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## SYMPOSIUM

### The Impact of Organismal Innovation on Functional and Ecological Diversification

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**Synopsis** Innovations in organismal functional morphology are thought to be a major force in shaping evolutionary patterns, with the potential to drive adaptive radiation and influence the evolutionary prospects for lineages. But the evolutionary consequences of innovation are diverse and usually do not result in adaptive radiation. What factors shape the macroevolutionary impact of innovations? We assert that little is known in general about the macroevolutionary outcomes associated with functional innovations and we discuss a framework for studying biological innovations in an evolutionary context. Innovations are novel functional mechanisms that enhance organismal performance. The ubiquity of trade-offs in functional systems means that enhanced performance on one axis often occurs at the expense of performance on another axis, such that many innovations result in an exchange of performance capabilities, rather than an expansion. Innovations may open up new resources for exploitation but their consequences for functional and ecological diversification depend heavily on the adaptive landscape around these novel resources. As an example of a broader program that we imagine, we survey five feeding innovations in labrid fishes, an exceptionally successful and ecologically diverse group of reef fishes, and explore their impact on the rate of evolution of jaw functional morphology. All of the innovations provide performance enhancements and result in changes in patterns of resource use, but most are not associated with subsequent functional diversification or substantial ecological diversification. Because selection acts on a specific performance enhancement and not on the evolutionary potential of an innovation, the enhancement of diversity may be highly serendipitous. The macroevolutionary potential of innovations depends critically on the interaction between the performance enhancement and the ecological opportunity that is exposed.

#### Introduction

The ecological and evolutionary impact of a functional innovation depends on the complex interaction between the strength of the performance increase provided by the change, ecological opportunity, and functional trade-offs. Thus, diversification following a change in morphology or physiology is not guaranteed (Levinton 1988). It may never happen or it may occur later, when ecological opportunities shift, for example due to climatic change, the loss of a competitor or after further functional changes (Liem 1973; Losos and Mahler 2010). When an innovation has had a positive impact on subsequent diversification it is often referred to as a “key innovation” (Jablonski and Bottjer 1990; Fig. 1). Key innovations have been central to discussions

of adaptive radiation (e.g., Simpson 1953; Seehausen 2006; Losos 2010) and represent a major way in which the evolutionary history of organismal function may have shaped the tempo and mode of life’s diversification (Simpson 1944, 1953; Stanley 2007; Gillespie and Baldwin 2010; Vermeij 2012). However, relatively little is known about the diversity of evolutionary outcomes of functional innovation or the factors that determine this impact (Vermeij 2001).

In this article, we revisit the interface between functional innovation and ecomorphological diversification. We offer a definition of innovation and comment on the potential role of the adaptive landscape and functional trade-offs in promoting or limiting the subsequent adaptive diversification.

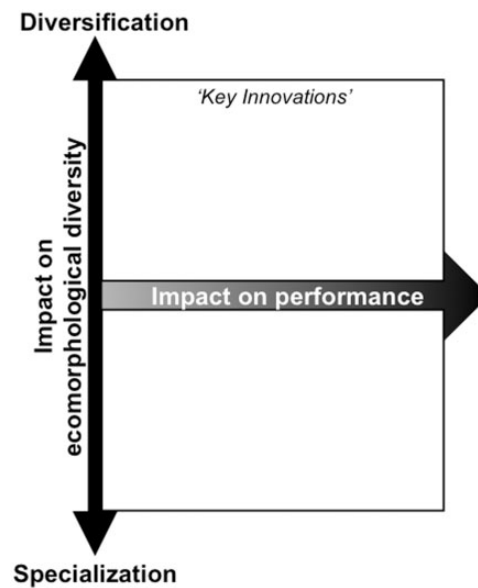
These considerations suggest a general approach to studying the macroevolutionary impacts of innovation, which we illustrate with a case study that explores innovations in the feeding mechanism of labrid fishes, an ecologically and functionally diverse group of reef fishes.

