

LETTER

Diversification and functional evolution of reef fish feeding guilds

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Abstract

A core eco-evolutionary aim is to better understand the factors driving the diversification of functions in ecosystems. Using phylogenetic, trophic, and functional information, we tested whether trophic habits (i.e. feeding guilds) affect lineage and functional diversification in two major radiations of reef fishes. Our results from wrasses (Labridae) and damselfishes (Pomacentridae) do not fully support the ‘dead-end’ hypothesis that specialisation leads to reduce speciation rates because the tempo of lineage diversification did not substantially vary among guilds in both fish families. Our findings also demonstrate a tight relationship between trophic habits and functional roles held by fish in reef ecosystems, which is not associated with a variation in the tempo of functional diversification among guilds. By illustrating the pivotal importance of the generalist feeding strategy during the evolutionary history of reef fishes, our study emphasises the role of this feeding guild as a reservoir for future diversity.

Keywords

Coral reef fish, ecological diversity, evolutionary rate, functional diversity, functional ecology, Labridae, Pomacentridae, trait evolution, versatility.

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INTRODUCTION

Evolutionary shifts in ecological attributes within a given lineage have long been thought to impact the pattern of diversification across the Tree of Life (Simpson 1944; Schluter 2000). According to the theory of adaptive radiation, the emergence of a novel trait – which allows the exploitation of untapped resources – may favour lineages’ radiation (Schluter 2000), and promote diversification and disparification (e.g. Near *et al.* 2012; Frédérick *et al.* 2014). However, an ecological specialisation (i.e. the use of a narrow range of resources) may also generate adverse effects by constraining changes along other axes of diversity and limiting evolvability (e.g. Buckling *et al.* 2003; Collar *et al.* 2009).

Since specialist organisms are designated as the ‘great losers’ of past and current global changes (Devictor *et al.* 2008), a growing number of studies focused on assessing evolutionary trends that underlie the generation of specialisation. Among others, two main hypotheses have emerged: (1) the ‘dead-end’ hypothesis that specialisation leads to reduced speciation and increased extinction risk (Simpson 1944; Colles *et al.* 2009), and (2) the ‘generalist-to-specialist’ hypothesis that generalists should produce specialists while the reverse is unlikely (Futuyma & Moreno 1988; Schluter 2000). In addition, some works have started to question the relationship between environmental niche specialisation (defined by a set of conditions such as temperature, precipitations, oxygen saturation) and rates of evolution in predicting the evolution of species’ distribution facing environmental changes (Smith &

Beaulieu 2009; Fisher-Reid *et al.* 2012; Litsios *et al.* 2012; Bonetti & Wiens 2014; Chejanovski & Wiens 2014; Gómez-Rodríguez *et al.* 2015).

Defining the degree of specialisation may be challenging as it depends on the context and variables used. For instance, the habitat of one marine fish could be quantified by various environmental variables (e.g. temperature, salinity) or a description of the landscape (e.g. seagrass bed, coral reef). Moreover, the importance of a given resource may also vary across species’ ontogeny, which can affect the degree of specialisation by restraining the use of the specialist-generalist binary categorisation (Devictor *et al.* 2010). To overcome these issues, grouping species according to their similar use of environmental resources [i.e. guilds (Blondel 2003)] may appear more suitable. Feeding guilds reflect traits related to diet and trophic interactions, and they have been largely used as a synonym for functional groups that represent clusters of species performing analogous ecosystem functions (Blondel 2003; Bellwood *et al.* 2004). Yet, this synonymy has often impaired a deeper understanding of the association between diet and other ecological attributes, which are part of the functional diversity and depict species’ ecosystem functions and life strategies (Rosenfeld 2002; Villéger *et al.* 2008). For example trophic evolution (i.e. a shift between two feeding guilds) is one major driver of lineage diversification (Price *et al.* 2012; Lobato *et al.* 2014) and phenotypic evolution (Frédérick *et al.* 2013; Fabre *et al.* 2016), but its effects on functional diversity remain to be explicitly tested. Little is known about how species’ ecological attributes affect

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functional diversification, albeit some studies have highlighted a link between phylogenetic diversity and ecosystem functioning (Cadotte *et al.* 2009; Srivastava *et al.* 2012). Overall, a specialisation along the trophic axis may impact the evolution of functions by (a) limiting trophic reversal and (b) impeding the diversification in the rest of the functional space and restraining the number of functional roles, which could ultimately result in an ecosystem functional vulnerability.

Here, we provide a quantitative macroevolutionary analysis of the tempo of functional evolution in two major radiations of reef fishes: the wrasses (Labridae) and the damselfishes (Pomacentridae). By combining time-calibrated phylogenies, functional data sets and phylogenetic comparative analyses, we assess the evolutionary conservatism of functional traits and test whether dietary preferences affect lineage and functional diversification in both families. Specifically, we first aim to test the 'dead-end' hypothesis that more specialised feeding guilds show reduced speciation rates and increased extinction risk. Then, under the prediction that a specialisation along the trophic axis may impact the evolution of fish functions, we expect to find variation in the (1) transition rates and (2) tempo of functional evolution as well as in the levels of functional diversity among feeding guilds.

MATERIALS AND METHODS

Trophic and functional data set

We compiled dietary data for 315 wrasses and 200 damselfishes at their adult stage mainly from Floeter *et al.* (2018), Baliga & Law (2016) and Frédérick *et al.* (2013) (Table S1). The evolution of feeding modes in Labridae was first explored by Cowman *et al.* (2009), and a recent update of this work was provided by Floeter *et al.* (2018). Four major feeding categories were used for Labridae: benthic feeders (i.e. herbivory, detritivory and foraminiferan specialists), generalist carnivores (i.e. vagile and sessile invertebrate eaters and molluscivory), pelagic feeders (i.e. piscivory and zooplanktivory) and tiny biters (i.e. ectoparasite eaters and coral-mucous eaters). For Pomacentridae, we assigned each species to one of three commonly recognised feeding guilds (Frédérick *et al.* 2009, 2016; Gajdzik *et al.* 2016): pelagic feeders picking zooplankton, benthic feeders grazing filamentous algae, and an intermediate group including species feeding on small invertebrates and algae in variable proportions.

