**LETTER**

## Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes

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### Abstract

Although coral reefs are renowned biodiversity hotspots it is not known whether they also promote the evolution of exceptional ecomorphological diversity. We investigated this question by analysing a large functional morphological dataset of trophic characters within Labridae, a highly diverse group of fishes. Using an analysis that accounts for species relationships, the time available for diversification and model uncertainty we show that coral reef species have evolved functional morphological diversity twice as fast as non-reef species. In addition, coral reef species occupy 68.6% more trophic morphospace than non-reef species. Our results suggest that coral reef habitats promote the evolution of both trophic novelty and morphological diversity within fishes. Thus, the preservation of coral reefs is necessary, not only to safeguard current biological diversity but also to conserve the underlying mechanisms that can produce functional diversity in future.

### INTRODUCTION

Understanding the origination and maintenance of global biodiversity is a core challenge in ecology, evolution and conservation science. In the marine biome, coral reefs are hotspots of species richness and endemism, with the 10 richest reefs accounting for between 44 and 54% of restricted-range marine species (Roberts *et al.* 2002). Coral reefs are particularly important for global vertebrate diversity as they harbour the greatest species richness of fishes on earth (Harmelin-Vivien 2002), with up to 1000 species coexisting within a single location (Bellwood *et al.* 2005). Coral reefs are also thought to be epicentres of speciation for fishes and other organisms; palaeontological data show that throughout the Palaeozoic the origination of marine genera is the fastest on biogenic reefs and that reefs have consistently exported diversity to other marine ecosystems (Kiessling *et al.* 2010). Similarly, a recent phylogenetic analysis of extant tetraodontiform fishes has revealed that there are increased rates of speciation in reef-associated clades, compared with non-reef relatives (Alfaro *et al.* 2007). These findings suggest that the study of coral reefs can play a critical role in the elucidation of the evolutionary and ecological dynamics that promote diversification and ensure ecosystem function.

Coral reefs are highly productive habitats (Fraser & Currie 1996), supported by a high flux of prey and nutrients from the surrounding oceans (Genin *et al.* 2009).In addition, the physical complexity of reefs provides topological and hydrodynamic diversity (e.g. Monismith 2006; Reidenbach *et al.* 2009). These mechanisms create a rich environment for niche partitioning and specialization, which is generally expected to increase the number of species that can stably co-exist (MacArthur & Levins 1964; Schoener 1974) and also potentially promote the evolution of morphological, functional and ecological diversity and novelty. We therefore predict that coral reefs will drive elevated rates of evolution in traits that underlie niche variation. Functional and eco-morphological diversity are vital in the identification of hotspots of biological diversity as they play a critical role in ensuring ecosystem function (e.g. Raymundo

*et al.* 2009) and future adaptability (Erwin 1991). In addition to the mechanisms of character displacement and ecological opportunity that may promote speciation and morphological diversification, the accumulation of taxonomic diversity on reefs may also potentially be driven by alternate mechanisms such as sexual selection. Thus, taxonomic diversity, which is far easier to measure, may not always be a useful proxy for functional diversity (see Devictor *et al.* 2010). Therefore, unless ecomorphological diversity is directly quantified and compared across habitats in a phylogenetic context we cannot determine if coral reefs promote the evolution of greater functional diversity. To the best of our knowledge no studies have so far attempted to address this question of whether functional ecomorphological diversity and novelty accumulate faster within coral reefs than in other tropical ecosystems.

The radiation of labrid fishes (Labridae: wrasses, weed-whitings and parrotfishes) is well suited to test the effects of coral reefs on ecological diversification because members of this group live in a diverse array of environments: including tropical shallow-water coral reefs, seagrass beds and temperate rocky reefs. Labridae consists of *c.* 600 species (Parenti & Randall 2000) and are characteristic of coral reef fish faunas around the world (Bellwood & Wainwright 2002). Labrids first appear in the fossil record around 50 million years ago (see Bellwood 1996) although recent fossil calibrations of molecular phylogenies suggest they may have originated up to 70 million years ago (Kazancioglu *et al.* 2009). Whether labrids originated on coral reefs is unclear but current phylogenetic and fossil evidence suggests that they are more likely to have a temperate deep-water origin (as reviewed by Bellwood & Wainwright 2002). The distribution of coral reef-associated species upon the phylogeny indicates that there have been multiple transitions to each habitat (see Fig. 1 for one possible history of reef living in labrids).

