number of transitions is much higher.

Table 2. Time-dependent patterns of trophic guild and morphological innovation evolution in labrid fishes.

Model	ln L	AICc	ΔAICc	δ	Prop.
Trophic guild					
Constant rate	−417.7 (−432.0 to −409.2)	841.4 (820.5–866.0)	0.0		0.757
Changing rate	−418.9 (−430.9 to −408.4)	841.8 (820.8–865.9)	0.4	1.578	0.243
Innovations					
Constant rate	−117.8 (−127.0 to −113.7)	237.6 (229.4–256.1)	0.7		0.000
Changing rate	−116.4 (−117.5 to −111.8)	236.8 (238.9–255.7)	0.0	0.296	1.000

Values depict the mean (range) log-likelihood (lnL) and Akaike Information Criterion corrected for sample size (AICc) and the mean difference in AICc scores (ΔAICc) across 1000 trees, mean estimate of the δ parameter, and the proportion (Prop.) of the 1000 trees in which the model was the best fit based on AICc scores.

Table 3. Morphological disparity through time in labrid fishes.

Trait	MDI	P	Prop. P	Prop. MDI
Fin aspect ratio	0.335 (0.237–0.427)	0.972 (0.921–0.992)	0.000	0.000
Gape	0.013 (−0.032–0.065)	0.830 (0.750–0.938)	0.000	0.196
Protrusion	0.197 (0.148–0.255)	0.941 (0.898–0.977)	0.000	0.000
Adductor mandibulae	0.315 (0.189–0.498)	0.968 (0.906–0.992)	0.000	0.000
Sternohyoideus	0.075 (0.009–0.146)	0.877 (0.789–0.945)	0.000	0.000
Levator posterior	0.136 (0.065–0.246)	0.915 (0.820–0.969)	0.000	0.000
Jaw closing lever	−0.210 (−0.235 to −0.176)	0.525 (0.375–0.742)	0.000	1.000
Jaw opening lever	0.0217 (−0.0160–0.069)	0.837 (0.758–0.922)	0.000	0.033
Jaw KT	0.165 (0.119–0.232)	0.928 (0.844–0.969)	0.000	0.000
Hyoid KT	−0.073 (−0.115 to −0.024)	0.759 (0.648–0.844)	0.000	1.000

Values depict the mean (range) of the MDI statistic and P-value summarized across 1000 trees. Prop. P depicts the proportion of trees that the Rank Envelope Test was significant. Prop. MDI depicts the proportion of trees in which the MDI statistic was negative.
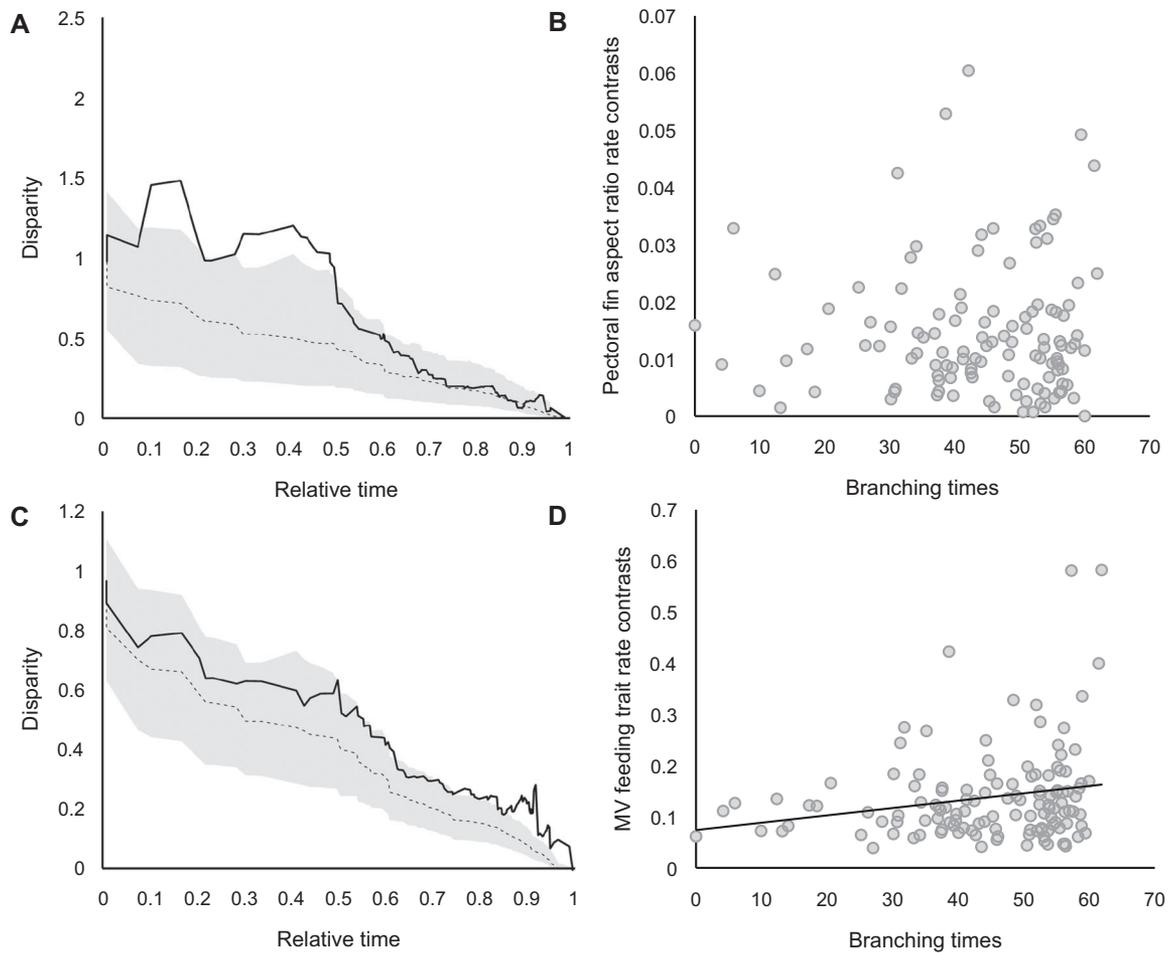
Figure 3. Morphological disparity and rates through time for the aspect ratio of the pectoral fin (A, B) and multivariate feeding traits (C, D). Plots are based on analyses with the MCC tree (see Tables 3 and 5 for summaries from 1000 trees and individual feeding traits).