### Innovation

Innovations are evolutionary novelties, or new traits or combinations of traits that result in enhanced performance of the organism in some task. While we see a continuous range in nature between minor adaptations and major innovations, as functional morphologists we regard innovations as adaptations that provide a novel functional mechanism that underlies increased performance. It seems likely that both complexity and the impact on performance are important axes of diversity among biological innovations. Much adaptive change involves small, simple changes, but the history of life also reveals cases of complex novelties with major consequences for organismal performance. How complex innovations are assembled from small evolutionary changes has been an issue of considerable interest for decades (Puzey et al. 2011; Wisecaver et al. 2013; Wainwright et al. 2015). It is important to recognize that the macroevolutionary impact of the innovation is separate from the processes driving the origination and establishment of the innovation, which occurs below the species-level (Cracraft 1990).

### Adaptive landscape

The adaptive landscape describes the fitness consequences of phenotypic combinations, with peaks and troughs in fitness that change over time (Simpson 1944), thereby providing a conceptual link between micro- and macroevolution (Arnold et al. 2001). Innovations change the shape of the adaptive landscape, some providing minor changes in fitness or advances in performance, while others confer major breakthroughs and potentially ecological opportunity (Fig. 1), an idea that has been central to previous thinking about the link between innovations and diversification (e.g. Simpson 1944; Vermeij 1974; Losos and Mahler 2010). Substantial performance enhancements may lead to specialization on existing or novel resources with no further ecological diversification (e.g., Westneat and Wainwright, 1989), while in other cases the lineage is able to diversify on a range of resources made accessible by the innovation (Duda et al. 2011). Thus, innovations lead to a range of outcomes from increased specialization on a resource that was already used, to a shift in resource



**Fig. 1.** Diagram illustrating the range of possible consequences of functional innovations on organismal performance and subsequent functional and ecological diversification. There is a potentially orthogonal relationship between the impact of innovations on the niche diversity of the lineage within which they arise and the magnitude of their performance enhancement. The capacity for an innovation to impact subsequent functional and ecological diversity depends on the adaptive landscape surrounding the niche that the innovation is a response to, but may not be a function of how strong the performance enhancement is.

use, which may allow subsequent ecological diversification. The potential for ecological diversification following innovation may require an adaptive landscape in which the strength of stabilizing selection around the novel resource is not so strong as to prevent populations from being drawn to nearby secondary peaks (Schluter 2000) otherwise it will result in specialization. The macroevolutionary impact of an innovation appears to be related to its ability to provide access to ecological opportunity (Simpson 1944; Liem 1973). Not all innovations with major impacts on performance will also open up considerable opportunity and lead to diversity. Indeed, even with the opportunity, subsequent diversification is not assured (Frazetta 1970; Vermeij 2001). The variation in macroevolutionary outcomes among instances of innovation deserves attention if we are to better understand how the evolution of organismal functional systems has impacted the history of life's diversification.

### Trade-offs

Ecological diversification depends on the potential for meaningful modifications of the innovation that confer performance changes that support the

ecological diversity. In general there is a strong expectation that functional diversity will underlie ecological diversity. It seems quite likely that innovations differ in their capacity for adaptive variation. This suggests that an important step in understanding the impacts of innovation is to explore consequences both for functional and ecological diversity. Trade-offs involved in the specific consequences of the functional novelties may result in the loss of considerable ecological opportunity even as new areas of the adaptive landscape are opened up. Inherent to the design of most functional systems is that some performance properties will be lost in trade-offs as other properties are enhanced (Walker 2007). Indeed, trade-offs are often credited with underlying ecomorphological patterns that are observed in nature, for example in bird wing shape (Norberg 1985), fish feeding systems (Wainwright and Bellwood 2002), or fish swimming systems (Langerhans 2008). The importance of trade-offs in shaping diversity implies that features of design that disrupt or limit the impact of trade-offs may have particularly important consequences for diversification. Complexity may permit considerable amelioration of the constraining impact of trade-offs (Wainwright 2007 ; Holzman et al. 2012).

