TROPHIC ECOLOGY

Specialization boosts reef fish functional diversity

Rapid evolution of morphological variations is shown to be linked to positions of coral reef fishes at trophic-web extremes. This finding suggests that current fishing practices on coral reefs that target top predators and seaweed-grazing fishes may undermine the potential for future species diversification.

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The diversity of fishes inhabiting tropical coral reefs encompasses an exuberant variety of colours, forms and functions. In addition to body sizes spanning across two orders of magnitude, coral reef fishes also exhibit striking variability in morphology and resource-acquisition strategies. Writing in *Nature Ecology & Evolution*, Borstein et al.[1] take advantage of this diversity to tackle the question of the relationship between species diversification rates and trophic specialization.

At the bottom of the reef-fish food chain are species specialized in browsing specific seaweed parts and others that tend algae gardens, often going to great lengths to defend them against other herbivores. There are even species adapted to feed on the organic matter available in detritus lying on the sea floor. On the other end of the food chain, top-predator fish-eaters engage in elaborate ways to pursue a meal. Some species chase their quarry in the water column, while others lie still, relying on camouflage to ambush non-suspecting prey. There are also morphological adaptations that allow predators to venture deep inside the convoluted structure of reefs to capture tiny cryptobenthic fishes. Species situated at these trophic extremes generally have a specialized diet, but situated between these extremes are groups with a broader dietary range, such as omnivores that consume both plant and animal material, and invertebrate eaters.

Feeding at the extremes of the food chain is challenging. At one end, species face low-protein and hard-to-digest plant organic compounds[2]. At the other end, they have to deal with energetic trade-offs between capturing high-caloric prey that are also highly evasive and often well defended[3]. How diversification rates respond to these constraints in food acquisition is a contentious issue. The niche variation hypothesis states that the ability to exploit a wider range of resources, presented by guilds at intermediate trophic positions, translates into higher phenotypic variation.