Functional morphological diversity is expected to have profound implications for ecological diversity, as the organization of morphological systems shape and constrain an organism's ability to perform tasks related to resource use and reproductive success. This is particularly apparent in coral reef fishes where the trophic guild is
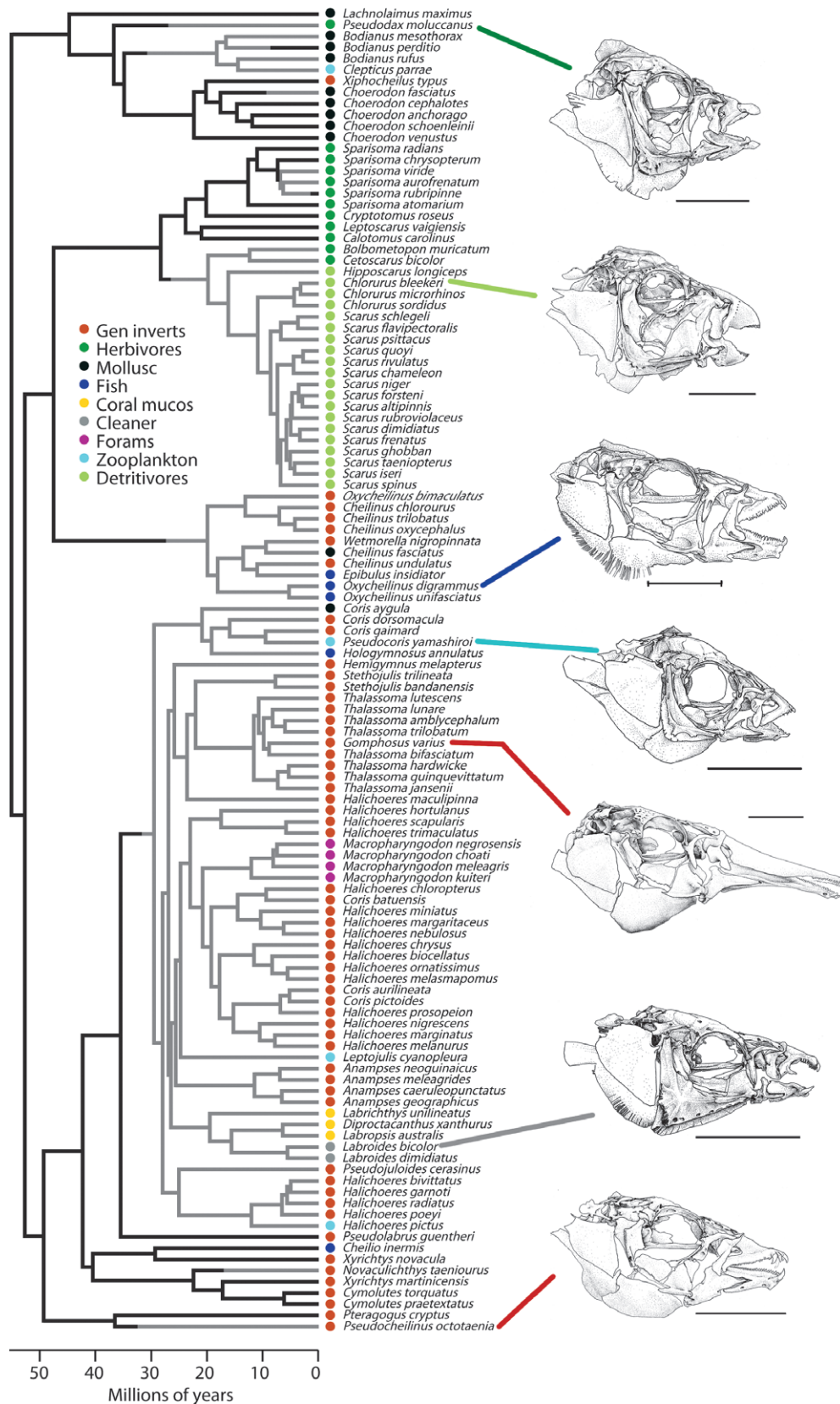
**Figure 1** A time-calibrated phylogeny of labrids (from Kazancioglu *et al.* 2009) with a single possible map of habitat (coral reefs in grey and non-reef in black) generated through stochastic character mapping using SIMMAP (Bollback 2006). Coloured circles at the tips of the tree indicate each species' diet. This habitat mapping illustrates a non-reef origin for labrids as it is the most common root state within the 500 character histories we generated and is in agreement with fossil information (Bellwood & Wainwright 2002). Diagrams illustrating the morphological diversity of the labrid feeding apparatus are also shown across the phylogeny, the scale bars are all 10 mm in length.

strongly influenced by the mechanics of the feeding apparatus (Wainwright & Bellwood 2002). Labrids are trophically diverse, ranging from generalist invertebrate predators to piscivores, molluscivores, planktivores, polychaete specialists, coral-mucous feeders, ectoparasite cleaners, herbivores and detritivores (Randall 1967), which is reflected in the interspecific variation of the feeding structures (Wainwright 1988; Wainwright *et al.* 2004; see Fig. 1). Patterns of prey use are constrained by the trade-offs resulting from the mechanics of jaws, for example the lever system that governs jaw motion can be modified for speed or force but not both, thus causing a trade-off between strength and speed of the bite and, thus, attached and elusive prey (Wainwright *et al.* 2004). If coral reefs also drive trophic novelty, as might be predicted by the abundance and diversity of possible prey items on reefs, we expect to find coral reef-specific trophic strategies, which should be reflected in the exploration of new regions of morphospace.

In this study we test the hypotheses that morphological diversity and trophic novelty are evolving at a higher rate in species associated with coral reefs than in tropical non-reef species, using labrid fishes as a case study. This is a global comparison of reef and non-reef tropical labrids, thus reef and non-reef species do not form a community assemblage in a single specific geographic location. We calculate the worldwide accumulation of disparity in coral reef and non-reef habitats in an evolutionary context. We do this because the diversity observed within a habitat is not simply a function of differential rates of morphological evolution; it is also dependent on the evolutionary history of the taxon and its association with the habitat. The age of the association between the habitat and its community is particularly important, as under a Brownian motion (BM) model, trait disparity is expected to accumulate in proportion to time. For each habitat we estimate the BM rate of morphological evolution across the traits mapped onto the phylogeny, which is a time- and phylogeny-corrected estimate of disparity (see Hutcheon & Garland 2004; O'Meara *et al.* 2006). We also perform a second analysis to determine if the observed rate changes are also associated with the occupation of novel morphospace by projecting the phylogeny into the morphospace (phylomorphospace *sensu* Sidlauskas 2007). We found that coral reef labrids exhibit faster rates of functional ecomorphological evolution and occupy more trophic morphospace than tropical non-reef labrids. This suggests that coral reefs promote the evolution of both morphological diversity and ecological novelty in fishes.

## METHODS

### Morphological data

We characterized the functional diversity of jaw mechanics across labrids, using species averages of eight musculoskeletal traits, which are part of the principal systems involved in prey capture, biting, suction feeding, jaw depression and handling of prey by the pharyngeal jaws (as described in Wainwright *et al.* 2004; Collar *et al.* 2008). The traits were three muscle masses, adductor mandibulae, levator posterior and sternohyoideus muscle, which primarily power the biting by the oral jaws, processing by the pharyngeal jaws and buccal expansion during suction feeding, respectively. Mouth-opening and -closing lever ratios, which contribute to bite force and velocity, premaxillary protrusion distance and gape, are integral to determining suction-feeding performance. Finally, kinematic transmission coefficient of the oral jaws four-bar linkage effects hyoid motion and the

expansion of the buccal cavity. Measurements of all eight traits were available for 122 species (34 parrotfishes and 88 wrasses) represented in the Kazancioglu *et al.* (2009) time-calibrated phylogeny, which is used throughout the article. However, we removed four species (*Calatomus spinidens*, *Scarus oviceps*, *S. globiceps* and *Hologymnus doliatus*) to ensure that no two species diverged more recently than 1 million years ago as very recent divergences can bias the calculation of the general evolutionary rate, especially if there is any measurement error (Martins 1994).