To grasp the functional diversity of reef fish, we collected functional data about the habitat, mobility, foraging, reproduction and defence for 156 wrasses and 200 damselfishes included in time-trees, which, respectively, represent 28 and 48% of the total number of species in each family (Table S1). These data were collected with an approach utilising primary scientific articles and online databases, and they were summarised into categorical traits. The six chosen functional traits contained information on body size, habitat affinity (i.e. maximum depth, water column position, habitat substratum and intensity of wave exposure) and physiology of reproduction (i.e. sex change). In addition to these six functional traits, we were able to collect information about two more traits for damselfishes: farming behaviour as well as group type and

territoriality. Categories and eco-functional relevance for each trait are detailed in Supporting Information. All these traits were recognised as of primary importance for describing the functional ecology of fishes (Villéger *et al.* 2017) and have already been used to study global and local patterns of fish functional diversity (Mouillot *et al.* 2013, 2014; Gajdzik *et al.* 2018).

Species richness and functional diversity

Under the hypothesis that trophic specialisation influences diversification and functional evolution, species richness and functional diversity are expected to vary among feeding guilds. For both families, species richness was appraised with the number of species assigned to each feeding guild. Functional diversity of each guild was estimated with two indices: functional entity (FE) and functional richness (FR). The set of functional traits and their respective number of categories produce a theoretical number of 2120 and 15, 120 unique combinations of these trait values (FEs) for Labridae and Pomacentridae respectively. The 156 wrasses filled in 138 FEs in total distributed in the four trophic guilds, whereas the 200 damselfishes corresponded to 154 FEs in total distributed in the three main trophic groups. For each guild, functional richness (FR) was measured as the volume inside the convex hull shaping all species.

To create the functional space, we calculated the functional distance between all pairs of fish species from each data set (i.e. the functional data set of Labridae and the one of Pomacentridae) using the Gower's metric. Then, we applied a Principal Coordinates Analysis (PCoA) on this distance matrix (Mouillot *et al.* 2014). As stressed by the quality test performed with the *quality_funct_space* function (Maire *et al.* 2015), we used species' coordinates on the first five and six principal axes of the PCoA through our analyses for Labridae and Pomacentridae respectively. Functional spaces were computed using the *MultidimFD* function (Villéger *et al.* 2008; Mouillot *et al.* 2013; Maire *et al.* 2015) in R.

Phylogenies, ancestral state reconstruction and stochastic mapping

We examined the tempo of diversification in Labridae and Pomacentridae, both families having a good phylogenetic resolution. The time-calibrated phylogenies of wrasses from Baliga & Law (2016) and the chronograms of damselfishes from Frédérick *et al.* (2013) were used throughout this work. These multigene phylogenies included 320 and 208 species of Labridae and Pomacentridae respectively (i.e. 50-55% of nominal species for each family). From the Bayesian posterior distribution generated by BEAST (version 1.8) (Drummond & Rambaut 2007), we randomly sampled 100 trees that we used throughout the study as a way of including uncertainty in tree topology and branch length into our phylogenetic comparative analyses.

Stochastic character mapping (Huelsenbeck *et al.* 2003) was used to infer possible trophic histories. It was produced using the function *make.simmap* in the R-package PHYTOOLS (version 0.6.60) (Revell 2012). One hundred character maps were simulated for each sampled tree, resulting in 10 000

trophic histories for each family. For the parameterisation of *make.simmap*, we used the estimated ancestral state and a fixed value of transition matrix (Q) from the best model for our empirical data. To assess the best model for the Q matrix, we fitted a model with an equal rate of transition between states and a model with all rates different using the function *ace* in the R-package *APE* (version 4.1) (Paradis *et al.* 2004). The likelihood of these two models was then compared using a likelihood ratio test, which suggested the use of unequal rates for trophic evolution in both fish families (see Results). Posterior probabilities of ancestral states, the statistics of transitions between trophic states and number of shifts per unit of time were retrieved using functions in *PHYTOOLS*.

Models of trophic transitions and lineage diversification rates

In order to test the ‘dead-end’ hypothesis that specialisation leads to reduced speciation and increased extinction risk (Simpson 1944), we explored the relationship between feeding guild evolution and lineage diversification by comparing the fit of ten evolutionary models using a maximum-likelihood approach from the ‘Multiple State Speciation Extinction’ (MuSSE) method (Maddison *et al.* 2007; FitzJohn *et al.* 2009). MuSSE is an extension of the ‘Binary State Speciation Extinction’ – BiSSE maximum likelihood-based test described in Maddison *et al.* (2007) and FitzJohn *et al.* (2009). These models allowed rates of speciation, extinction and transition between feeding guilds to be either independent of trophic state (rates to be equal across all strategies) or constrained by trophic state (separate rates for each strategy). In addition, in order to widen our modelling, we considered the generalist carnivores of wrasses and the intermediate group of damselfishes as generalist guilds. Although these two guilds are not analogous in their feeding preferences, they both include species feeding on food sources from the entire benthic-pelagic compartment (Westneat 1994; Frédérix *et al.* 2016). On the other hand, the other guilds are more specialised in their dietary habits as they mainly feed in one of the two compartments (i.e. either benthic or pelagic). This simplified classification allowed us to constrain the rates according to the specialist or generalist status.