Several recent studies have highlighted the potential for trade-offs to have a dramatic impact on diversification following the introduction of innovations (e.g. Higham et al. 2015; McGee et al. 2015). Often the constraining impact of the trade-off is overshadowed by the dramatic positive impacts of the innovation. An example is found in the impact of pharyngognathy, a well-studied major innovation of the pharyngeal jaws found in several major groups of teleost fishes, including cichlids, labrids, and damselfishes (Stiassny and Jensen 1987). Pharyngognathy involves a set of three modifications of the generalized pharyngeal jaw condition that results in a stronger and more robust bite: fusion of the left and right lower jaw bones into a single element, a muscular sling that suspends the lower jaw below the neurocranium, and well-developed joints between the underside of the neurocranium and upper pharyngeal jaw. Pharyngognathy has evolved several times independently within spiny-rayed fishes (Mabuchi et al. 2007; Wainwright et al. 2012) and is famously associated with trophic diversity (Liem and Osse 1975), particularly elevated rates of evolution of diets that involve tough or hard prey, such as plants, algae, and shelled invertebrates (McGee et al. 2015). However, pharyngognathy results in a restricted pharyngeal gape, which limits the size of prey that can readily pass posteriorly to the esophagus, and as a result

evolutionary transitions to a fish-eating diet occur at a lower rate in pharyngognathous lineages than other spiny-rayed fishes (McGee et al. 2015). Thus, while pharyngognathy opened up ecological opportunity in the form of diets that involve tough and hard prey, this came at the cost of diets that involve swallowing large whole prey.

Another example involves an insight where the constraining impact of the innovation becomes apparent when it is lost secondarily. Toe pads are a well-studied innovation independently evolved in geckos, anoles and some skinks. They allow lizard feet to cling to smooth flat vertical surfaces or even the underside of structures (Stewart and Higham 2014). The innovation has opened up a number of habitats to use by these lineages of lizards that are not as accessible to lizards without toe pads, including vertical rock surfaces, trees, and ceilings. Toe pads provide access to novel habitats but their presence may limit the diversity of locomotor kinematics in lineages with toe pads. This hypothesis was tested recently, by comparing the locomotor kinematics of a closely related group of African geckos, with several species that have lost the toe pads (Higham et al. 2015). These researchers found that the kinematic diversity of lineages that lack toe pads was greater than in the lineages with toe pads, and that rates of evolution of locomotor kinematics were higher in the lineages that had experienced secondary loss of toe pads (Higham et al. 2015). The results are consistent with the interpretation that toe pads constrain the evolution of locomotor kinematics and limit the ecological opportunity of lizards to habitats and lifestyles that capitalize on the toe pads.

### Studying macroevolutionary impacts of innovation

A phylogenetic approach allows researchers to test hypotheses about the impact of innovations on subsequent niche evolution, functional and ecological diversification. The phylogenetic distribution of an innovation can be used to estimate the history of the novelty and can form the basis of tests for comparisons of the rates of evolutionary change in functional morphology and ecology between lineages that possess the innovation and those that do not. When the innovation has evolved multiple times this approach can be used to identify whether there is a consistent evolutionary impact and if not, start to tease apart the influence of additional factors that promote or limit diversification. Additionally, if the innovation can be inferred within extinct lineages the inclusion of fossils within the phylogenetic framework enables the potentially obscuring effect of

extinction to be taken into account. The comparative approach is well suited to surveying the macroevolutionary impact of innovations to determine whether the trait has been associated with changes in niche, diversification, or increased specialization. Rather than focus on the total range of morphology and niches that evolves subsequent to the innovation we estimate the impact of the innovation on the diversification of functional morphology and potentially ecology. Examples are drawn from the feeding biology of labrid fishes using simple adaptive landscapes as described by Ornstein-Uhlenbeck models in a phylogenetic context (Hansen 1997; Beaulieu et al. 2013). Phylogenetic comparisons help control for the different amounts of time that groups have had to diversify since the origin of innovations and the effects of shared evolutionary history.