To ensure that the magnitude of character change was unrelated to the trait value (larger changes are less likely when trait values are small) we log transformed all linear measurements. Masses were cube-root transformed prior to log transformation so that all non-ratio traits were on a linear scale. Our initial analyses indicated that all morphological traits had a strong association with size but there was no evidence of strong clade-specific allometric differences or grade-shifts. We therefore calculated size-corrected values for all traits across labrids using the phylogenetic methods outlined by Revell (2009). We then conducted a phylogenetic principal components analysis (following Revell 2009) to create orthogonal characters. We performed all dataset manipulations and statistics in the R software environment for statistical computing (R Development Core Team 2008) using the ape (Paradis *et al.* 2004) and geiger (Harmon *et al.* 2008) phylogenetic packages.

### Dietary data

We compiled dietary data using literature reports as a guide (Randall 1967; Wainwright 1988; Bellwood *et al.* 2006). As each source varied in the number and description of dietary categories, we created nine categories that we felt captured the most variation in primary prey type. These were: general invertebrate eater, molluscivore, piscivore, zooplanktivore, ectoparasite eater, coral-mucous eater, herbivore, detritivore and foraminiferan specialist.

### Reconstructing 'coral reef' living

The purpose of this study is to compare the rates of morphological evolution in coral reef and non-reef-dwelling species and since coral reefs only occur in the tropics, temperate species were excluded. We assigned each species to either a 'coral reef' (CR) or 'non-coral reef' (NCR) habitat based on published information (e.g. Randall 2005) and field observations by PCW and RH at several locations in the Caribbean, Indo-Pacific and the Red Sea. Species are qualified as coral reef fishes only if they are intimately associated with coral reefs, feeding and taking refuge on coral reefs. Many of the species in our study live in habitats that are adjacent to coral reefs, such as sandy plains and seagrass (e.g. *Xyrichtys* and *Cryptotomus* respectively); we classified these as non-coral reef.

We used stochastic character mapping (Huelsenbeck *et al.* 2003 and references therein) to sample possible histories of coral reef living in proportion to their posterior probability, as implemented in the program SIMMAP V1.0 (Bollback 2006). SIMMAP uses a symmetrical β prior on the morphological state frequencies; the shape of the distribution is described by the α parameter, which is discretized using κ categories. As α becomes larger the distribution forms a narrower peak around a state frequency of 0.5, very large α values give equal prior probabilities for each state. We used a smaller α value (α = 5 and κ = 19) to give a broad peak, which allowed the possibility of reconstructing a reef as well

as non-reef origin of the Labridae. We then sampled 500 character histories in proportion to their posterior probability and integrated the parameter estimates over these sampled histories (following Collar *et al.* 2009) and calculated standard errors (SE). Unlike parsimony or maximum likelihood methods of ancestral state reconstruction these 500 character maps allow us to incorporate the uncertainty associated with the timing of the transitions between the coral reef and non-reef habitats into our parameter estimates and SE.

## Trophic novelty

To calculate the amount of unique morphospace occupied by reef and non-reef species we used a bivariate plot of the phylogenetically corrected principal components analysis for the first two PC axes (which account for *c.* 50% of the total morphological disparity, see Table 1) and created two minimum convex polygons using the aspace package in R (Builung & Remmel 2008). These two polygons represent the amount of morphospace occupied by coral reef species and non-reef species, respectively. We then created a third polygon using the co-ordinates of all labrids, which represents the total morphospace occupied by all labrids. Finally, we calculated the percentage of morphospace within PC1 and PC2 that was unique to each habitat relative to the total area occupied by all labrids. We also compared the number of unique dietary categories that evolved in each habitat.

## Evolutionary rates

There are many ways to estimate morphological diversity (see review by Ciampaglio *et al.* 2001). In the phylogenetic context it is frequently measured as the rate parameter from a BM model of phenotypic evolution (see Hutcheon & Garland 2004; O'Meara *et al.* 2006; Thomas *et al.* 2006): the faster the Brownian rate the more morphological diversity is generated per unit of time. Therefore, we chose to estimate the rate of morphological evolution in coral reef and non-reef fishes using a BM model of evolution. We do not include Ornstein-Uhlenbeck (OU) models, which are a BM model with a selection parameter that

pulls the traits towards one or more optima (Butler & King 2004 and references therein). Our hypotheses predict differing rates of evolution in coral reef and non-reef fishes and current implementations of OU models only allow the location of the optima to vary while the BM rate and selection parameters are kept the same. In addition, we do not expect coral reef fishes to share a single-optimal morphology, as they are trophically and functionally diverse, ranging from coral scrapers to planktivores. However, for completeness we do repeat the analyses in an OU framework in Data S1.

We estimated the maximum likelihood Brownian rate parameter for each PC axis on the time-calibrated phylogeny of Kazancioglu *et al.* (2009) across the 500 stochastic maps using code written by Liam Revell (available from http://anolis.oeb.harvard.edu/~liam/R-phylogenetics/) based on O'Meara *et al.* (2006) and implemented in the statistical software R (R Development Core Team 2008). In the first model we fit a single Brownian rate of morphological evolution across the whole tree, representing the same rate of morphological evolution for coral reef and non-reef-associated fishes. In the second model we fit a two-rate model, allowing species living on coral reefs to evolve at different rates to those that do not live on reefs. We assessed the fit of the one and two-rate BM models using the modified Akaike Information Criterion (AICc) that takes into account small sample sizes (Hurvich & Tsai 1989), this is a function of the likelihood of the data given the model, the number of parameters in the model and the size of the sample. The lower the AICc value the better the fit. To integrate over uncertainty in the history of coral reef living we calculated the difference in the average AICc scores across the 500 character histories to select the best fitting model for each PC axis. A ΔAICc value of two or more was taken as an indication of support for one model over the other following Burnham & Anderson (2002). The SE of the rate estimate includes the variance due to uncertainty in the history of coral reef living using the 500 character maps and the variance due to the likelihood surface taken from the Hessian.

