Title

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Trophic ecology is thought to exert a profound influence on biodiversity, but the specifics of the process are rarely examined at large spatial and evolutionary scales. We investigate how trophic position and diet breadth influence functional trait evolution in one of the most species-rich and complex vertebrate assemblages, coral reef fishes, within a large-scale phylogenetic framework. We show that, in contrast with established theory, functional traits evolve fastest in trophic specialists with narrow diet breadths at both very low and high trophic positions. Top trophic level specialists exhibit the most functional diversity, while omnivorous taxa with intermediate trophic positions and wide diet breadth have the least functional diversity. Our results reveal the importance of trophic position in shaping evolutionary dynamics while simultaneously highlighting the incredible trophic and functional diversity present in coral reef fish assemblages.

One of the central issues limiting progress towards a generalized theory of biological organization involves integrating the interplay of current ecological conditions with long-term macroevolutionary dynamics. Trophic interactions are critically important for understanding how variation in resource acquisition shapes diversity, food webs and community assembly[1,2]. While studies have provided valuable insights into how trophic ecology affects community assembly, trophic cascades and ecosystem-level processes[3–5], there remains a need to quantify how trophic interactions might shape evolutionary dynamics over macroevolutionary timescales using phylogenetic comparative methods[6–8]. Large comparative studies of trophic ecology on phylogenies have provided valuable insights into the evolutionary dynamics of families[9–15], yet further comparative studies investigating the impact of trophic ecology on global assemblage-wide patterns remains crucial.

Studies focused on single species or small clades suggest that the evolution of high trophic position should constrain rates of functional trait evolution due to the constraints imposed by feeding on evasive energy-rich prey items relative to lower trophic levels[16–19]. We term this the height constraint hypothesis (HCH). The niche variation hypothesis (NVH) predicts a direct positive relationship between niche breadth and phenotypic variation[20]. While the NVH has been investigated at the individual[21,22], population[23,24] and species level[25], it is less commonly examined at a macroevolutionary scale[26], where we predict that guilds composed of species with wider niches might also exhibit greater phenotypic variation. Thus, guilds occupying intermediate trophic positions, which exploit a more diverse set of resources compared with species feeding very high or very low in a food web, might therefore be expected to exhibit faster rates of functional trait evolution as there would be more phenotypic variance at the tips of the phylogeny among members of a guild. A third possibility, which we term the 'trophic extremes' hypothesis (TEH), posits that species with extremely high or low trophic position experience elevated rates of evolution compared with species at intermediate trophic levels. Increased rates of functional trait evolution may also be associated with the difficulty of accessing resources at very low or very high trophic levels. In the case of herbivory, this

may require functional traits related to crushing tough cell walls, as well as adaptations to a diet containing fewer proteins and fats[27–30]. At the highest trophic level, predators experience physical and energetic constraints related to the capture of highly evasive, large and/or defended prey items[31–34].

Here, we examine how trophic position and diet breadth affect the functional dynamics of trait evolution, using one of the most species-rich vertebrate assemblages—coral reef acanthomorph fishes. Coral reefs are known biodiversity hotspots that promote elevated rates of diversification, morphological diversity and ecological novelty due to the high amount of habitat partitioning and available trophic niches[35–40]. Reef acanthomorph fishes dominate this habitat and occupy numerous trophic levels, ranging from strict herbivores to specialized apex predators, and these feeding modes have evolved not once but many times[34,40]. Unfortunately, coral reefs are highly at-risk habitats due to various anthropogenic changes to their environment[41–43]. Understanding the ecological processes governing the evolutionary dynamics of reef assemblages is critical to successful conservation efforts.

We examine how trophic position affects the rate of functional trait evolution in a comparative context that accounts for evolutionary history, as well as the effect of trophic position on diet breadth. If the HCH drives evolution, we would expect to see high trophic level species (that is, top predators) evolving more slowly than other trophic levels. However, if the NVH is the primary driver, we would expect the highest rates of functional trait evolution in intermediate trophic levels. If the TEH is operating, we should see that the trophic extremes (species with very low or very high trophic levels) experience faster rates of functional trait evolution than species with intermediate positions.