Table 4. Best-fit evolutionary model and parameter estimates for traits associated with locomotion and feeding performance.

Trait	Best model	Comp. models	δ	α	Prop.
Fin aspect ratio	BM	OU, delta	1.39	0.006	0.962
Gape	OU	delta	1.81	0.014	0.985
Protrusion	OU	—	2.88	0.052	1.000
Adductor mandibulae	OU	—	2.90	0.048	1.000
Sternohyoideus	OU	—	2.88	0.037	1.000
Levator posterior	delta	BM, OU	1.75	0.010	0.522
Jaw closing lever	OU	—	2.43	0.025	1.000
Jaw opening lever	OU	—	2.90	0.052	1.000
Jaw KT	OU	delta	2.32	0.019	1.000
Hyoid KT	OU	—	2.73	0.056	1.000

The best-fit and comparable (Comp.) models, mean parameter estimates of δ and α, and the proportion (Prop.) of the 1000 trees in which the model was the best fit based on AICc scores.

correlations between absolute contrasts and the heights of the nodes at which they were calculated were either nonsignificant or exhibited a significant positive relationship (Fig. 3 and S6). The aspect ratio of the pectoral fin, jaw protrusion, masses of the leva-

tor posterior and sternohyoideus, jaw closing lever ratio, and hyoid KT consistently had nonsignificant relationships across the 1000 trees, whereas the mass of the adductor mandibulae, jaw opening lever ratio, and jaw KT consistently had significant positive

Table 5. Rates of morphological evolution through time based on node-height tests.

Trait	r^2	P	Prop. $P < 0.05$
Fin aspect ratio	0.001 (0.000–0.008)	0.497 (0.073–0.988)	0.000
Gape	0.004 (0.000–0.014)	0.801 (0.211–0.999)	0.000
Protrusion	0.032 (0.015–0.060)	0.162 (0.039–0.691)	0.014
Adductor mandibulae	0.051 (0.033–0.074)	0.043 (0.003–0.165)	0.698
Sternohyoideus	0.049 (0.032–0.069)	0.103 (0.021–0.472)	0.086
Levator posterior	0.001 (0.000–0.008)	0.626 (0.138–0.999)	0.000
Jaw closing lever	0.014 (0.001–0.024)	0.504 (0.123–0.990)	0.000
Jaw opening lever	0.049 (0.030–0.067)	0.038 (0.005–0.116)	0.758
Jaw KT	0.048 (0.027–0.076)	0.050 (0.008–0.221)	0.573
Hyoid KT	0.020 (0.006–0.034)	0.343 (0.074–0.962)	0.000