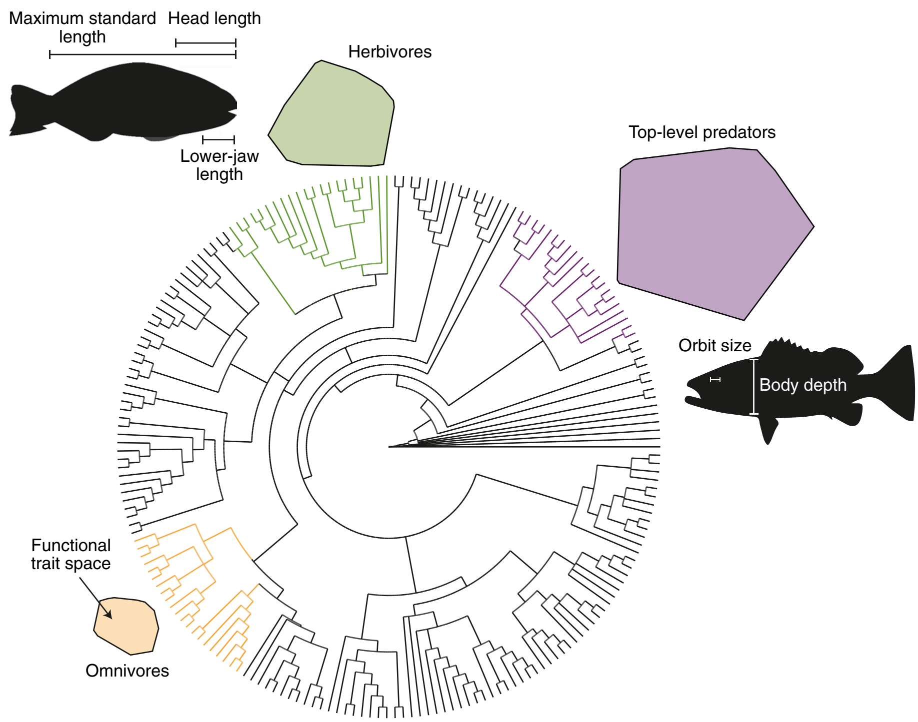

Fig. 1 | Evolution of functional diversity across reef fish trophic groups. Borstein et al.[1] show that reef fish species occupying the trophic-web extremes — top-level predators and herbivores — have evolved faster and developed greater phenotypic diversity when compared with generalists. Of seven functional traits (body measures) examined by the authors, herbivores exhibited the fastest evolutionary rates for maximum standard length, head length and lower-jaw length, and top-level predators exhibited the fastest evolutionary rate for orbit size and body depth. The functional diversity of predators occupies a greater space relative to herbivores (illustrated by the polygons), whereas omnivores showed lower levels of phenotypic functional diversity overall.

Conversely, there are studies suggesting that having a generalized diet by feeding on multiple food items hampers diversification[4], and that specialized herbivores and carnivores evolve faster and to greater phenotypic diversity than generalists[5].

Borstein et al. used a large database encompassing a broad phylogenetic sample of 1,545 reef fish species in 92 families, seven functional traits (body measures) and their prey items. By combining tools for mapping trophic level transitions across the phylogeny, measuring trait evolutionary rates and functional space analysis, the authors show that the pace of functional trait evolution has been faster for specialists at the extremes of the trophic web (Fig. 1). Conversely, omnivorous reef fishes, with broader dietary range, were associated with the slower rate of morphological evolution (Fig. 1). Yet the pace and magnitude of trait diversification at those functional extremes show some inconsistencies. When combined, both top predators and herbivores exhibit the faster diversification rate for all traits. However, while top predators translated that diversification into the highest functional diversity across all groups, herbivores had intermediate levels of phenotypic functional diversity.

Borstein and colleagues suggest that a herbivorous lifestyle may constrain the occupation of the functional space, hence the lower functional diversity presented by this group when compared with top predators (Fig. 1). However, every functional ecology study is limited by the set of traits used[6]. It may well be that the addition of further morphological traits that relate more to the herbivorous foraging strategy, such as tooth shape[7] or length of the digestive tract[8], would be more accurate in capturing the functional diversity of herbivores.

Borstein and colleagues also point out another possibility for the lower than expected functional diversity in herbivore reef fishes — time. Transitions to herbivory and other low-caloric-content diets are relatively recent in reef fishes, and it may be that herbivores did not have as long to build up the phenotypic diversity shown by top predators. Reef fish lineages have been evolving since the Eocene epoch (56–34 million years ago), yet feeding modes were not all established in ancient reefs at that time. Although herbivory in fishes had already originated back then, specialized herbivores such as scraper parrotfishes (Fig. 1) appeared in reef fish lineages in only the last 18 million years[9]. In other words, for some trophic categories there has been a shorter period of time for trait novelty emergence. Contrasting the tempo of trait evolution across lineages with distinct dietary modes and origins in the tree of life is an aspect that deserves attention for future research[10].

This study shows that diet has a clear association with the diversification dynamics of reef fishes. The finding that omnivorous reef fishes had both the lowest diversification rate and the lowest functional diversity across trophic groups is opposite to that expected by the niche variation hypothesis. Nevertheless, this finding is in line with recent research showing the same trend for mammals and birds[4,5]. These results challenge the long-standing expectation that ecological generalists are sources of future diversity and ecological specialists are evolutionary dead-ends. Rather, it suggests quite the opposite.

Studies across gradients of human population and fishing densities have found that piscine predators have historically been the first group to be overfished, followed by grazing herbivores, with high absolute losses of biomass occurring under relatively low fishing pressure[11]. Local extinctions caused by overfishing are severely reducing functional diversity, potentially leading to a loss of critical functional roles necessary for reef ecosystems to persist, and thereby resulting in a loss of phylogenetic diversity that may alter the capacity for adaptive evolution[12]. There is, therefore, an urgent need to integrate evolutionary ecology together with functional traits into fisheries management to ensure the sustainability of ecosystem functions and future diversification. ❐

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Competing interests

The authors declare no competing interests.