We also calculated AICc weights from the mean AICc scores; these describe the proportion of support a model receives in relation to support for all models (Burnham & Anderson 2002). We then

**Table 1** Principal component analysis: loadings and percentage variance from the phylogenetic PCA

| | Trait | pc1 | pc2 | pc3 | pc4 | pc5 | pc6 | pc7 | pc8 |
|---|---|---|---|---|---|---|---|---|---|
| Full dataset | Gape | 0.353 | −0.572 | 0.215 | −0.028 | −0.696 | 0.027 | 0.092 | −0.094 |
| | Protrusion | 0.549 | 0.104 | −0.686 | 0.245 | −0.057 | 0.279 | −0.127 | −0.244 |
| | AM mass | 0.766 | 0.041 | 0.259 | −0.259 | 0.175 | −0.34 | −0.217 | −0.291 |
| | SH mass | 0.809 | 0.061 | −0.179 | 0.243 | −0.103 | −0.23 | −0.117 | 0.417 |
| | LP mass | 0.742 | −0.103 | −0.103 | −0.41 | 0.238 | 0.149 | 0.421 | 0.066 |
| | Jaw closing | 0.139 | 0.731 | 0.201 | −0.449 | −0.265 | 0.292 | −0.194 | 0.107 |
| | Jaw opening | 0.077 | 0.825 | 0.088 | 0.324 | −0.196 | −0.2 | 0.322 | −0.137 |
| | Jaw KT | −0.455 | 0.057 | −0.634 | −0.48 | −0.223 | −0.327 | 0.027 | 0.001 |
| | % variance | 30.6 | 19.6 | 13.5 | 11.1 | 9.3 | 6.3 | 5.1 | 4.5 |
| Novel feeding strategies removed | Gape | 0.367 | 0.203 | 0.669 | −0.450 | −0.405 | −0.085 | 0.065 | 0.010 |
| | Protrusion | 0.380 | 0.187 | −0.763 | −0.304 | −0.220 | −0.229 | −0.180 | 0.111 |
| | AM mass | 0.782 | 0.085 | 0.208 | 0.406 | −0.032 | 0.258 | −0.223 | 0.237 |
| | SH mass | 0.768 | 0.152 | −0.278 | −0.280 | 0.036 | 0.424 | 0.089 | −0.204 |
| | LP mass | 0.784 | 0.132 | −0.093 | 0.320 | 0.064 | −0.255 | 0.431 | 0.041 |
| | Jaw closing | 0.401 | −0.750 | −0.021 | 0.355 | −0.278 | −0.119 | −0.135 | −0.203 |
| | Jaw opening | −0.079 | −0.876 | −0.123 | −0.305 | −0.046 | 0.174 | 0.215 | 0.199 |
| | Jaw KT | −0.652 | 0.309 | −0.257 | 0.366 | −0.441 | 0.227 | 0.179 | 0.014 |
| | % variance | 33.6 | 19.4 | 15.5 | 12.4 | 6.2 | 5.8 | 4.7 | 2.4 |

calculated the average BM rate parameter for coral reef and non-reef fishes across both one and two-rate models weighted by the AICc weights. This model-averaging approach incorporates uncertainty about model choice as well as the ancestral habitat into the parameter estimate. We calculated SE on the model-averaged results using the methods outlined in Burnham & Anderson (2002).

We re-ran these analyses on a subset of the original dataset, which excluded species with dietary strategies that only appear on coral reefs (ectoparasite feeding, coral-mucous eating, detritivory, planktivory and foraminferan specialists). This allowed us to investigate whether any increase in rate on coral reefs was purely driven by the adaptation to novel feeding niches or if there may be other processes promoting morphological diversification, such as increased niche partitioning. We also repeated the analyses excluding the genera *Scarus*, *Hipposcarus* and *Chlorurus*. This clade has previously been shown to have much faster rates of oral jaw evolution compared to other labrids (Price *et al.* 2010) and we wanted to ensure they were not driving our results (see Data S2).

Finally, to ensure that the prevalence of shallow nodes in the coral reef clades (see Fig. 1) was not artificially elevating the estimated rates of morphological evolution due to the overestimation of the rate parameter over short time scales we ran two analyses. To assess the probability of Type I errors due to the structure of the tree, we first simulated 100 traits on the phylogeny under a single-rate BM model and then repeated our analyses with the 500 stochastic character maps to see if we could recover faster rates of evolution on coral reefs. Recovery of significantly faster rates on coral reefs using the simulated dataset would indicate a significant effect of the shorter node heights. The second was a rarefaction analysis in which we sub-sampled coral reef clades in a phylogenetically over-dispersed manner. This analysis consisted of 500 mapped trees, each with an equal number of reef and non-reef species (42 species in total). The 500 trees were selected so that the mean time spent in reef and non-reef states was equal, thus reducing the shallowness of the nodes (see Data S3 for details).

## RESULTS

### Principal components analysis

The amount of variance explained and the morphological traits that the PC axes load heavily onto are remarkably consistent between the full dataset and the subset that excludes all coral reef species with novel feeding strategies (see Table 1). PC1 is the primary axis of morphological variation after correcting for body size and explains *c.* 30% of the total variance. It is a synthetic measure of morphological variability in labrids as all three muscle masses: adductor mandibulae, levator posterior, sternohyoideus, as well as gape, jaw protrusion and jaw linkage kinematic transmission are all highly correlated with PC1. PC2 explains *c.* 20% of the variance and loads heavily onto the two traits in the dataset not included in PC1: jaw opening and closing lever ratios along with gape. The first four PC axes together explain *c.* 75% of the total variance.