relationships across the 1000 trees (Table 5). Results with mass of the adductor mandibulae, jaw opening lever, and jaw KT were variable among trees, being significant across 698, 758, and 573 of the 1000 trees, respectively (Table 5). All significant relationships were positive, suggesting an increase in rates of morphological evolution over time. We tentatively interpret these increasing rates because datasets simulated with BM were favored over delta and OU models across 821 and 869 of the 1000 trees, respectively, indicating some limitations in distinguishing between BM and these models that often are consistent with accelerating rates of morphological evolution (Cooper et al. 2016). In contrast, BM was favored over EB models across 957 of the 1000 trees using BM-simulated data, indicating a more robust ability to distinguish between those models.

ORIGINS OF FUNCTIONAL INNOVATIONS

The origins of functional innovations were also well distributed across the phylogeny (Fig. 4A) and through time (Fig. 4B). The evolution of innovations best fit a changing rate model on all 1000 of the 1000 trees. Estimates of the δ parameter were less than one across all trees, ranging from 0.30 to 0.32, indicating a decrease in origination rate over time (Pagel 1999). (Table 2; Fig. 4C). Innovation diversity began sharply accumulating concurrently with trophic guild diversity approximately 38 Mya (Fig. 4D).

Discussion

Labrids failed our tests for diversity-dependent lineage diversification and dietary diversification as well as our tests for early bursts of trait evolution. Instead, labrid diversification is mostly characterized by constant rates throughout their 65 My history. Since the end-Cretaceous mass extinction event that substantially altered coral reef biomes (Wood, 1999), labrids have diversified steadily, ultimately producing extensive variation in their swimming and feeding systems, while also giving rise to innovations that contributed to a continuous and ongoing expansion in trophic

niches that reaches its zenith in today's oceans. The overall picture that emerges from our analyses is that the pace of labrid diversification has changed little through their history and is very much ongoing.

The early burst pattern is generally viewed as a response to a sudden expansion of ecological opportunity, whether due to invasion of a new region, loss of major antagonists, or key innovation (Schluter 2000; Simpson 1953). The scenarios that most commonly accompany bursts of diversification in the empirical literature involve invasion of new regions rich with ecological opportunity (Burress and Tan 2017; Mahler et al. 2010) or key innovations that allow access to a novel adaptive zone (Donoghue 2005; Litsios and Salamin 2014). But, while labrids have achieved both numerical abundance and exuberant diversity on coral reefs, the pace of their diversification clearly does not fit with this prevailing view of adaptive radiation. What combination of factors might explain their capacity for evolving diversity while giving insight into the absence of an early burst?

Coral reefs clearly are a biome with extensive ecological opportunity. Diversity and abundance of many marine metazoan groups is highest in the tropics and particularly on coral reefs (Tittensor et al. 2010), and has been rising throughout most of the Cenozoic following the loss of biodiversity at the end-Cretaceous mass extinction (Budd 2000; Buzas et al. 2002; Renema et al. 2008; Yashura et al. 2016). This pattern of increasing biodiversity through time was somewhat reversed in several major reef groups, although not fishes, in the Plio-Pleistocene (Renema et al. 2008). But, for the first 55 My of labrid history, taxonomic richness in reef communities, and thus the range of potential prey and habitat resources appear to have represented an ever-expanding substrate for functional and ecological exploitation.