#### Case study: labrid innovations and rates of functional morphological evolution

Labridae is a group of about 600 species of predominantly reef fishes that includes the dominant lineages of diurnally active generalized invertebrate predators and benthic grazing herbivores on coral reef systems around the world. The group is renowned for its trophic diversity, with many well-studied functional innovations associated with shifts in trophic habits (Wainwright et al. 2004). We determined the macroevolutionary impact of five innovations on the evolutionary dynamics of the morphology of the oral and pharyngeal jaws of labrid fishes using evolutionary model-fitting. The choice of these five innovations, rather than other feeding innovations, was arbitrary, however they all are at least 5 million years old and allow us to illustrate a range of evolutionary outcomes using our approach. Each innovation is found within a single monophyletic group of labrids: (1) *Anampses*—share a unique combination of enlarged fleshy lips and large flattened anterior teeth that curve anteriorly. Species of *Anampses* feed mostly on small invertebrates that live in turf algae. The *Anampses* species within our dataset last shared a common ancestor approximately 11.5 million years ago. (2) *Choerodon*—share an enlarged set of caniniform teeth in the anterior part of the oral jaws that are used in gripping and removing attached invertebrate prey. The *Choerodon* species within our dataset last shared a common ancestor approximately 22.4 million years ago. (3) *Labroides*—share a unique split in middle of the lower lip that expose the mandibular teeth, allowing these fish to approach host fish at a very shallow angle as they swim over them searching

for the ectoparasites they remove. The *Labroides* species within our dataset last shared a common ancestor approximately 5.6 million years ago. (4) *Scarinae*—parrotfish share unique modifications of the pharyngeal jaw apparatus enabling them to pulverize the mixture of dead coral skeletons, algae, and assorted invertebrate and microbial organisms they ingest. The *Scarinae* species within our dataset last shared a common ancestor approximately 28.3 million years ago. (5) *Scarus/Chlorurus/Hipposcarus*—Members of this clade of parrotfishes share an intra-mandibular joint between the dentary and articular bones of their mandible (Bellwood 1994; Price et al. 2010), which is thought to permit more complex motions of the mandible (Konow et al. 2008). In our dataset the species within these three genera last shared a common ancestor approximately 16.2 million years ago.

We sought to quantify the impact of each innovation on diversification of functional morphological traits of the feeding mechanism. Morphological data from the feeding mechanism in 125 labrid species were taken from Wainwright et al. (2004) and consisted of: gape width, levator posterior (LP) muscle mass, stenochoideus (SH) muscle mass, adductor mandibulae (AM) muscle mass, premaxillary jaw protrusion, mouth-closing lever ratio, mouth-opening lever ratio, and the kinematic transmission coefficient of the oral jaws four-bar linkage (Jaw KT). We refer the reader to this previous work for a full discussion of the functional importance of these traits (Wainwright et al. 2004). One could imagine extending this study to also quantify the impact of each innovation on diversification of aspects of the feeding niche.

The five innovations vary in their inferred age and thus the amount of time the lineages have had to realize any subsequent diversification. Older innovations can be expected to have given rise to greater diversity, all else being equal. In order to separate the effects of time and evolutionary rate on subsequent macroevolutionary patterns, we analyzed the data by fitting four variants of the Ornstein-Uhlenbeck (OU) model. OU models describe trait evolution as an adaptive process pulled towards a primary optimum ( $\theta$ ), with the trait variance around the optimum determined by the strength of pull towards the optimum ( $\alpha$ ) and the stochastic rate ( $\sigma^2$ ) calculated as  $\sigma^2/2\alpha$  (Hansen 1997). The faster the rate and the weaker the strength of pull towards the optimum, the greater the expected disparity between closely related species. We fit one OU model that allowed the innovation to influence the primary optimum of the morphological trait (OUM, or multipeak) and

another fit a single optimum for each trait across all labrids (OU1). If there is no optimum shift or if the optimum shift moves randomly over time then there is no pull towards the peak ( $\alpha=0$ ) and the OU model collapses to Brownian motion (BM), which models trait evolution as a random walk with trait variance proportional to time. Two Brownian motion (BM) models were fit to each trait, one (BMS) allowed the innovation to influence the rate of morphological evolution ( $\sigma^2$ ) and the other fit a single rate across all labrids (BM1).