### Dietary diversity & trophic novelty

The morphospace of PC1 vs. PC2 (Fig. 2), with each species point joined by the phylogeny and coloured with respect to dietary category and habitat, illustrates that coral reef species occupy more functional morphospace than non-reef species. The area of the minimum convex polygons that delimit the morphospace represented in PC1 and PC2 by coral reef and non-coral reef species reveals that 68.6% of the total morphospace occupied by tropical labrids is unique to reef species while only 4% is unique to non-reef species. Within tropical labrids there are five dietary strategies unique to species that live on coral reefs, including the detritivorous strategy employed by most parrotfishes as well as the less common strategies of planktivory, coral-mucous, ectoparasite (cleaning) and foraminiferan specialism. There is a partial connection between morphological diversity and the occurrence of trophic novelty in coral reef-dwelling labrids as the five novel dietary categories account for 25% of the morphospace unique to coral reef fishes. There is no dietary strategy unique to tropical non-reef species; they are mainly molluscivores and general invertebrate eaters with a few piscivores and herbivores.

### Rates of morphological evolution

The results are summarized as model-averaged rates for reef and non-reef taxa with SE (see Fig. 3 and Table 2) as well as means and SE across the 500 character histories for the one and two-rate models separately (see Table 2). All eight PC axes evolve faster in coral reef-associated fishes according to the model-averaged rates. Using model selection PC1, PC4 and PC7 are best fit by a two-rate model ($\Delta$AICc 7.8, 2.3 and 9.1 respectively), support for one- and two-rate models is
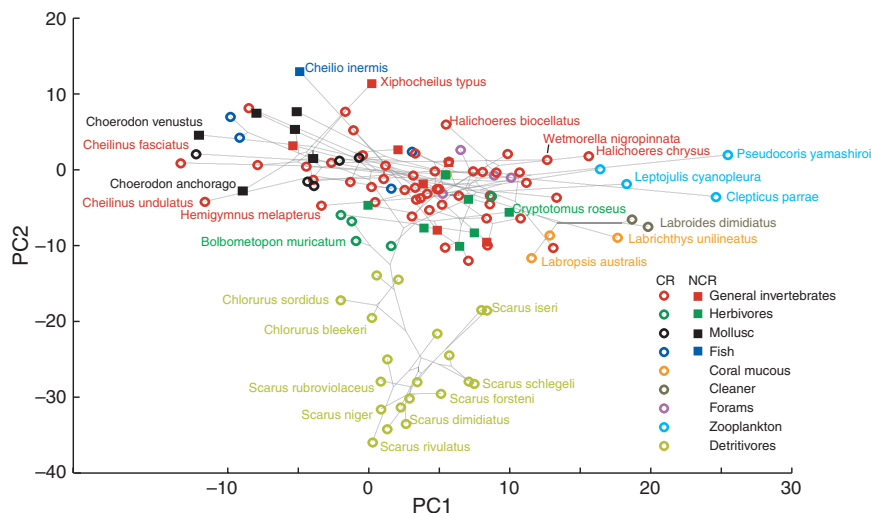


**Figure 2** A morphospace of all 118 labrids that superimposes the branching patterns of the phylogeny (light grey lines) on the plot of the first two PC axes from the phylogenetic PCA. Species are coloured with respect to their dietary category and the shape indicates whether they live on coral reefs (circles) or not (squares).
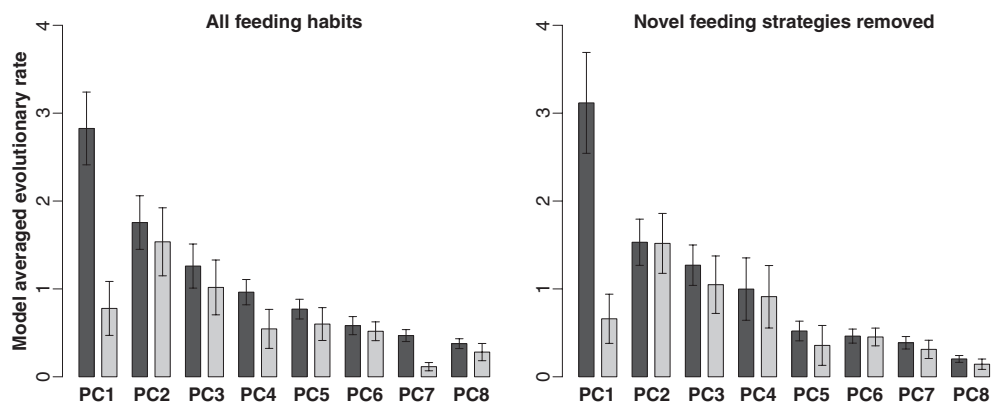
**Figure 3** Model-averaged rates of ecomorphological evolution for coral reef (black bars) and non-coral reef (grey bars) labrids. Data includes all PC axes of the complete dataset (a) and the dataset which excludes the novel trophic strategies (b). Rates of evolution are the fastest on coral reefs for all morphological axes, however, in a model selection framework only PC1, PC4 and PC7 have strong support ($\Delta$AICc > 2) for the two-rate Brownian model in the complete dataset. Data are model-averaged estimates of the Brownian motion rate parameters with standard errors from a set of 500 character maps of reef/non-reef habitat.