The link between feeding guild evolution and lineage diversification was first investigated with MuSSE because this is the only method allowing the exploration of state-dependent lineage diversification rates between more than two groups. However, some issues with this approach have been recently raised (Maddison & Fitzjohn 2015; Rabosky & Goldberg 2015), and thus we further explored this relationship in a simplified framework using the ‘Hidden State Speciation and Extinction’ (HiSSE) method (Beaulieu & O’Meara 2016). For these comparative analyses, species were grouped into only two guilds: the generalists (i.e. species feeding on both benthic and pelagic food sources) and the specialists (i.e. grouping all specialist guilds of each family). In this comparative framework, we compared ten two-state character-dependent and -independent diversification models. These BiSSE/HiSSE models differed by (1) the presence/absence of hidden states in the guild of generalists and the group of all specialists and (2) the

constrained or unconstrained net turnover rates, extinction fractions and transition rates.

We used the R-packages *DIVERSITREE* (version 0.9.10) (FitzJohn 2012) and *HiSSE* (version 1.8.5) (Beaulieu & O’Meara 2016) to compare the fit of the ten different MuSSE and HiSSE/BiSSE models respectively. In these analyses, we assumed that the missing species are randomly distributed on phylogenetic trees. Acknowledging that trophic data on some missing species are unavailable and that feeding habits may vary within genera, we assumed that the addition of missing species would not modify the proportion of species within each guild. The fit of models was compared using Akaike’s Information Criterion (AIC) scores and weights (Burnham & Anderson 2002). A Δ AIC value of four or more was taken as an indication of support for one model over the others (Burnham & Anderson 2002). To examine the uncertainty in the parameter estimates, the best-fitting MuSSE model from the maximum-likelihood analysis was analysed using Bayesian Markov Chain Monte Carlo (MCMC) methods.

Functional dissimilarity and functional diversification

Under the prediction that trophic specialisation influences the type and diversity of functions, we expect feeding guilds to differ in their functional diversity and tempo of functional evolution. Divergence in the occupancy of the portions of the total functional space was tested using the index of functional dissimilarity (Villéger *et al.* 2011). It was performed on the three-dimensional functional space with the R source code ‘*multidimFbetaD.R*’ made available by S. Villéger. The higher the values of this index (closer to one than zero), the more it implies a high degree of functional dissimilarity among guilds (Villéger *et al.* 2011). In addition, we performed phylogenetic Procrustes ANOVA to test any divergence in the occupancy of the functional space among trophic guilds using the function *procD.pgls* in the R-Package *GEOMORPH* (version 3.0.5) (Adams & Otárola-Castillo 2013). To test whether the evolutionary rate of functional traits varied among feeding guilds, we estimated the multivariate evolutionary rate (σ^2_{mult}) of functional diversification for each guild and compared them using the function *compare.evol.rates* from the R-package *GEOMORPH* with 10^5 iterations. Since it is based on distances rather than covariances, this test was proven to be highly efficient for describing evolution occurring in a multivariate-trait space (Adams 2014b).

In addition to these tests, we also attempted to describe the conservatism of functions across phylogenetic histories. One commonly expected evolutionary corollary is that closely related species co-occur more often in the niche space because of their shared environmental tolerances. This outcome may result in a higher phylogenetic structure, indicative of some phylogenetic conservatism. It is usually estimated with a test of phylogenetic signal, which corresponds to the degree of phylogenetic dependency of a given character (Blomberg & Garland 2002). We used all five and six dimensions of the functional space into the function *physignal* from the R-package *GEOMORPH* for Labridae and Pomacentridae respectively. This test was done with 10^5 iterations. Similar to the interpretation of Blomberg’s K (Blomberg *et al.* 2003; Adams 2014a), a $K_{\text{mult}} = 1$ indicates a strong phylogenetic signal that

perfectly follows Brownian motion. A K_{mult} value > 1 means a stronger resemblance of closely related species in functional trait values than expected under a Brownian motion model, whereas a value < 1 suggests a greater lability of trait values and a departure from a strong phylogenetic signal.

RESULTS

Feeding strategies are not evenly distributed within each family (Fig. 1), sustaining our hypothesis that species richness differs among feeding guilds. The majority of wrasses (64%) belong to the generalist carnivore group, whereas half of the damselfish species (54%) are zooplanktivore (Fig. 2a). In both families, the other guilds include $\leq 30\%$ of the species richness (Fig. 2a). The results of dietary reconstructions suggested that the last common ancestor of all living wrasses was a generalist carnivore (99% of posterior probabilities), whereas it was a benthic feeder (70%) for damselfishes. In both families, the probabilities of some transitions between feeding guilds are very low (Table S2) and most trophic shifts occurred during the last 25 millions of years (Fig. S1). Within the 10 000 reconstructed trophic evolutionary histories of damselfishes, no transitions occur from the benthic feeding guild to the pelagic feeding guild, whereas between 17 and 27 trophic transitions originate from the intermediate group to the two other guilds. Similarly, evolutionary trophic shifts in wrasses mainly occur from the generalist carnivores to the other guilds and transition from benthic feeders to tiny biters or pelagic feeders never happen (Table S2).

The impact of trophic evolution on the rates of lineage diversification differs between the two fish families. Taking $\Delta\text{AIC} > 4$ (Akaike Information Criterion) as a strong indication of the best model, we cannot reject a model where there is no variation in the net diversification rates among guilds for Labridae (Models #3 & #5; Table 1). On the other hand, the models allowing speciation and extinction rates to vary among feeding guilds fit better than others in Pomacentridae (Table 1). According to the credible intervals for lineage diversification rates provided by Bayesian MCMC methods, the lineages belonging to the intermediate group in damselfishes have a higher net diversification rate (0.142 ± 0.024)

than pelagic (0.086 ± 0.018) and benthic feeders (0.062 ± 0.017 ; Fig. 3). In both families, the tempo of transitions between trophic strategies is unbalanced (Tables S3 and S4). The best-fitting models provide evidence that the transitions occurring between ‘specialist’ guilds do not happen (Table 1), and simple models considering only transitions between ‘specialists’ and ‘generalists’ may explain the pattern of trophic evolution in both families (Table 1). However, the tempo of trophic transition out of the generalists differs between the two families. The highest transition rates occur from the intermediate group into specialists in damselfishes, whereas the transition rates between specialists and the generalist carnivore are close to symmetrical in Labridae (Fig. 3; Tables S3 and S4).