Using the maximum clade credibility tree from Kazancıoğlu et al. (2009) each innovation was mapped onto the phylogeny by assigning the “innovation” category to every internal branch related to the most recent common ancestor of the clade for which the innovation was a synapomorphy. All other branches were assigned to the “non-innovation” category. The four evolutionary models (BM1, BMS, OU1, and OUM) were fitted using the R package “OUwie” (Beaulieu et al. 2012). Preliminary analyses indicated that assuming  $\theta$ , the optimum, at the root is distributed according to the stationary distribution of the OU process helped to stabilize the estimates of  $\theta$  for all analyses, we therefore set `root.station=TRUE`. We checked the results of the OUwie analyses to ensure that the eigenvalues of the Hessian were positive, as this is an indicator that the parameters were reliably estimated (Beaulieu et al. 2012). When a negative value was found the results for that model and tree combination were removed from the data. We calculated the relative strength of the evidence for each model in the set using the Akaike Weight (Burnham and Anderson 2002) calculated from the Akaike Criterion corrected for small sample size (AICc, Hurvich and Tsai 1989).

To compare the impact of the innovations on the lineages’ potential to generate trait disparity, we calculated the ratio of rates ( $\sigma^2_{\text{innovation}} : \sigma^2_{\text{non-innovation}}$ ) from the multi-rate Brownian motion model. All else being equal, faster evolutionary rates generate greater disparity within a given time period. This parameter was chosen in preference to more simple measures of disparity, such as trait variance, and more complex measures, using OU models that allow  $\theta$ ,  $\alpha$  and  $\sigma^2$  to vary, as it provided a balance between the information within our limited sample size and the need to control for time and phylogeny. As some of the innovations had very low sample sizes, which reduces our power to estimate the three OU parameters, we calculated 95% confidence intervals around the BM rate ratio using parametric bootstrapping. We ran 1000 simulations for each innovation were generated

using the parameters from the two-rate model, the two-rate model was then re-fitted and the ratio  $\sigma^2_{\text{innovation}} : \sigma^2_{\text{non-innovation}}$  estimated.

## Results

According to the Akaike weights (Table 1) traits within each innovation are best-fit by a variety of models but over half the analyses run provide substantial support for the hypothesis that the innovation had no impact on the evolution of the trait, i.e., OU1 or BM1. However, given the small number of species possessing some of the innovations (see Fig. 2) the power to detect an influence of the innovation upon the trait will be low. Possibly because of this, only the innovations associated with the two largest clades (*Scarus/Chlorurus/Hipposcarus* and Scarinae) have substantial support for the two-rate BM model. This result is echoed by the estimates of the relative rate of morphological evolution (see Fig. 3): the only strong support for higher rates of morphological evolution being associated with innovations comes from these two larger clades and even then the levator posterior muscle mass evolves at significantly slower rates in the innovation clade. It should be noted that the influence of the pharyngeal innovations and the intra-mandibular joint innovations associated with these clades might not be independent. Our previous analyses of this dataset indicated that the higher rates found in Scarinae relative to the rest of the labrids may be the result of a trickle-down effect from the *Scarus*, *Chlorurus* and *Hipposcarus* clade (Price et al. 2010).

## Discussion

Our estimates of the consequences of five feeding innovations in labrid fishes for the rates of evolution of feeding functional morphology reveal what is likely a common pattern among innovations: many innovations do not lead to an elevated rate of subsequent diversification. There may be considerable obstacles to the realization of enhanced functional morphological diversification following assembly of an innovation. In many cases, the innovation itself may represent an adaptation to a specific niche. For example, the unusual split in the lower lip of *Labroides* allows these fish to bring their teeth into close proximity of the surface of fish that they swim over, while searching for ectoparasites (Baliga and Mehta 2015). While the split lip may enhance ectoparasite cleaning, the ecological landscape around this trophic niche may not provide many opportunities for further specialization or diversification.

**Table 1.** Results from model fitting for oral jaw traits in several groups of labrid fishes that possess feeding innovations. Best model fits are indicated in bold font.