**Table 2** Model fitting and model parameters from the one- and two-rate Brownian motion models

| | | One-rate model | | | | Two-rate model | | | | | Model averaged | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Log likelihood | BM rate ± SE | $\Delta$AICc | AICc weight | Log likelihood | Coral reef Brownian rate ± SE | Non-reef Brownian rate ± SE | $\Delta$AICc | AICc weight | Coral reef Brownian rate ± SE | Non-reef Brownian rate ± SE |
| Full dataset | PC1 | −115.93 | 2.43 ± 0.32 | 7.83 | 0.02 | −110.86 | 2.83 ± 0.41 | 0.74 ± 0.28 | 0 | 0.98 | 2.83 ± 0.41 | 0.78 ± 0.3 |
| | PC2 | −89.74 | 1.56 ± 0.20 | 0 | 0.66 | −89.23 | 1.654 ± 0.24 | 1.16 ± 0.39 | 1.31 | 0.44 | 1.75 ± 0.3 | 1.54 ± 0.38 |
| | PC3 | −67.4 | 1.07 ± 0.14 | 0 | 0.58 | −66.54 | 1.15 ± 0.17 | 0.72 ± 0.24 | 0.61 | 0.56 | 1.26 ± 0.25 | 1.02 ± 0.31 |
| | PC4 | −56.34 | 0.89 ± 0.12 | 2.33 | 0.24 | −54.02 | 0.99 ± 0.14 | 0.44 ± 0.15 | 0 | 0.76 | 0.96 ± 0.14 | 0.55 ± 0.22 |
| | PC5 | −45.61 | 0.74 ± 0.10 | 0.01 | 0.5 | −44.45 | 0.80 ± 0.12 | 0.46 ± 0.15 | 0 | 0.5 | 0.77 ± 0.11 | 0.6 ± 0.18 |
| | PC6 | −22.38 | 0.50 ± 0.07 | 0 | 0.68 | −21.99 | 0.52 ± 0.08 | 0.39 ± 0.13 | 1.55 | 0.46 | 0.58 ± 0.1 | 0.52 ± 0.1 |
| | PC7 | −9.72 | 0.401 ± 0.05 | 9.13 | 0.01 | −3.99 | 0.47 ± 0.07 | 0.11 ± 0.05 | 0 | 0.99 | 0.47 ± 0.06 | 0.11 ± 0.04 |
| | PC8 | −2.99 | 0.358 ± 0.05 | 0.3 | 0.46 | −1.97 | 0.39 ± 0.06 | 0.22 ± 0.08 | 0 | 0.54 | 0.38 ± 0.05 | 0.28 ± 0.09 |
| Novel feeding strategies removed | PC1 | −80.6 | 2.65 ± 0.44 | 8.29 | 0.02 | −75.29 | 3.13 ± 0.57 | 0.63 ± 0.25 | 0 | 0.98 | 3.12 ± 0.57 | 0.66 ± 0.28 |
| | PC2 | −60.49 | 1.53 ± 0.25 | 0 | 0.75 | −60.45 | 1.54 ± 0.29 | 1.49 ± 0.57 | 2.24 | 0.25 | 1.53 ± 0.26 | 1.52 ± 0.34 |
| | PC3 | −52.38 | 1.22 ± 0.20 | 0 | 0.59 | −51.6 | 1.34 ± 0.25 | 0.79 ± 0.31 | 0.76 | 0.41 | 1.27 ± 0.23 | 1.05 ± 0.32 |
| | PC4 | −44.29 | 0.98 ± 0.16 | 0 | 0.7 | −43.97 | 1.04 ± 0.19 | 0.75 ± 0.29 | 1.68 | 0.3 | 1 ± 0.35 | 0.91 ± 0.35 |
| | PC5 | −18.66 | 0.49 ± 0.08 | 0.35 | 0.46 | −17.32 | 0.55 ± 0.11 | 0.25 ± 0.11 | 0 | 0.54 | 0.52 ± 0.11 | 0.36 ± 0.22 |
| | PC6 | −16.72 | 0.46 ± 0.08 | 0 | 0.75 | −16.67 | 0.47 ± 0.09 | 0.43 ± 0.16 | 2.23 | 0.25 | 0.46 ± 0.08 | 0.45 ± 0.1 |
| | PC7 | −8.83 | 0.37 ± 0.06 | 0 | 0.59 | −8.02 | 0.41 ± 0.08 | 0.23 ± 0.10 | 0.71 | 0.41 | 0.39 ± 0.07 | 0.31 ± 0.1 |
| | PC8 | 15.56 | 0.190 ± 0.04 | 0.22 | 0.47 | 16.83 | 0.22 ± 0.04 | 0.1 ± 0.04 | 0 | 0.53 | 0.2 ± 0.04 | 0.14 ± 0.06 |

Summary of model fit comparisons and rate parameter estimates averaged across the 500 sampled histories of reef living for the full dataset and a subset that excludes novel feeding strategies found upon reefs. Standard errors (SE) for the one- (1 d.f.) and two-rate models (2 d.f.) are also given. Model-averaged rate parameters were calculated as average Brownian motion rate parameter for coral reef and non-reef fishes across both one- and two-rate models weighted by the AICc weights, SE were calculated following Burnham & Anderson (2002).

equivalent across all other PC axes (see Table 2). Overall, the weighted average rate of morphological evolution over all eight axes is 2.2 times faster on reefs relative to non-reefs. Analyses of the data subsets that removed species with dietary strategies unique to coral reef environments or a clade of parrotfishes that had previously been shown to have elevated rates of morphological evolution (Price *et al.* 2010) gave similar results, most PC axes evolve faster in coral reef species (see Data S3).

There is also no indication that shallow nodes in the coral reef clades are strongly elevating the estimated rates of morphological evolution. The dataset simulated under a single-rate Brownian model yielded similar rates on and off reefs with only a very slight bias towards overestimating reef rates and the rarefaction analysis estimated faster rates on coral reefs (see Data S3 for details).

Furthermore, the rarefaction analysis also confirms that although the maximum likelihood rate estimator is known to estimate rates that are too low when sample sizes are small (see O'Meara *et al.* 2006) it was not driving our results, as the estimated rate is faster in CR fishes when equal numbers of reef and non-reef species are sampled.

Finally, it should be noted that like all model fitting analyses these results are only as accurate as the *a priori* models tested, thus we cannot rule out that another unknown evolutionary model is not a better fit to the labrid morphological data.

## DISCUSSION

Our data indicate that within the highly diverse Labridae, coral reef species exhibit faster rates of trophic ecomorphological evolution and

occupy more trophic morphospace than tropical non-reef fishes. Some of the morphological diversity in the feeding apparatus of coral reef labrids can be explained by adaptation to novel niches; of the 68.6% of labrid morphospace that is unique to coral reef species 25% of it is associated with trophic strategies only found on reefs. However, even when trophic strategies unique to reefs are removed, coral reef species still exhibit higher rates of morphological evolution. This result suggests that coral reef habitats promote the evolution of both trophic novelty and morphological diversity within these fishes perhaps due to the ecological, as well as the physical complexity within coral reef ecosystems.