The comparative approach using the HiSSE method helped to refine and even strengthen the MuSSE results. We found strong evidence for the presence of a hidden trait in the guild of generalists in Labridae (Table 2). Indeed, a small fraction of the generalist carnivores show lower net diversification rates than the other generalists, but this second subset of generalist carnivores has diversification rates slightly higher than specialists (Fig. S2 and Table S5). For Pomacentridae, we cannot reject a simple model where there is no variation in the diversification rates between specialists and generalists (Table 2). The best-fitting models also suggest that the highest transition rates arise from generalists into specialists in wrasses, whereas the transition rates between specialists and generalists are symmetrical in Pomacentridae (Table S5). Overall, stochastic maps and results from models of lineage diversification confirm our expectation that some trophic transitions are constrained, but HiSSE and MuSSE results do not validate the ‘dead-end’ hypothesis.

In Labridae, we observed the highest number of functional entities (FEs) in the generalist carnivore group (76) and the lowest one for the tiny biters (10; Fig. 2b). Functional richness (FRs) also varied with generalist carnivores occupying the largest functional space (0.63) and the tiny biters having the lowest space (0.002; Figs 2c and 4). In Pomacentridae, the pelagic feeders have the highest number of FE (74) and the intermediate group the lowest number (28; Fig. 2b). However, benthic feeders occupied the largest functional space (0.28)

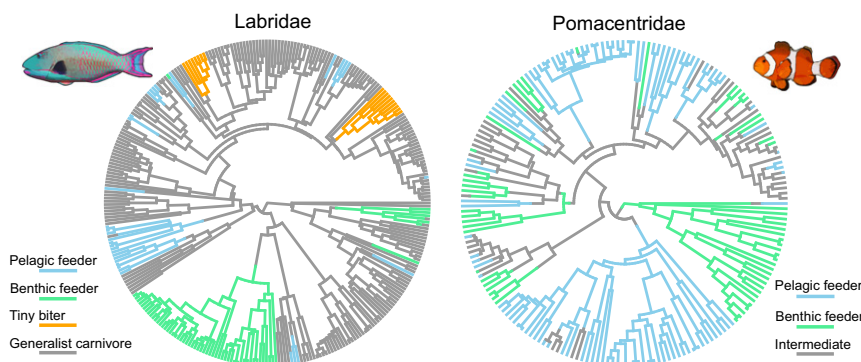


Figure 1 Evolution of feeding guilds in Labridae and Pomacentridae. Mapping of trophic guilds on the consensus phylogenetic tree of Labridae and Pomacentridae. Through stochastic mapping, these trees represent one possible trophic history. Dietary behaviours were represented by different colours on branches.

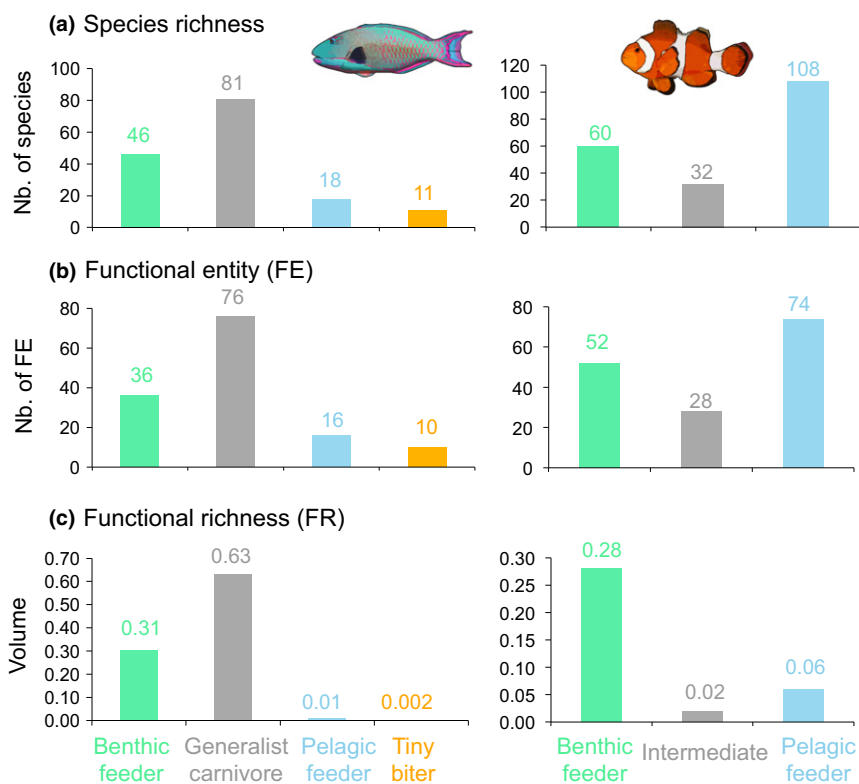


Figure 2 Metrics of species richness and functional diversity. For each trophic guild, histograms show (a) the species richness (exact number of species is provided on top of each bar); (b) the number of FEs (Functional Entities; exact number on top of each bar); and (c) the size of the functional space or Functional Richness (FR) (absolute size on top of each bar).

and the intermediate group the lowest one (0.02; Figs. 2c and 4). The high values of functional dissimilarity (0.83–0.98) between the majority of trophic guilds for both Labridae and Pomacentridae indicated that, in each family, the great majority of feeding guilds occupy different portions of the total functional space. Only in Labridae, the benthic feeders and generalist carnivores appeared to be not so dissimilar to one another (functional dissimilarity = 0.54). However, phylogenetic Procrustes ANOVAS revealed no significant differences in mean niche position between species of different feeding guilds in the functional space (Labridae: $F_{3,148} = 0.23$, $P = 0.14$; Pomacentridae: $F_{2,192} = 2.14$, $P = 0.13$). Consequently, we cannot reject the null hypothesis that functional dissimilarities among feeding guilds occurred by chance along the evolutionary history of both fish families.