Innovation	Trait	1-rate BM AICc weight	2-rate BM AICc weight	1-optimum OU AICc weight	2-optimum OU AICc weight
Anampses	jawclosingleverratio	<b>0.3899</b>	0.1501	0.3336	0.1264
Anampses	jawkt	0.0000	0.0000	0.1454	<b>0.8546</b>
Anampses	jawopeningleverratio	0.0000	0.0000	0.2571	<b>0.7428</b>
Anampses	log cuberootAM	0.0005	0.0002	<b>0.6683</b>	0.3310
Anampses	log cuberootlp	<b>0.3592</b>	<b>0.3723</b>	0.1952	0.0734
Anampses	log cuberootsh	0.0000	0.0004	<b>0.7044</b>	0.2953
Anampses	log gape	0.4057	0.1426	<b>0.2058</b>	<b>0.2459</b>
Anampses	log protrusion	0.0000	0.0000	<b>0.6760</b>	0.3240
Choerodon	jawclosingleverratio	<b>0.3411</b>	0.2597	0.2918	0.1074
Choerodon	jawkt	0.0000	0.0000	<b>0.5841</b>	0.4158
Choerodon	jawopeningleverratio	0.0001	0.0001	<b>0.7176</b>	0.2822
Choerodon	log cuberootAM	0.0005	0.0002	<b>0.6815</b>	0.3177
Choerodon	log cuberootlp	0.3232	<b>0.4080</b>	0.1757	0.0931
Choerodon	log cuberootsh	0.0000	0.0000	0.3750	0.6249
Choerodon	log gape	<b>0.4703</b>	0.1710	0.2386	0.1202
Choerodon	log protrusion	0.0000	0.0000	0.3523	0.6477
Labroides	jawclosingleverratio	<b>0.3838</b>	0.1671	0.3284	0.1208
Labroides	jawkt	0.0000	0.0000	0.4569	0.5431
Labroides	jawopeningleverratio	0.0001	0.0000	0.6502	0.3497
Labroides	log cuberootAM	0.0005	0.0003	0.5884	0.4108
Labroides	log cuberootlp	<b>0.3765</b>	0.1688	0.2046	0.2501
Labroides	log cuberootsh	0.0000	0.0000	0.3430	<b>0.6570</b>
Labroides	log gape	<b>0.4857</b>	0.1745	0.2464	0.0934
Labroides	log protrusion	0.0000	0.0000	<b>0.6910</b>	0.3090
Scaridae	jawclosingleverratio	0.0000	<b>0.9942</b>	0.0000	0.0058
Scaridae	jawkt	0.0000	0.0000	<b>0.7256</b>	0.2743
Scaridae	jawopeningleverratio	0.0000	<b>0.5661</b>	0.2933	0.1405
Scaridae	log cuberootAM	0.0006	0.0006	<b>0.7367</b>	0.2621
Scaridae	log cuberootlp	0.0035	<b>0.9937</b>	0.0019	0.0009
Scaridae	log cuberootsh	0.0000	0.0000	0.1030	<b>0.8969</b>
Scaridae	log gape	<b>0.4476</b>	0.1662	0.2271	0.1591
Scaridae	log protrusion	0.0000	<b>0.5509</b>	0.0043	0.4448
Scarus/Chlorurus/Hipposcarus	jawclosingleverratio	0.0000	<b>0.9996</b>	0.0000	0.0004
Scarus/Chlorurus/Hipposcarus	jawkt	0.0000	0.0008	<b>0.6593</b>	0.3398
Scarus/Chlorurus/Hipposcarus	jawopeningleverratio	0.0000	<b>0.9929</b>	0.0002	0.0068
Scarus/Chlorurus/Hipposcarus	log cuberootAM	0.0006	0.0054	<b>0.7288</b>	0.2652
Scarus/Chlorurus/Hipposcarus	log cuberootlp	0.0081	<b>0.9858</b>	0.0044	0.0016
Scarus/Chlorurus/Hipposcarus	log cuberootsh	0.0000	0.0000	0.2353	<b>0.7647</b>
Scarus/Chlorurus/Hipposcarus	log gape	<b>0.4606</b>	0.2005	0.2336	0.1052
Scarus/Chlorurus/Hipposcarus	log protrusion	0.0000	0.0423	<b>0.6989</b>	0.2588

These analyses also highlight some of the issues when investigating the evolutionary impacts of an innovation and in particular the problem of taxon sampling and power. Several of the important

functional innovations within labrids have evolved only once in a clade with very few extant species, therefore we cannot rule out the possibility that the lack of a subsequent shift in peak or rate following

