The evolution of traits and functions in herbivorous coral reef fishes through space and time

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Supplementary methods

(a) Phylogenetic inferences

For each of our herbivorous fish groups, we downloaded overlapping gene sequences for all available species from Genbank using Geneious Pro version 11.1 [1]. For the Acanthuridae, we downloaded two mitochondrial (*Cox1* and *Cytb*) and seven nuclear genes (*ENC1*, *myh6*, *plagl2*, *Rag1*, *Rh*, *zic1* and *ETS2*) belonging to 72 species (~90% total diversity) from all extant genera. Two species were used as outgroups, one from the family Zanclidae (*Zanclus cornutus*) and one from the family Luvaridae (*Luvarus imperialis*). The Siganidae phylogeny was based on two mitochondrial markers (*Cytb* and *16s*) and the nuclear rRNA internal transcribed spacer 1 (*ITS1*) region. It contained 24 species (~80% total diversity) in its single genus *Siganus*, and included the species *Zanclus cornutus* (Zanclidae) and *Prionurus scalprum* (Acanthuridae) as outgroups. Finally, the Scarini phylogeny was based on five mitochondrial (*Cox1*, *Cytb*, *12s*, *16s* and control region) and six nuclear markers (*Bmp4*, *Dlx2*, *Otx1*, *Rag2*, *S7I1* and *Tmo-4C4*), for 87 species (~87% total diversity) belonging to all extant genera. Nine species from the family Labridae (two Hypsigenyines and seven Cheilines) were included to act as outgroups for the parrotfishes. The Majority of these genetic sequences have been deposited by previous studies performed with the focal taxa [2–6]. Species and accession numbers are given in Supplementary tables 4-6. Gene datasets were aligned using the Muscle algorithm [7] in Geneious Pro version 11.1 [1] and checked by eye. The resulting concatenated alignments consisted of 7,229 (Acanthuridae), 3,001 (Siganidae) and 6,296 (Scarini) base pairs. Model testing was performed using PartitionFinder2 [8] and indicated the best gene partitioning scheme for each taxa (Supplementary tables 7-9).

For the phylogenetic inferences, we benefited from the CIPRES Science Gateway [9] computing environment. Firstly, we ran maximum likelihood (ML) analyses using the GTR + G model and 1000 bootstraps per taxa in RAxML [10]. The resulting ML tree for each taxa was converted to an ultrametric tree using the penalized likelihood method in 'ape' R package (function '*chronos*'; [11]), and subsequently used as a starting tree in BEAST2 [12] for Bayesian estimation of topology, branch lengths and node ages. For this analysis, we set gene partitions according to the results from PartitionFinder (Supplementary tables 7-9) and we used relaxed lognormal clock priors. We also set birth-death models with node calibration points according to fossil information for each of our groups, all of which had lognormally distributed priors with soft upper bounds. For the surgeonfishes, we placed a calibration point in the crown Acanthuridae lineage to represent the acanthurid fossils from Monte Bolca at 50 Myr [13]. We also placed a prior on the stem lineage of Acanthuridae to represent the fossil *Kushlukia permira*, described as a stem Luvaridae from 55.8 Ma [14]. For the rabbitfishes, the root node representing the stem Siganidae lineage was calibrated at 55 Myr representing *Siganopygeus rarus*, the oldest fossil described for the family [15]. We also calibrated the outgroup stem Zanclidae lineage to represent the only fossil described for that family from Monte Bolca at 50 Myr [13]. Finally, for the Parrotfishes, we used the only two fossils described for the group as internal calibration points: *Calotomus preisli* as a stem *Calotomus* at 14 Myr and the stem *Bolbometopon* fossil at 5 Myr [16]. We also calibrated the crown Hypsigenyines outgroup at 50 Myr to represent the labrid *Phyllopharyngodon longipinnis* from Monte Bolca [17]. Five independent MCMC runs were conducted per group for 100 million generations each, storing trees every 10,000 generations (10,000 trees per run). All runs were assessed for convergence and stationarity in Tracer v1.7.0 [18] using effective sample size (ESS) scores. After removing 20% burnin from each run, all trees were combined in LogCombiner v2.5.0 [12] and compiled into a maximum clade credibility (MCC) tree in TreeAnnotator v2.5.0 [12].