Results

Trophic level distribution. Trophic levels for the 1,545 species of reef acanthomorphs ranged from 2.0 for species consuming solely autotrophs and/or detritus to 4.5 for species consuming solely higher trophic level prey. Our final dataset was composed of 186 species of herbivores, 200 species of omnivores, 844 low-level

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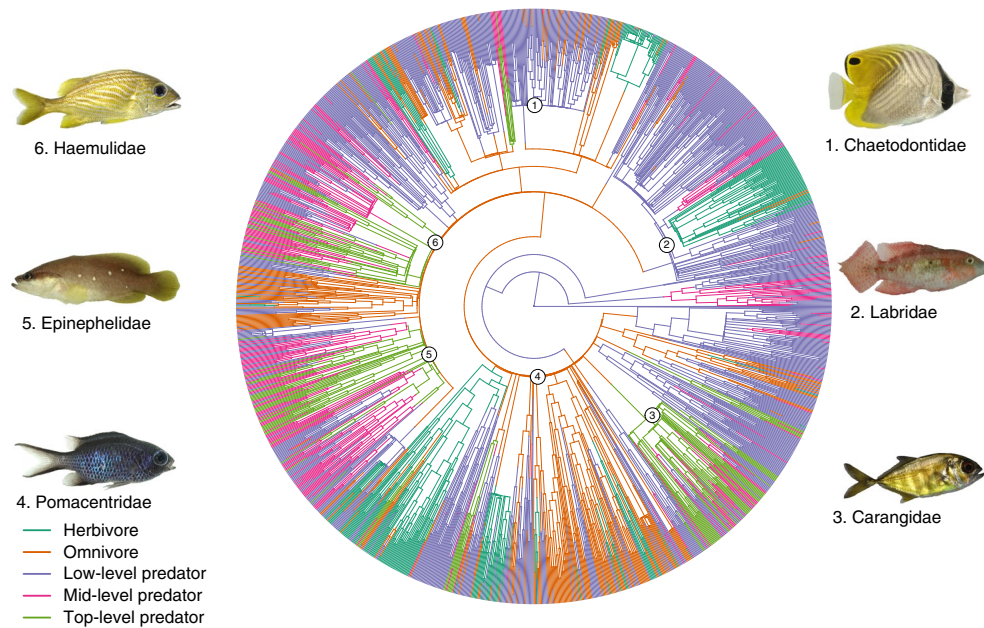
Fig. 1 | Stochastic character mapping reveals over 600 trophic level transitions across the phylogeny of 1,545 acanthomorph reef taxa. Trophic levels range from 2.0 for species consuming solely autotrophs and detritus to 4.5 for species consuming entirely large nekton. Transitions between the five trophic levels (herbivores, omnivores, low-level predators, mid-level predators and top-level predators) occur frequently throughout the phylogeny. Numbered node labels indicate the phylogenetic position of the families Chaetodontidae (1), Labridae (2), Carangidae (3), Pomacentridae (4), Epinephelidae (5) and Haemulidae (6).

predators, 217 mid-level predators and 98 top-level predators (Fig. 1 and Supplementary Tables 4 and 6). A total of 1,000 stochastic character maps of trophic level on the phylogeny recovered a range of 548 and 662 trophic level transitions across the phylogeny with a mean of 602 transitions across all 1,000 mappings.

Morphospace. Morphospace generation through principal component analysis (PCA) recovered four axes that each accounted for at least 10% of the morphological variation (Fig. 2 and Supplementary Table 7). The first axis was composed of traits representing overall body depth or elongation, and accounted for 31.32% of the variation. Axis two represented 18.82% of the variation and was composed of caudal fin aspect ratio and maximum standard length. Species with high aspect ratios and large maximum standard lengths, such as jacks, tended to occupy similar regions of morphospace to one another, while species with smaller maximum standard lengths and smaller aspect ratios, such as gobies, also tended to occupy similar areas of morphospace to one another. The third axis of variation represented a second elongation axis that was driven by species having deep bodies but elongate lower jaws, such as frogfish, representing 17.52% of the variation. However, in contrast with the first PCA axis, this axis was predominantly dominated by differences in body shape as they relate to jaw size. Axis four represented variation in caudal peduncle traits between species with short and deep peduncles, such as angelfish, and species with elongate and narrow peduncles, such as pipefish. These results largely conform with morphospaces obtained in other studies as body depth and elongation is commonly found to be the main axis of variation in fishes[44–46].

Rates of morphological evolution. Herbivores were found to have the fastest rates of overall morphological evolution, as well as the fastest rate of locomotor prey acquisition morphology, caudal fin aspect ratio, head length, lower jaw length and peduncle length (Table 1). Top-level predators had the fastest rates of evolution for rate of prey acquisition morphology, body depth, eye diameter, maximum standard length and caudal peduncle depth. Top-level predators

had the slowest rates of lower jaw length evolution. We found that omnivores had the slowest rates of overall morphological evolution, as well as for prey acquisition morphology, body depth, eye diameter, maximum standard length and peduncle depth. Mid-level predators had the slowest rates of morphological evolution for the multivariate rate of locomotor traits associated with prey capture, aspect ratio, head length and peduncle length.