Finally, the evolutionary conservatism of functional traits was assessed using tests of phylogenetic signal. The values of the multidimensional equivalent of Blomberg's K (Adams 2014a) were lower than 1 in both families (Labridae: $K_{\text{mult}} = 0.05$; $P = 0.87$; Pomacentridae: $K_{\text{mult}} = 0.08$; $P = 0.001$), delineating an overall low degree of phylogenetic dependency of the functional characters and thus, that closely related species seem to exhibit different trait values than would be expected under a Brownian motion model. Despite no support for phylogenetic conservatism, we found that the evolutionary rate of functional diversification (σ^2) does not significantly differ among feeding guilds in Pomacentridae ($P = 0.69$). On the other hand, the rates of functional

evolution vary among trophic guilds in Labridae ($P = 0.02$). The benthic feeders showed a higher rate of functional evolution (median $\sigma^2 = 0.021$) than the others (median values: $\sigma^2_{\text{generalist_carnivore}} = 0.002$; $\sigma^2_{\text{pelagic_feeder}} = 0.001$; $\sigma^2_{\text{tiny_biter}} = 0.001$). These analyses sustain our predictions that dietary specialisation affects the diversity of fish functions. Functional diversity varies among feeding guilds despite very low variation in the tempo of functional diversification.

DISCUSSION

Integrative work combining phylogenetic and functional information is needed to shed light on factors impacting the diversification of functions in ecosystems. Our results from two conspicuous reef fish families reveal that (1) feeding strategies influence the rise of species richness and functional diversity and (2) the generalist trophic strategy (i.e. feeding on food sources from the whole benthic-pelagic compartment) has a key role during evolution. However, we found no strong evidence for the 'dead-end' hypothesis because the variation in diversification rates among feeding guilds remains limited.

The relationship between feeding habits, functional diversity and the pattern of functional evolution

Functional diversity varies among feeding guilds and every guild occupies different subspaces of the functional space, emphasising the tight link between dietary strategies and

Table 1 Results from fitting lineage diversification and transition rate models using MuSSE method

	Model	Model specification			# Of parameters	AIC	Δ AIC	wtAIC
		Speciation rate	Extinction rate	Transition rate				
Labridae	#1	All constrained	All constrained	All constrained	3	2434.74	5.57	3.25 E ⁻⁰²
	#2	All constrained	All constrained	Free	14	2439.92	10.75	2.44 E ⁻⁰³
	#3	All constrained	All constrained	Bf, Pf, Tb (specialist) Vs Gc (generalist) Transitions within specialists = 0	8	2429.17	0.00	0.53
	#4	All constrained	All constrained	Bf, Pf, Tb (specialist) Vs Gc (generalist) Rates of transition between specialist and generalist	7	2437.57	8.40	7.89 E ⁻⁰³
	#5	All constrained	All constrained	Bf, Pf, Tb (specialist) Vs Gc (generalist) Rates of transition between specialist and generalist & Transitions within specialists = 0	4	2431.95	2.79	0.13
	#6	Free	Free	All constrained	9	2438.82	9.65	4.22 E ⁻⁰³
	#7	Free	Free	Free	23	2441.46	12.30	1.13 E ⁻⁰³
	#8	Free	Free	Bf, Pf, Tb (specialist) Vs Gc (generalist) Transitions within specialists = 0	17	2430.51	1.34	0.27
	#9	Free	Free	Bf, Pf, Tb (specialist) Vs Gc (generalist) Rates of transition between specialist and generalist	13	2441.19	12.02	1.29 E ⁻⁰³
	#10	Free	Free	Bf, Pf, Tb (specialist) Vs Gc (generalist) Rates of transition between specialist and generalist & Transitions within specialists = 0	11	2435.38	6.21	2.36 E ⁻⁰²
Pomacentridae	#1	All constrained	All constrained	All constrained	3	1641.40	36.79	3.75 E ⁻⁰⁹
	#2	All constrained	All constrained	Free	8	1615.83	11.22	1.34 E ⁻⁰³
	#3	All constrained	All constrained	Bf, Pf (specialist) Vs In (generalist) Transitions within specialists = 0	6	1614.74	10.13	2.32 E ⁻⁰³
	#4	All constrained	All constrained	Bf, Pf (specialist) Vs In (generalist) Rates of transition between specialist and generalist	5	1611.78	7.17	1.02 E ⁻⁰²
	#5	All constrained	All constrained	Bf, Pf (specialist) Vs In (generalist) Rates of transition between specialist and generalist & Transitions within specialists = 0	4	1613.18	8.57	5.04 E ⁻⁰³
	#6	Free	Free	All constrained	7	1636.14	31.53	5.21 E ⁻⁰⁸
	#7	Free	Free	Free	12	1607.24	2.63	0.10
	#8	Free	Free	Bf, Pf (specialist) Vs In (generalist) Transitions within specialists = 0	10	1606.35	1.74	0.15
	#9	Free	Free	Bf, Pf (specialist) Vs In (generalist) Rates of transition between specialist and generalist	9	1604.61	0.00	0.37
	#10	Free	Free	Bf, Pf (specialist) Vs In (generalist) Rates of transition between specialist and generalist & Transitions within specialists = 0	8	1604.63	0.02	0.36