(b) Herbivorous reef fish data

We categorized all parrotfish, surgeonfish and rabbitfish species present in the phylogenetic trees based on seven traits related to feeding. Firstly, we collected data on the maximum size recorded for each species in Fishbase [19]. This was the only continuously variable trait included in our analysis. We then assigned species according to categories of tooth morphology and alimentary tract, traits that are related to food processing. To classify the types of alimentary tract found in herbivorous coral reef fishes, we considered the most important feature of internal food processing in each of our groups. In parrotfishes, the Pharyngeal Jaw Apparatus is modified in a structure specialized for

grinding food, known as Pharyngeal Mill. Considering that this is a synapomorphy for the tribe Scarini (formerly the Scaridae) [20], we classified the alimentary tract of all our parrotfish species as having a Pharyngeal Mill. All parrotfishes lack a stomach and must thus rely on the pharyngeal jaws for triturating food particles. By contrast, surgeonfishes and rabbitfishes mainly rely on stomach features for initial food processing [21]. Therefore, we divided the stomachs of these groups into two categories as being either thin-walled or gizzard-like (following [21,22]). Thin-walled stomachs are associated with acid lysis of food items and is found in rabbitfishes and some surgeofishes (*Naso* and some *Acanthurus*), while gizzard-like stomachs rely on thick, muscly walls to triturate food and is found in other surgeonfishes (*Ctenochaetus* and some *Acanthurus*). For the tooth morphology categorization, we used the most prominent feature of the tooth structure of each herbivorous group. All rabbitfishes have a bicuspid tooth, while in the surgeonfishes, tooth can be conical (*Naso*), multi-denticulate (*Acanthurus*) or brush-like (*Ctenochaetus*) (following [23–25]). For the parrotfishes, the tooth morphology was based on the intensity of fusion of the dental plates and on the dental margin pattern, which resulted in the following categories: not-fused (*Calotomus*, *Cryptotomus* and *Nicholsina*), weakly-fused (most *Sparisoma*), fused-crenelated (*Cetoscarus*, *Bolbometopon*, *Chlorurus* and some *Sparisoma*), and fused-even (*Hipposcarus* and *Scarus*) (following [20,26]).

We also classified four important behavioural traits related to food acquisition that included feeding mode, diet, feeding habitat and schooling behaviour. Each of these traits are related to different components of the feeding behaviour of herbivorous fishes on coral reefs. For instance, we classified each of our species according to the mode how they acquire food, which included browsing (i.e. species that browse on macroalgae larger than 10 mm), scraping (i.e. parrotfishes that remove the epilithic algal matrix), excavating (i.e. parrotfishes that excavate the surface of the reef matrix), planktivory (i.e. surgeonfishes that feed in the water column), cropping (i.e. surgeonfishes and rabbitfishes that crop short turf algae from the benthos), sucking (i.e. surgeonfishes that use suction to feed on particulate material on the benthos), and brushing (i.e. surgeonfishes that brush particulate material from the benthos) (classification modified after [20,23,26–30]). We also classified the typical diet of each species. The food items classified included: cyanobacteria, coral, detritus, epilithic algal matrix (EAM), macroalgae, seagrass, sponges, turf-algae and zooplankton (data drawn from [20,23,26–43]). For feeding habitat, we considered the location where each species predominantly feed on, which included: concealed, open or sandy parts of the reef, the water column and off-reef species (classification modified after [26,30,34,44–48]). Finally, our classification of schooling behaviour included species that feed solitarily, in pairs or in schools [23,24,30].

The combination of traits that we classified provides an indication of each species' ecological role in terms of ecosystem processes. However, different trait combinations can result in similar ecosystem functions (i.e. the movement or storage of energy through trophic or bioconstructional pathways [49]) performed by herbivorous fish species on coral reefs. Therefore, we also categorized each species according to their role in ecosystem processes and consequently to the cycling of matter and nutrients in reef systems. Our ecosystem function categories included: Turf-algae removal, Macroalgae removal, Sediment removal (which includes the rework and transport of sediment particles), Zooplanktivory, Crevice cleaning (i.e. species that are capable of feeding in concealed parts of the reef), Bioerosion, Coralivory and Spongivory. We assigned these ecosystem functions to all species in our database considering that each species could potentially perform more than one function simultaneously.

(c) Ancestral range estimation

To assess the ancestral ranges in each of our herbivorous fish groups, we built biogeographical models using the 'BioGeoBEARS' R package [50]. This package allows the comparison of candidate models for ancestral range estimation built in a maximum likelihood framework. We used this framework to build models according to the notation of the three most widely recognized models in historical biogeography: DEC [51]; DIVA [52]; and BayAREA [53]. We built combinations of models including the founder-speciation event parameter *j* [54], which considers the inheritance of a new area by a daughter lineage while the sister-splitting lineage inherits the original ancestral range. All our models were built considering time-constraints from the past geological history of marine environments that are well known to influence coral reef fish biogeography [55,56]. We constrained the root nodes of each group to be present in the ancestral (now extinct) Tethys sea, reflecting the presence of fossil species in a region that used to connect major ocean basins (Atlantic and Indo-Pacific) in the geological past [57]. Since our chronogram for the Siganidae shows that the extant species in the family are a product of a recent radiation (~ 25 Ma; Supplementary Fig. 1), we included their outgroup to allow the stem node to be sampled in the biogeographic analysis. From 65 Ma to 12 Ma, we allowed the dispersal of lineages between the adjacent EA and WI regions, connected via Tethys seaway. From 12 Ma onwards, we excluded the Tethys sea from the analysis and we set very low dispersal multiplier values between EA and WI to reflect the final closure of the Tethys seaway [58], but allowing the possibility of dispersal around the South African coast [59]. We also constrained the dispersal between TEP and WA from 3.1 Myr onwards, reflecting the final closure of the Isthmus of Panama [60]. Finally, we assigned a low dispersal value between CP and TEP to reflect