One possible key to understanding labrid history is that, while early Cenozoic coral reefs offered considerable ecological opportunity, they have supported a rich fish fauna throughout this period that has increased in richness in parallel with labrid expansion. The oldest Cenozoic reef fish fossil assemblage is found in the
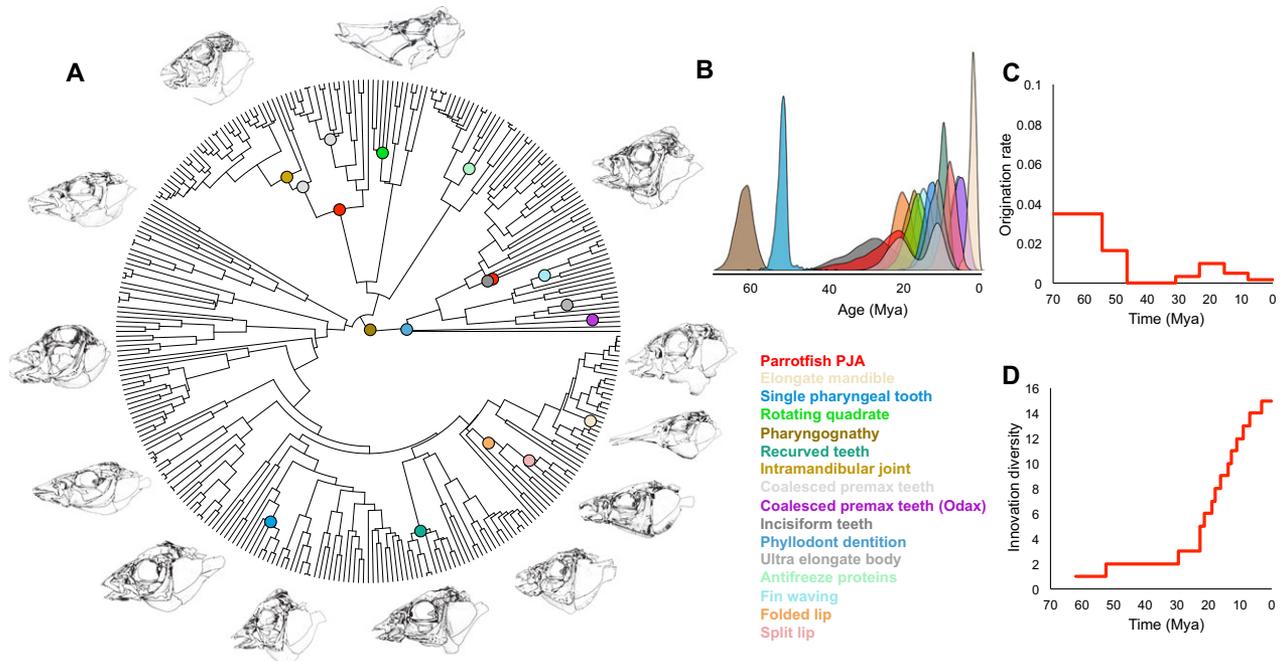
Figure 4. The origins of morphological innovations across the labrid phylogeny (A), through time (B), and their origination rate in 5 My bins (C) and accumulation (D) through time. Origin nodes were identified based on 1000 stochastic histories. Labeled nodes correspond to the most frequent earliest reconstruction of each innovation, based on 1000 stochastic mappings with the MCC tree. The age distributions in B correspond to the age estimates of the clades defined by the origin nodes across 1000 trees randomly sampled from the posterior distribution. Note that D displays the accumulation of unique innovations, but because some innovations evolved more than once the total number of transitions is higher. Inset skull diagrams illustrate the morphological diversity of the adjacent lineage.

Eocene deposits of Monte Bolca, in Northern Italy. This fauna shows an assemblage strongly reminiscent of modern reefs, with most of the major lineages found on modern coral reefs already well represented (Bellwood et al. 2017). Thus, it appears that in the aftermath of the end Cretaceous mass extinction, labrids became established in reef systems that were inhabited by a rich diversity of competitors and predators. While potential prey were aplenty and quite diverse, other lineages of fishes were present and likely represented competition for those resources and predators on labrids themselves.

These observations suggest that conditions during the first third of labrid diversification were markedly different from those encountered by cichlids following their invasion of recently formed rift lakes in Africa or encountered by the silverswords and honeycreepers upon their arrival to Hawaii. In these latter examples, ecological opportunity seems to have been considerable and paired with relatively few incumbent antagonists (Baldwin and Sanderson 1998; Lovette et al. 2002; Seehausen 2006). In contrast, for labrids, abundant ecological opportunity was paired with a community heavy with incumbency.

INNOVATIONS AND LABRID ADAPTIVE RADIATION

Another key to labrid diversification appears to be an unusual capacity for functional innovations that underpin the invasion of numerous novel niches, some with profound implications for reef ecosystems. Labrid trophic diversity is centered on a relatively rare core ability to successfully handle hard-shelled prey (Randall 1967; Yamaoka 1978; Wainwright 1988), an ability they owe in large part to pharyngognathy, a novel condition of the pharyngeal jaw apparatus that is a synapomorphy of labrids (Fig. 4; Stiassny and Jensen 1987; Wainwright et al. 2012). This condition strengthens the prey-crushing bite and allows many labrids, even at small body sizes, to crush the shells of gastropods, bivalves, heavily armored crabs, and echinoderms (Randall 1967; Liem and Sanderson 1986; Wainwright 1987; 1988; Bellwood et al. 2006). A considerable fraction of labrid trophic diversity involves moving up and down the hardness axis of benthic invertebrate prey taxa. These changes involve hypertrophy of jaw muscles and strengthening of skeletal elements supporting the jaws in the case of mollusc-feeding or a reduction in jaw muscle strength in taxa that feed on softer-bodied invertebrates, like polychaetes, and smaller crustaceans such as amphipods and isopods. As an indication of how extensive crushing strength diversity is, the muscle that powers the pharyngeal jaw bite of labrids varies 500-fold in mass across species, after accounting for body size (Wainwright et al. 2004).