The models are compared with AIC scores and Akaike weights (wtAIC). Median AIC values over the 100 time-trees are provided. Δ AIC scores indicate the difference between the candidate model and the best-fitting model. The best-fitting models are highlighted in bold, assuming that a Δ AIC value of four or more was taken as an indication of support for one model over the others (Burnham & Anderson 2002). The name of trophic guilds was abbreviated: Labridae – Bf, Benthic feeding; Pf, Pelagic feeding; Gc, Generalist carnivore; Tb, Tiny biter – Pomacentridae – Bf, Benthic feeding; Pf, Pelagic feeding; In, Intermediate group.

functional roles. Yet, counter to our simple prediction, we found that reef fish guilds having more diverse feeding habits do not necessarily yield high rates of functional diversification and, in contrast, dietary specialisation does not inevitably impede the tempo of evolution in the functional space. Rates of functional evolution among feeding guilds were similar in Pomacentridae and only slightly varied in Labridae. The benthic feeding guild in wrasses had a higher rate of functional diversification than others and is mainly represented by parrotfishes (Scarinae). Species from this subfamily has modified

jaws that are, in contrast to other wrasses, associated with an increased species richness (Kazancioglu *et al.* 2009) and morphological diversity (Price *et al.* 2010). Our results further demonstrate that parrotfishes have both high rates of lineage and functional diversification. As suggested by previous studies (Alfaro *et al.* 2009; Price *et al.* 2010; Choat *et al.* 2012), the rapid functional diversification of parrotfishes on tropical reefs is certainly driven by a combination of factors including morphological innovations, sexual selection, genetics and ecological circumstances.

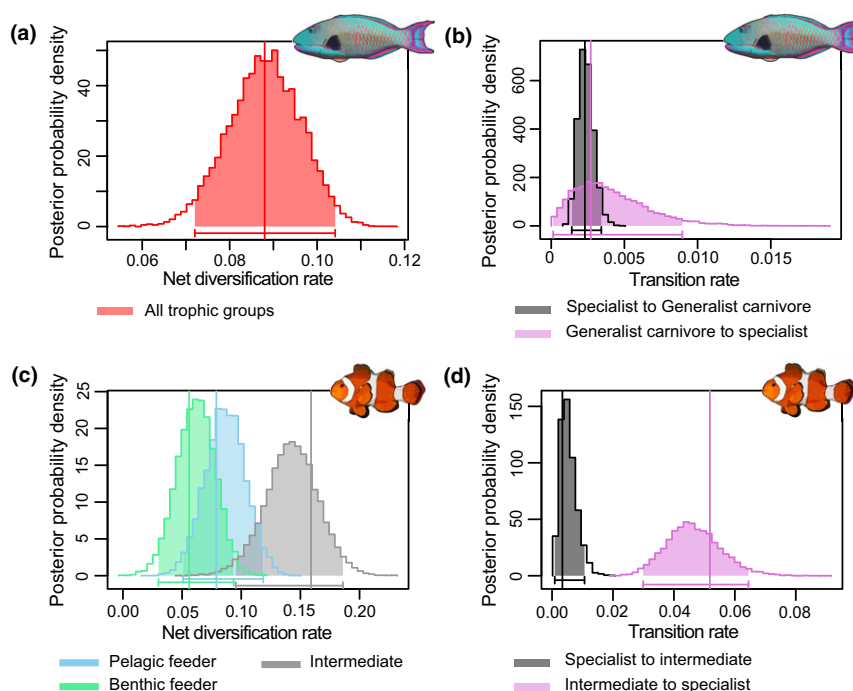


Figure 3 Parameter estimates for the best model of trophic evolution and lineage diversification using the MuSSE method. Plot of the posterior density of the parameter estimates for the best fitting MuSSE model having the lowest number of parameters analysed using Bayesian MCMC methods on the consensus time-tree. Illustration of (a) the net diversification rate and (b) the transition rates in Labridae for all trophic guilds and (c) the net diversification rate and (d) the transition rates in Pomacentridae for all trophic guilds.

Table 2 Results from fitting lineage diversification and transition rate models using HiSSE and BiSSE methods

	Model	Hidden states	Tau	Epsilon	q	AICc	Δ AIC	wtAIC
Labridae	bisse #1	No hidden states	Equal	Equal	Equal	2384.08	10.28	0.01
	bisse #2	No hidden states	Free	Free	Equal	2386.01	12.22	2.07×10^{-3}
	bisse #3	No hidden states	Equal	Equal	Free	2382.65	8.85	0.01
	bisse #4	No hidden states	Free	Free	Free	2384.86	11.06	3.69×10^{-3}
	hisse #1	Hidden state present for both generalists & specialists	Free	Free	Equal	2380.19	6.39	0.04
	hisse #2	Hidden state present for generalists	Free	Free	Equal	2384.11	10.32	0.01
	hisse #3	Hidden state present for specialists	Free	Free	Equal	2387.27	13.48	1.10×10^{-3}
	hisse #4	Hidden state present for both generalists & specialists	Free	Free	Free	2386.93	13.13	1.31×10^{-3}
	hisse #5	Hidden state present for generalists	Free	Free	Free	2373.80	0.00	0.93
	hisse #6	Hidden state present for specialists	Free	Free	Free	2391.61	17.81	1.26×10^{-4}
Pomacentridae	bisse #1	No hidden states	Equal	Equal	Equal	1540.68	25.06	2.04×10^{-6}
	bisse #2	No hidden states	Free	Free	Equal	1536.21	20.60	1.90×10^{-5}
	bisse #3	No hidden states	Equal	Equal	Free	1516.39	0.78	0.38
	bisse #4	No hidden states	Free	Free	Free	1515.61	0.00	0.57
	hisse #1	Hidden state present for both generalists & specialists	Free	Free	Equal	1532.23	16.61	1.40×10^{-4}
	hisse #2	Hidden state present for generalists	Free	Free	Equal	1541.23	25.62	1.55×10^{-6}
	hisse #3	Hidden state present for specialists	Free	Free	Equal	1526.12	10.51	2.96×10^{-3}
	hisse #4	Hidden state present for both generalists & specialists	Free	Free	Free	1536.00	20.39	2.12×10^{-5}
	hisse #5	Hidden state present for generalists	Free	Free	Free	1526.62	11.00	2.31×10^{-3}
	hisse #6	Hidden state present for specialists	Free	Free	Free	1520.68	5.06	0.04