The high productivity of coral reefs (Fraser & Currie 1996) is expected to play an important role in the evolution of ecomorphological diversity. The variety and abundance of potential prey is likely to promote both diversity and novelty within the feeding apparatus of reef fishes and other coral reef organisms, as species adapt to new prey items. This is illustrated by the two clades of labrids that have evolved to exploit corals; the herbivorous/detritivorous parrotfishes (*Scarus* and their relatives) and the coral-mucous eating tubelip wrasses exploit this resource in very different ways as illustrated by their position in the morphospace (Fig. 2). Parrotfishes share a unique set of modifications of the pharyngeal jaw that allow them to grind coral skeletons (Gobalet 1989) to extract the algae, infaunal invertebrates and detritus that colonize the skeletons of dead corals, and some species have evolved beak-like jaws that enable efficient scraping and excavating of dead coral. In contrast, the tubelip wrasses have evolved to eat mucous from the surface of living corals, although they do damage the surface to elicit the secretion of mucous by using sharp raptorial teeth that wound the soft external surface of the coral.

Furthermore the greater variety and abundance of prey items as well as a broader spectrum of prey size on coral reefs may promote niche partitioning, even within a single trophic strategy. For example the closely related coral reef taxa *Cheilinus undulatus* and *Wetmorella nigropinnata* are both general invertebrate eaters but they have very different functional morphologies (see Fig. 2) and diets. The first functional difference is size, which can have a huge effect on diet even when jaw mechanics are similar (Wainwright 1988); *C. undulatus* is an extremely large wrasse weighing *c.* 28 kg while *W. nigropinnata* is tiny, weighing *c.* 4 g. In addition, PC1 reveals that even after taking into account differences in body mass *C. undulatus* still has large muscle masses and protrusion, while *W. nigropinnata* has smaller muscle masses and shorter protrusion for its size. These differences are associated with distinct feeding strategies; *C. undulatus* primarily feeds on non-evasive hard-shelled prey which requires modification for force while *W. nigropinnata* feeds on approximately equal amounts of evasive soft-shelled and non-evasive hard-shelled prey (Westneat 1995) which requires a more versatile functional morphology. This example illustrates how niche partitioning can occur within a single dietary category.

The physical complexity of coral reefs may also contribute to elevated rates of morphological evolution. It has been shown that, at least within tropical marine environments around the Virgin islands, coral reefs are the most structurally complex habitat (Gratwicke & Speight 2005). As total niche space increases with structural complexity, niche partitioning is expected to be higher on coral reefs, promoting species co-existence (MacArthur & Levins 1964; Schoener 1974). It is well-known that species richness and diversity within coral reefs increases with habitat complexity (Risk 1972; Luckhurst & Luckhurst 1978). We also expect structurally complex coral reefs to promote morphological diversity within ecologically important traits

involved in niche partitioning, such as those in this study involved with prey capture and processing. It has been found that, within fish assemblages in a Neotropical floodplain river, morphological diversity is the highest in the most complex habitats (Willis *et al.* 2005) but this was not examined in a phylogenetic context and little is known about morphological diversity on coral reefs.

There are a variety of additional factors that may also lead to different rates of functional morphological evolution in coral reef and non-reef habitats. Intrinsic biological traits such as increased genetic diversity or innovations (Vermeij 1973) may promote morphological diversification on reefs. Though we do show that the two key innovations identified in a previous study as promoting morphological diversification in the jaws of a small clade of parrotfishes (Price *et al.* 2010) do not drive the results reported here (see Data S2). Finally, functional constraints on the feeding morphology of non-reef fishes may lead to the appearance of faster rates of evolution in coral reef species.

Coral reefs are one of the most diverse ecosystems on earth and yet we know little about the evolutionary and ecological mechanisms that generate or maintain such spectacular diversity. Our results suggest that coral reefs are not only hotspots of taxonomic diversity but are also centres of morphological diversification: functional morphological diversity evolves faster in labrids on coral reefs than in other tropical environments. Within labrids the diversity on coral reefs is at least partially due to the occupation of novel regions of morphospace but even when species with novel feeding ecologies were omitted from the analysis, reef lineages still showed faster morphological diversification. These results are perhaps driven by the ecological opportunities provided by high abundance and variety of prey items endemic to coral reefs and imply that habitat complexity, in terms of physical and biological diversity, can lead to elevated rates of morphological evolution within trophic structures. We predict that habitat complexity should drive similar patterns of functional ecomorphological diversity in other coral reef taxa, except those that exploit very narrow niches both on and off coral reefs. If our predictions are correct, the preservation of coral reefs is necessary, not only for safeguarding current biological diversity, but also for conserving the mechanisms that can generate future functional diversity and allow future adaptability in the face of global change.

## REFERENCES

Alfaro, M., Santini, F. & Brock, C.D. (2007). Do reefs drive diversification in marine teleosts? Evidence from the pufferfishes and their allies (order Tetraodontiformes). *Evolution*, 61, 2104–2126.

Bellwood, D.R. (1996). The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblages. *Coral Reefs*, 15, 11–19.

Bellwood, D.R. & Wainwright, P.C. (2002). The history and biogeography of fishes in coral reefs. In: *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (ed. Sale, P.F.). Academic Press, Boston, pp. 5–32.

Bellwood, D.R., Hughes, T.P., Connolly, S.R. & Tanner, J. (2005). Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecol. Lett.*, 8, 643–651.

Bellwood, D.R., Hughes, T.P. & Hoey, A.S. (2006). Sleeping functional group drives coral reef recovery. *Curr. Biol.*, 16, 2434–2439.

Bollback, J.P. (2006). SIMMAP: stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics*, 7, 88.

Builung, R.N. & Remmel, T. (2008). Open source, spatial analysis, and activity travel behaviour research: capabilities of the aspace package. *J. Geogr. Syst.*, 10, 191–216.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information Theoretic Approach*, 2nd edn. Springer-Verlag, New York.

Butler, M.A. & King, A.A. (2004). Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.*, 164, 683–695.

Ciampaglio, C.N., Kemp, M. & McShea, D.W. (2001). Detecting changes in morphospace occupation patterns in the fossil record: characterization and analysis of measures of disparity. *Paleobiology*, 27, 695–715.

Collar, D.C., Wainwright, P.C. & Alfaro, M. (2008). Integrated diversification of locomotion and feeding in labrid fishes. *Biol. Lett.*, 4, 84–86.