Secondary functional innovations have also permitted labrids to diversify along a prey elusiveness axis (Westneat 1995). In the

case of the slingjaw wrasse, *Epibulus*, piscivory is associated with a major novelty in the jaw mechanism that gives this genus the most protrusible jaws known in ray-finned fishes (Westneat and Wainwright 1989). Like many other lineages of reef fishes, labrids have evolved specialized zooplankton feeding typically associated with high-aspect ratio pectoral fins, swift swimming behavior (Wainwright et al. 2002), and an overall reduction in the size of feeding structures (Schmitz and Wainwright 2011). The labrichthyine wrasses contain the only origin of dedicated coral mucus feeding in labrids (Huertas and Bellwood 2017, 2018), a relatively recent novel trophic niche among reef fishes (Fig. 2; see also Huertas and Bellwood 2018). Coral feeding in labrids is intimately associated with highly folded lips that are richly endowed with mucus that may protect the fish from the coral's stinging cells and enhance the suction feeding behavior these fish use to remove coral tissue (Huertas and Bellwood 2017). Within this lineage, specialized ectoparasite feeding has also evolved, in association with a split in the lower lip that may facilitate exposure of the teeth of the lower jaw to the epithelium (Baliga et al. 2017).

Finally, the most striking and consequential trophic transition in labrids is found in parrotfishes, with a change to herbivory that occurred about 32 Ma (Fig. 2). Within parrotfishes there has been subsequent diversification of herbivory to detritivory (Tebbett et al. 2017) and recent work indicates that the diet of most parrotfish is dominated by autotrophic bacteria (Clements et al. 2017). The parrotfish transition to herbivory is associated with a substantial modification of the parrotfish pharyngeal jaw (Bellwood 1994), producing a system with considerable anterior-posterior grinding motion for pulverizing the mixture of benthic turf algae, sediment, and other material that is eaten by parrotfish (Gobalet 1989; Wainwright and Price 2018). Within parrotfish there appear to be two origins of coalesced teeth that form the beak-like oral jaw dentition that is key to their ability to scrape the rocky surface of reefs. One origin is at the base of the scarinine radiation, about 21 Ma, and a second at the base of *Sparisoma*, about 10 Ma (Fig. 4). Finally, within the scarinines an intra-mandibular joint arose about 18 Ma that is found in all species of *Scarus* (52 spp), *Chlorurus* (18 spp), and *Hipposcarus* (2 spp). It is thought that this novel joint facilitates greater dexterity in fitting the scraping jaws to the complex surfaces on reefs (Konow et al. 2008). The consistent evolution of these and other functional innovations gradually expanded the ecological repertoire of labrids.

The prevalence and sustained evolution of functional innovations seen in labrids may occur in other fish adaptive radiations. Cichlids have also evolved some functional innovations coupled with ecological and evolutionary consequences; however, the tempo in which they arose is not yet known. Pharyngognathy is found convergently in cichlids and likely provided similar access to hard and tough prey (Liem 1973; McGee et al. 2015),

mouth-brooding is a derived reproductive strategy that may facilitate offspring survivorship in response to high predation pressure (Hert 1989), and the evolution of egg-spots on the anal fin of males may serve as sexual advertisements that attract females and improve fertilization success (Hert 1989; Wickler 1962). These innovations have likely played a role during the evolutionary history of cichlids (Salzburger et al. 2002), but this adaptive radiation has been more strongly linked to ecological opportunity provided by the colonization of novel ecosystems (Seehausen 2006; Elmer et al. 2014; Wagner et al. 2014; Burress and Tan 2017). Consequently, a large fraction of cichlid diversity arose via recent bouts of diversification, most notably within the East African Great Lakes (Seehausen 2006), in contrast to the consistent tempo observed in labrids.