the East Pacific Barrier [61] in all time-slices considered, but still permitting the dispersal given the soft nature of the barrier [56,62]. Although we set the dispersal multiplier matrices to reflect realistic dispersal probabilities relative to the presence of major biogeographical events/barriers through time, we also built models in which the matrices could be adjusted according to the data. This was achieved by setting the matrix power exponential (parameter *w*) to be free and estimated with maximum likelihood, which reduces the subjectivity in user-defined values for dispersal multiplier matrices [63]. In total, we fitted 12 biogeographical models to each phylogeny. These models were compared using AIC scores to assess the best estimates for ancestral range reconstructions in our fish groups.

(d) Uncertainties in ancestral state reconstructions

We assessed the robustness of our trait space results against two issues that could potentially affect our ancestral state reconstructions: phylogenetic uncertainties (topology and node dates); and uncertainties of reconstructed node states. Firstly, to deal with the topological and dating uncertainties in the phylogenies, we randomly sampled 1000 trees for each group from the combined post-burnin posterior sets derived from the Bayesian inferences. In each sampled tree, we retrieved the ancestral states of all traits per time-slice (20, 15, 10 and 5 Ma). This was achieved by re-rooting (function '*reroot*' in 'phytools' R package [64]) the trees in all edge points cut by the time-slices and reconstructing states in each re-rooted node point. For the discrete traits, we performed reconstructions using the '*ace*' function from 'ape' R package [11]. This function implements maximum likelihood joint estimation based on a transition matrix between character states. These reconstructions were performed using single-rate models, chosen based on likelihood ratio tests over other reconstruction models. For the continuous trait, we used the function '*fastAnc*' [64], which estimates ancestral character states for continuous traits through maximum likelihood. The most probable state for the discrete traits and the reconstructed value for the continuous trait for each re-rooted node point (lineage) were used in subsequent analysis. After retrieving the ancestral states, we constructed 1000 trait space polygons (see main Methods), each based on a combined set of three sampled phylogenies (one per taxa). We then overlapped all the polygons with a high transparency value to create a "heatmap" for the most likely area occupied in each time-slice (Supplementary Fig. 14).

Secondly, we assessed the effect of uncertainty in the reconstructed states of our categorical traits. To do that, we performed two new analyses of the multidimensional trait space. In the first one, we used the results of our Bayesian ancestral state reconstructions (see main Methods) to reclassify the nodes

in which the modal posterior probability (PP) was bellow 0.67. If this was the case, we classified the node with the second most likely state. This threshold means that the modal PP values of the most probable state was at least twice as likely than the second best-supported state. In the second analysis, we selected which state to consider for each node by comparing the posterior probability distributions. In case the best-supported state comprised less than 95% of the PP samples, we retrieved the second best-supported state. With the results of each analysis combined with the main results for the continuous trait reconstructions, we once again plotted the multidimensional trait space (see main Methods) for each biogeographic realm (Supplementary Figs. 15-16).

Finally, we performed ancestral reconstructions with a recently developed hidden Markov model (SecSSE - version 0.1.12, privately provided by the author; [65]) for discrete trait evolution. We used this maximum likelihood framework to perform ancestral reconstructions accounting for state-dependent diversification and the existence of more than one transition matrix for each character state. For each of our classified traits, we built one model by allowing speciation and extinction rates to vary between observed and concealed states ($\lambda_{0A} \neq \lambda_{1A} \neq \lambda_{0B} \neq \lambda_{1B}$; $\mu_{0A} \neq \mu_{1A} \neq \mu_{0B} \neq \mu_{1B}$ - in a two-state example), and by setting a transition rate matrix with one concealed rate regime (B) for all character states. We then used the resulting maximum likelihood parameter estimates, to retrieve the ancestral states for each node using the '*secsse_loglik*' function in the 'SecSSE' R package [65]. These results were combined with the main results for the continuous trait reconstructions to plot the multidimensional trait space (see main Methods) for each biogeographic realm (Supplementary Fig. 17). This maximum likelihood model complements the main Bayesian analysis, to ensure the robustness of our results against trait-dependent diversification and the existence of rate heterogeneity in trait evolution within the trees.

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