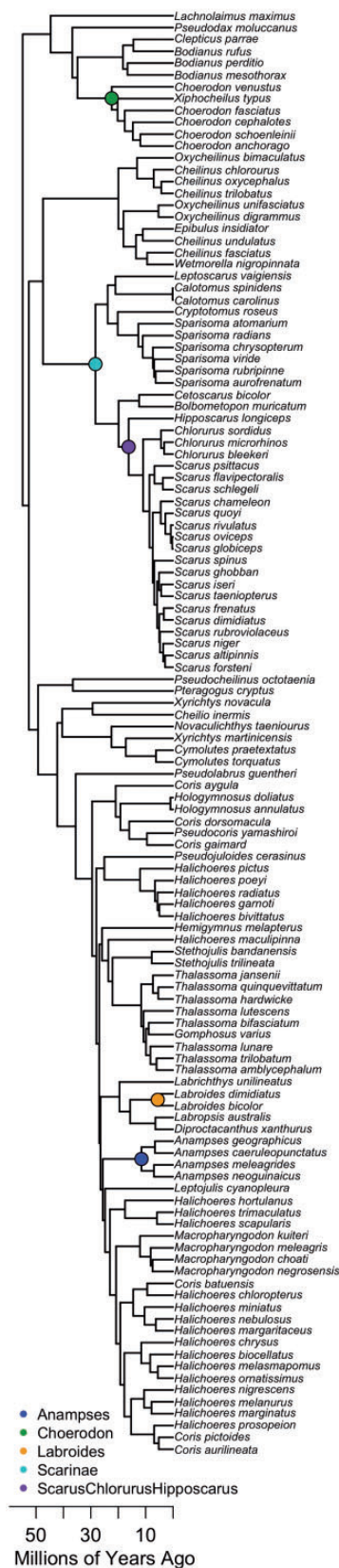
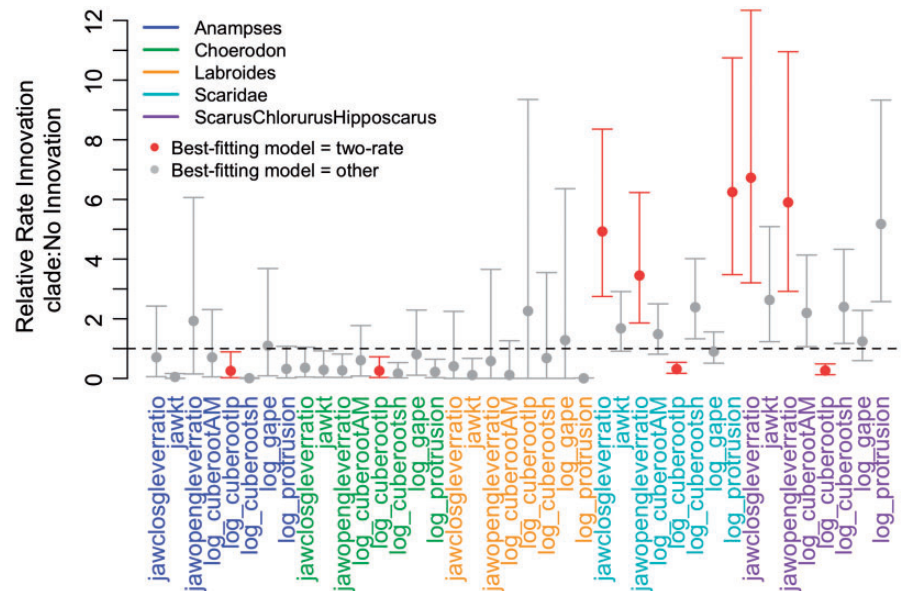


Fig. 2. Phylogenetic relationships among labrid fishes indicating the inferred origin of the five innovations to the feeding mechanism discussed in the text. Phylogeny is taken from Price et al. 2010.