Collar, D.C., O'Meara, B.C., Wainwright, P.C. & Near, T.J. (2009). Piscivory limits diversification of feeding morphology in Centrarchid fishes. *Evolution*, 63, 1557–1573.

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W. & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.*, 13, 1030–1040.

Erwin, T.L. (1991). An evolutionary basis for conservation strategies. *Science*, 253, 750–752.

Fraser, R.H. & Currie, D.J. (1996). The species richness-energy hypothesis in a system where historical factors are thought to prevail – coral reefs. *Am. Nat.*, 148, 138–159.

Genin, A., Monismith, S.G., Reidenbach, M.A., Yahel, G. & Koseff, J.R. (2009). Intense benthic grazing of phytoplankton in a coral reef. *Limnol. Oceanogr.*, 54, 938–951.

Gobalet, K.W. (1989). Morphology of the parrotfish pharyngeal jaw apparatus. *Am. Zool.*, 29, 319–331.

Gratwicke, B. & Speight, M.R. (2005). The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J. Fish Biol.*, 66, 650–667.

Harmelin-Vivien, M.L. (2002). Energetics and fish diversity on coral reefs. In: *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (ed. Sale, P.F.). Academic Press, Boston, pp. 265–274.

Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. (2008). GEIGER: investigating evolutionary radiations. *Bioinformatics*, 24, 129–131.

Huelsenbeck, J.P., Nielsen, R. & Bollback, J.P. (2003). Stochastic mapping of morphological characters. *Syst. Biol.*, 52, 131–158.

Hurvich, C.M. & Tsai, C.-L. (1989). Regression and time series model selection in small samples. *Biometrika*, 76, 297–307.

Hutcheon, J.M. & Garland, T. (2004). Are megabats big? *J. Mamm. Evol.*, 22, 257–277.

Kazancioglu, E., Near, T.J., Hanel, R. & Wainwright, P.C. (2009). Influence of sexual selection and feeding functional morphology on diversification rate of parrotfishes (Scaridae). *Proc. R. Soc. Lond. Ser. B*, 276, 3439–3446.

Kiessling, W., Simpson, C. & Foote, M. (2010). Reefs as cradles of evolution and sources of biodiversity in the Phanerozoic. *Science*, 327, 196–198.

Luckhurst, B.E. & Luckhurst, K. (1978). Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol.*, 49, 317–323.

MacArthur, R.H. & Levins, R. (1964). Competition, habitat selection, and character displacement in a patchy environment. *Proc. Natl Acad. Sci.*, 51, 1207–1210.

Martins, E.P. (1994). Estimating the rate of phenotypic evolution from comparative data. *Am. Nat.*, 144, 193–209.

Monismith, S.G. (2006). Hydrodynamics of coral reefs. *Annu. Rev. Fluid Mech.*, 39, 37–55.

O'Meara, B.C., Ane, C., Sanderson, M.J. & Wainwright, P.C. (2006). Testing for different rates of continuous trait evolution using likelihood. *Evolution*, 60, 922–933.

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.

Parenti, P. & Randall, J.E. (2000). An annotated checklist of the species of the labroid fish families Labridae and Scaridae. *Ichthyol. Bull. J.L.B. Smith Inst. Ichthyol.*, 68, 1–97.

Price, S.A., Wainwright, P.C., Bellwood, D.R., Kazancioglu, E., Collar, D.C. & Near, T.J. (2010). Functional innovations and morphological diversification in parrotfishes. *Evolution*, 64, 3057–3068.

R Development Core Team. (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at: http://www.R-project.org. Last accessed: 2 March 2011.

Randall, J.E. (1967). Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.*, 5, 655–847.

Randall, J.E. (2005). *Reef and Shore Fishes of the South Pacific. New Caledonia to Tahiti and the Pitcairn Islands*. University of Hawaii Press, Honolulu.

Raymundo, L.J., Halford, A.R., Maypa, A.P. & Kerr, A.M. (2009). Functionally diverse reef-fish communities ameliorate coral disease. *Proc. Natl Acad. Sci.*, 106, 17067–17070.

Reidenbach, M.A., Koseff, J.R. & Koehl, M.A.R. (2009). Hydrodynamic forces on larvae affect their settlement on coral reefs in turbulent, wave-driven flow. *Limnol. Oceanogr.*, 54, 318–330.

Revell, L. (2009). Size-correction and principal components for interspecific comparative studies. *Evolution*, 63, 3258–3268.

Risk, M.J. (1972). Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.*, 153, 1–6.

Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E. *et al.* (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, 295, 1280–1284.

Schoener, T.W. (1974). Resource partitioning in ecological communities. *Science*, 185, 27–39.

Sidlauskas, B.L. (2007). Testing for unequal rates of morphological diversification in the absence of a detailed phylogeny: a case study from characiform fishes. *Evolution*, 61, 299–316.

Thomas, G.H., Freckleton, R.P. & Székely, T. (2006). Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proc. R. Soc. Lond. Ser. B*, 273, 1619–1624.

Vermeij, G.J. (1973). Adaptation, versatility, and evolution. *Systematic Zoology*, 22, 466–477.

Wainwright, P.C. (1988). Morphology and ecology: the functional basis of feeding constraints in Caribbean labrid fishes. *Ecology*, 69, 635–645.

Wainwright, P.C. & Bellwood, D.R. (2002). Ecomorphology of feeding in coral reef fishes. In: *Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem* (ed. Sale, P.F.). Academic Press, Boston, pp. 33–56.

Wainwright, P.C., Bellwood, D.R., Westneat, M.W., Grubich, J.R. & Hoey, A.S. (2004). A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. *Biol. J. Linn. Soc.*, 82, 1–25.

Westneat, M.W. (1995). Feeding function and phylogeny: analysis of historical biomechanics in labrid fishes using comparative methods. *Syst. Biol.*, 44, 361–383.

Willis, S.C., Winemiller, K.O. & Lopez-Fernandez, H. (2005). Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river. *Oecologia*, 142, 284–295.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Data S1** Re-analysis in an Ornstein-Uhlenbeck framework.
**Data S2** Re-analysis removing the rapidly evolving *Scarus*, *Chlorurus* and *Hipposcarus* clade.
**Data S3** Effects of shallow nodes on the estimated rate of morphological evolution.

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