IMPLICATIONS FOR THE CONCEPT OF ADAPTIVE RADIATION

Our results indicate that the most ecologically diverse fish lineage that inhabits coral reefs, Labridae, does not fit the classic notion of adaptive radiation in which diversification slows over time as the clade becomes more diverse and fills available niches (Simpson 1953; Schluter 2000). The requisite features of adaptive radiation, especially the role of tempo, have been debated previously (reviewed in Givnish 2015). While some classic adaptive radiations, such as Australian marsupials, exhibit early bursts in lineage and morphological diversification (Garcia-Navas et al. 2018), some equally famous adaptive radiations, such as Darwin's finches, do not (Burns et al. 2017). Cichlid fishes, another pillar in the adaptive radiation literature, exhibit dramatic shifts in lineage diversification rates following the colonization of novel ecosystems (Seehausen 2006); however, many of these lineages, including the mega-diverse assemblages in Lakes Malawi and Victoria, may be in the expansion phase and have yet to enter the latter stages of adaptive radiation in which their diversification slows (Burress and Tan 2017; Burress et al. 2018). Of the older lineages, including the radiation within Lake Tanganyika, there is also little evidence of early bursts (Harmon et al. 2010).

Labrids likely faced a very different landscape than lineages that colonized young islands or lakes in which resources were underutilized. Since the end-Cretaceous mass extinction, coral reefs appear to have supported a diverse fish community (Bellwood et al. 2017) that may have constrained early labrid diversification and prevented an abrupt response to ecological opportunity. In this sense, "continental radiations" that have largely diversified in the presence of antagonists may provide a better analogy for labrids; however, in four such radiations in which tests for early bursts of lineage and/or morphological evolution have been performed (Neotropical cichlids, South American rodents, and North American warblers and minnows), these clades have largely corroborated early burst patterns of diversification (Rabosky and

Lovette 2008; López-Fernández et al. 2013; Arbour and López-Fernández 2016; Burress et al. 2016; Schenk and Steppan 2018). There are clearly a wide array of circumstances in which adaptive radiations occur and the early burst model does not fit all. Some authors have adopted broader definitions of adaptive radiation, focusing on the expansion of morphological and ecological diversity within a lineage (Losos 2010; Givnish 2015), rather than emphasizing the tempo of diversification.

Conclusions

The repeated and consistent evolution of functional innovations appears to have facilitated the ecological expansion of labrids in the face of competition and predation from incumbents. Our reconstruction of labrid diets indicates that for the first 30 My of the radiation the group may have been restricted to two diet categories, shelled invertebrates and molluscivory (Fig. 2). But, over the subsequent 30 My most of the tropic diversity seen in this group originated, as eight additional diets evolved (Fig. 2). This pattern is also seen in the history of functional innovations. Pharyngognathy and phyllodont dentition were introduced in the first 35 My of the radiation, allowing access to hard shelled prey like gastropods, bivalves, thick-shelled crabs, and echinoderms. Over the subsequent 30 My, 13 additional innovations were introduced, each underlying access to a novel niche, gradually expanding the ecological diversity of labrids (Fig. 4). This conspicuous role for repeated and phylogenetically nested functional innovations being linked to ecological expansion seems to be a key feature of the labrid adaptive radiation. Perhaps the most remarkable feature of the radiation is that after 65 My of steady diversification, culminating in high species richness and exceptional ecological diversity, labrids show no signs of slowing down, only signs of ongoing expansion.

AUTHOR CONTRIBUTIONS
P.C.W. conceived the study and assembled the data sets. E.D.B. analyzed the data. Both authors contributed to writing the manuscript; P.C.W. wrote the abstract, introduction and discussion, and E.D.B. wrote the methods, results, and prepared the figures and tables. Both authors contributed to revisions.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

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Supporting Information
Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Evolutionary models fit to locomotion and feeding performance traits.
Figure S1. Maximum clade credibility phylogenetic tree used in the paper (originally from Baliga and Law 2016) and that appears in Figures 2 and 4 of the main text.
Figure S2. Assessment of sensitivity to the prior number of shifts in speciation rates during analyses of diversification using TESS.
Figure S3. Plots demonstrating the scaling of trait values with body size.
Figure S4. Histograms demonstrating the extreme jaw length (A) and body elongation (B) values observed in *Gomphosus* and *Siphonognathus*, respectively, used to justify treating these cases as discrete innovations.
Figure S5. Disparity through time plots based on the MCC tree, for the 10 traits included in the paper.
Figure S6. Node-height tests, based on the MCC tree, for the 10 traits included in the paper. Best fit lines depict significant relationships.
Supporting Information