The models are compared with AIC scores and Akaike weights (wtAIC). Median AIC values over the 100 time-trees are provided. Δ AIC scores indicate the difference between the candidate model and the best-fitting model. The best-fitting models are highlighted in bold, assuming that a Δ AIC value of four or more was taken as an indication of support for one model over the others (Burnham & Anderson 2002). Tau (τ), epsilon (ϵ) and q refer to 'net turnover' rate, extinction fraction and transition rates, respectively.

There is an absence of phylogenetic conservatism on functional traits in both fish families, as revealed by the tests of phylogenetic signal. The evolutionary corollary is that closely

related species show stronger differences in functional trait values than expected under a Brownian motion model. Natural selection, favouring ecological divergence to minimise the

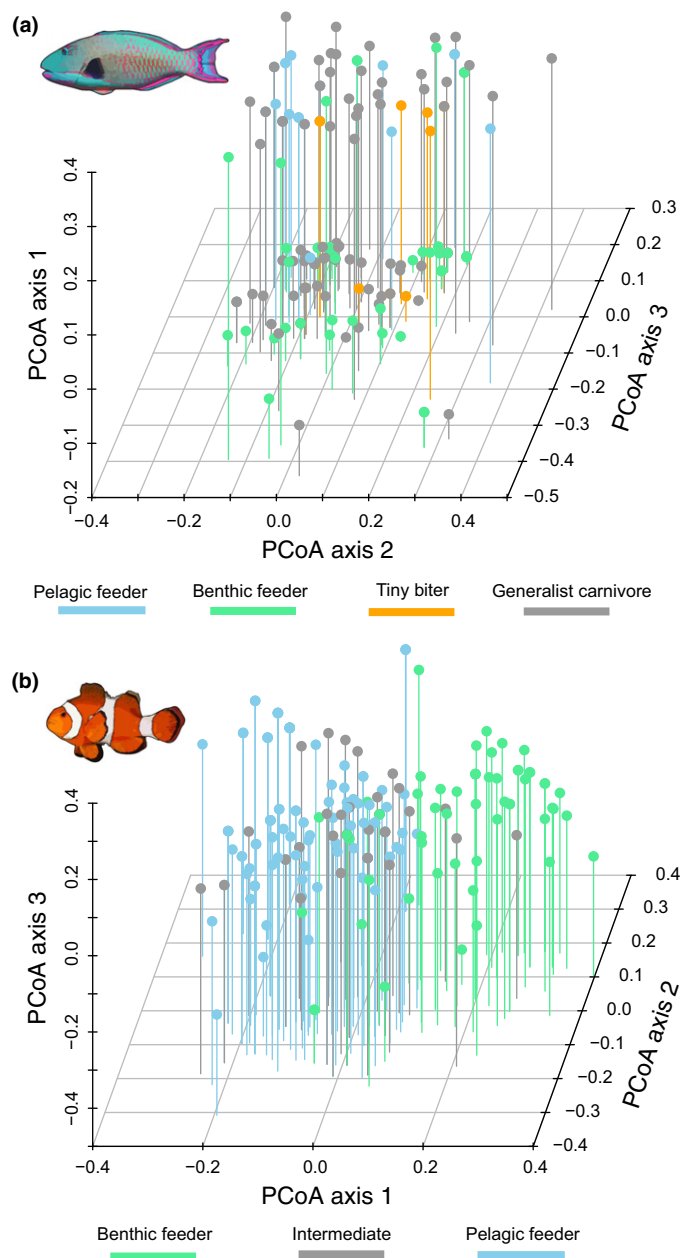


Figure 4 Functional spaces of Labridae and Pomacentridae. Distribution of the species in functional spaces where axes represent PCoA1 – PCoA3 from a Principal Coordinate Analysis of functional traits. (a) Labridae and (b) Pomacentridae.

intensity of interspecific interactions (Losos 1994), probably sustains variation in functions among closely related species. The absence of phylogenetic conservatism cannot be fully elucidated in view of varying rates of functional evolution among feeding guilds, but diverse evolutionary processes can explain the observed low *K* values (Revell *et al.* 2008). Among others, models of variable selection or models with bounded functional space may lead to low values of phylogenetic signal (Revell *et al.* 2008) and fit the evolution of functional traits in Pomacentridae and Labridae. The phylogenetic procrustes ANOVA showed that, in each family, the mean functional niche was not significantly different among trophic groups.

Accordingly, we hypothesise that feeding strategies do not drive functional diversity by stabilising selection towards optimal values. However, additional investigations, where fitting alternative models of trait evolution, should be considered to disentangle the evolutionary processes sustaining the diversification of functional roles of fish in reef ecosystems.