the innovation may be due to low statistical power to detect such a change. It will always be difficult to unambiguously determine whether innovations found in a limited number of species resulted in diversification or specialization (although see Nunn and Zhu 2014). However, as morphological disparity and lineage diversity can be evolutionarily decoupled (e.g., Derryberry et al. 2011) it is still possible to identify instances of specialization following innovation as illustrated by the parrotfishes. Our previous analyses show that faster rates of evolution found within Scarinae (Fig. 3) are an artifact; they are the result of a trickle-down effect from the more recently evolved second innovation, the intramandibular joint within the *Scarus/Chlorurus/Hipposcarus* clade (Price et al. 2010). When the parrotfishes with the second innovation are excluded, lineages with only the pharyngeal jaw innovation show slower rates of oral jaw evolution than non-scarine labrids. While the modified pharyngeal jaw is crucial to their ability to feed on the overgrowth of exposed benthic substrates, and within this *Scarus/Chlorurus/Hipposcarus* clade is associated with elevated rates of functional morphological evolution, the stabilizing selection surrounding this niche appears to be very strong, as no parrotfish lineages appear to stray from benthic herbivory and detritivory.

Parrotfishes with an intramandibular joint (*Scarus/Chlorurus/Hipposcarus* clade) exhibit higher rates of evolution of jaw functional morphology than other labrids. Thus, this innovation leads to enhanced evolutionary diversification of functional morphology. This result presents something of a paradox, however, because while the novel joint is thought to substantially change the functional morphology of the jaws and represent a substantial innovation for a benthic grazing fish (Konow et al. 2008), there is not known to be any substantial ecological diversification within this group. Parrotfish in this group differ from most other groups by mostly feed on microbes and detritus that colonize recently disturbed hard surfaces on reefs (as opposed to feeding on turf algae and epiphytes). Although one lineage within this group shows enhanced oral jaw strength and they are known to take deep gouging bites compared to the superficial scraping bites of other species (Bellwood and Choat, 1990), other axes of ecological diversity that correspond to jaw mechanics have not been recognized. In this case, it appears that the innovation—a novel joint in the mandible—facilitates further mechanical modification of the feeding apparatus, which may or may not further enhance performance. This group of parrotfish is species-rich and is thought to have undergone a





**Fig. 3.** Results of estimates of evolutionary rate changes in feeding traits following each of five innovations to the labrid feeding mechanism. The y-axis depicts the ratio of the rate of evolution of the trait in the group with the innovation versus all other labrids. Hence, a value greater than one indicates a higher rate in the group with the innovation. Only the values shown in red represent transitions where the best fitting model supports different rates in the two regimes. See also Price et al. 2010.

shift in speciation rate (Alfaro et al. 2009) but any ecological basis for this diversity has yet to be discovered and thus may be driven by sexual selection (Kazancıoğlu et al. 2009). Perhaps the *Scarus/Chlorurus/Hipposcarus* parrotfish clade represents an ecological adaptive peak that has fostered considerable functional diversification that is mostly neutral with respect to its implications for diet. This would represent a novel model for adaptive radiation of functional morphology as it is unclear how natural selection has driven the changes in jaw mechanics under a mostly constant feeding niche. It is possible that elevated rates of morphological evolution in this clade represent a release of constraint on the traits necessary for suction feeding, although this should apply to all Scarinae (Price et al. 2010).

## Conclusion

Innovations may lead to an increased ability to use specific resources and ecological specialization, or they may lead to ecological diversification as the lineage with the innovation ascends multiple adaptive peaks made accessible by the performance enhancement. The difference between specialization and adaptive radiation may lie in the nature of the interaction between the adaptive landscape surrounding the new resource, the innovation's consequence for performance and related functional trade-offs.

Both the proximity of nearby adaptive peaks and secondary factors that promote access of those peaks may be important. Such factors might include interactions with other community members and the presence of sufficient phenotypic variation to allow the drawing influence of these secondary adaptive peaks. The potential for subsequent diversification is not likely to be a direct target of selection, suggesting that the link between innovation and diversification is complex and depends on the alignment of many factors.

The idea that a functional innovation can impact subsequent functional and ecological diversification is a cornerstone of macroevolutionary thinking. But it is important that innovations be tested for their impact. It seems likely that most innovations lead to increased specialization rather than functional diversification. More must be learned about the conditions under which innovations stimulate diversification versus specialization and the extent to which intrinsic properties of functional design limit or expand the macroevolutionary potential of life's innovations.

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