The pattern of functional evolution does not lead to functional redundancy

When several species perform similar functions, this functional redundancy is thought to ensure against the loss of ecosystem functioning following declines in species diversity (Fonseca & Ganade 2001). Here, the unequivocal relationship between the numbers of species and functional entities (FEs) indicates that the functions occupied by feeding guilds appear speciose. These findings emphasise that the pattern of diversification within monophyletic groups of reef fishes results in limited levels of functional redundancy. The pelagic feeding guild in damselfishes displays some degree of functional redundancy (1.4 species per FE; Fig. 2), which is illustrated by the relatively smaller portion of the functional space they occupy given their species (Fig. 2a) and functional richness (Fig. 2c). At the macroevolutionary time scale, bounded functional subspace of pelagic feeders could be a source of redundancy in the roles they occupy. Ecological factors, such as the large abundance of food sources in the water column, could also sustain a high number of species varying in other aspects of their ecology and behaviour. For example a partitioning of the same resources on a diurnal temporal scale may contribute to this apparent functional redundancy (Kronfeld-Schor & Dayan 2003). However, such an apparent redundancy does not ineluctably guarantee a functional resilience if species are unevenly grouped into a small subset of FEs (Mouillot *et al.* 2014). In contrast to pelagic feeders, the benthic feeders in Pomacentridae are more widely distributed in their functional subspace (Figs 2 and 4). If functional vulnerability is inversely related to the number of species that share similar trait values (Mouillot *et al.* 2013), the very distinct functional characteristics exhibited by these benthic feeding species allowed them to disperse the most in the functional space, further suggesting that they hold the highest pool of ecosystem functions.

The generalist feeding guild is not an evolutionary sink

Our models of trophic evolution reveal that the ‘generalist’ guild in both families is systematically involved in all trophic transitions, indicating that the generalist carnivore guild in Labridae and the intermediate trophic guild in Pomacentridae may act as a stepping-stone state towards more specialised strategies. This key role of generalised feeding strategies during evolution is somewhat expected because shifting from one dietary specialisation to another would also imply extensive physiological and morphological changes. For instance pelagic-feeding damselfish lineages changing to a grazing feeding mode (Frédérich *et al.* 2014; Olivier *et al.* 2016) must possess specific gastric enzymes to be able to digest algae (Clements *et al.* 2009). Wrasses able to feed on corals should have particular morphological and physiological adaptations (Huertas

& Bellwood 2017). Yet, stochastic maps (Table S2) and the study of Cowman *et al.* (2009) indicate that a direct shift from one dietary specialisation to another can also happen, although the presence of a generalist phase during the transition between two specialist states may have been undetected. Interestingly, we also highlight that most trophic shifts occurred during Oligocene and Miocene suggesting intensive functional diversification during the rise of modern coral reef systems (Bellwood *et al.* 2017).

Guilds of generalist species hold future diversity. Lineages of wrasses and damselfishes with a generalist feeding strategy show equal or higher rates of net diversification than others (Fig. 3 and Table S5). Accordingly, the generalist carnivore guild in Labridae exhibits the highest functional and species richness. These characteristics exhibited by the generalist carnivore guild could have also been driven by biogeography as it includes species from all marine tropical and temperate regions, whereas specialist guilds are not ubiquitously distributed (e.g. tiny biters are absent from the Atlantic Ocean (Cowman *et al.* 2017)). This difference with other guilds also suggests that the generalist carnivorous feeding mode in wrasses had certainly facilitated diversification along various ecological axes such as fine-scale habitat partitioning. In Pomacentridae, the intermediate trophic guild shows the lowest species richness, which is probably due to a competition with specialist feeding guilds and less efficient use of dietary resources. Nevertheless, this generalist feeding guild displays low rates of extinction (Table S4), implying that this feeding mode is a strategy for surviving fluctuations in resource availability (Ingram *et al.* 2009) and that generalist lineages may generate future diversity. In light of these findings and considering that dietary specialised descendants emerged from generalised trophic groups, we argue that the generalist guilds of damselfishes and wrasses are not evolutionary 'dead-ends' (as defined in Eldredge 1982). This result contrasts with studies on mammals (Price *et al.* 2012) and birds (Burin *et al.* 2016) that designated a generalist dietary habit (omnivory) as a macroevolutionary sink. The dissimilar outcomes between our research and theirs might be attributed to the types of variables used to describe the trophic strategies. Instead of scoring food types (Price *et al.* 2012; Burin *et al.* 2016), we built our fish feeding categories on functional demands associated with the capture of prey in the benthic and/or pelagic compartments. The generalist feeding guilds of both wrasses and damselfishes have more diverse morphological attributes than others (Bellwood *et al.* 2006; Olivier *et al.* 2017), and our trophic categorisation probably translates to phenotypic traits linked to versatility. According to the predictions of Bellwood *et al.* (2006), we suggest that such a trophic versatility may sustain high rates of lineage diversification by (1) relaxing interspecific competition and facilitating local co-occurrence of ecologically similar species and (2) enhancing reef colonisation ability.

CONCLUSION

Our macroevolutionary analysis of reef fishes does not corroborate the 'dead-end' hypothesis, in which the variation in lineage diversification rates among feeding guilds is limited. Our results also clearly indicate that trophic attributes affect the

diversification of species' functions. Feeding habit has a low effect on the tempo of functional diversification, but the type and the diversity of functional roles hosted by fish in reef ecosystems are tightly linked to their dietary specialisation. The absence of a phylogenetic signal for functional traits suggests an overall malleability of these traits during the evolutionary history of Labridae and Pomacentridae. Finally, we argue that the generalist feeding strategy is an evolutionary stepping-stone state towards specialisation and may serve as a reservoir of future diversity.

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AUTHOR CONTRIBUTIONS

BF and LG designed the research. LG and RAM compiled the functional data set; LG and BF performed all comparative analyses and led the writing of the manuscript with RAM who gave final approval for publication.

DATA ACCESSIBILITY STATEMENT

Supporting Information, trophic and functional data are available from Figshare: <https://doi.org/10.6084/m9.figshare.7528748.v1> and from IMIS: <https://doi.org/10.14284/327>. Time-calibrated trees of Labridae and Pomacentridae can be found in Baliga & Law (2016) and Frédéricich *et al.* (2013), respectively. Scripts to compute functional diversity indices are made available by Sébastien Villéger (<http://villeger.sebastien.free.fr/Rscripts.html>) and in the supplementary materials of Maire *et al.* 2015.

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SUPPORTING INFORMATION

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

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