We found minimal differences between the full dataset and both the Bellwood and Wainwright dataset[47] and the dataset for 50% of extant taxa occurring on coral reefs (Supplementary Tables 8 and 9 and Supplementary Figs. 4 and 5). For both datasets, herbivores were found to have the fastest rates of morphological evolution for all traits and trait sets, except for body depth, eye size and caudal peduncle depth, for which the fastest rate of evolution was found to be in top-level predators. Omnivores had the slowest overall rate of morphological evolution, as well as the slowest rate for prey acquisition feeding morphology, eye diameter and maximum standard length, while mid-level predators had the slowest rates for locomotor prey acquisition morphology, caudal fin aspect ratio and body depth. Top-level predators had the slowest rates of morphological evolution for lower jaw length and peduncle length in both datasets. The slowest rate of evolution for head length was found to be the mid- and top-level predators for the Bellwood and Wainwright dataset and the dataset for 50% of extant taxa occurring on coral reefs, respectively.

Analyses limited to the family level exhibited few significant differences in rates of phenotypic evolution, and these differences were not always congruent with the global pattern in our dataset (Supplementary Table 18). Significant rates within a family were often the result of very few dietary transitions and serve to highlight the issues involved in inferring general patterns from small taxonomic groups with few transitions in the character of interest (Supplementary Information).

Diet breadth. Herbivores had the narrowest diet breadth (with a mean breadth of 0.018), followed by top-level predators, mid-level
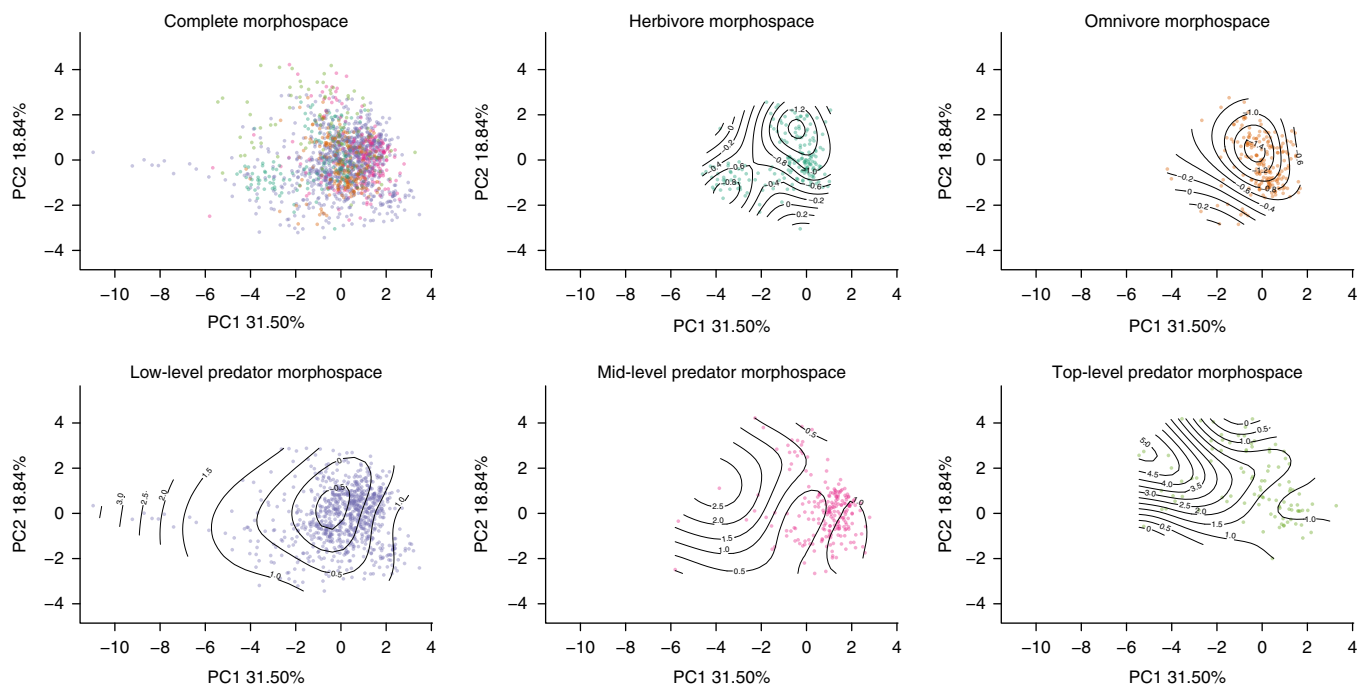
Fig. 2 | Morphospace by trophic level of 1,545 reef acanthomorphs based on 8 phenotypic functional traits. The morphospace was generated via PCA. Principal component 1 (PC1) was composed of traits representing differences in body depth and elongation, representing 31.46% of the variation in the morphological data. Principal component 2 (PC2) represented 18.85% and was driven by changes in body size and caudal fin aspect ratio. Contour lines represent principal component 3, which accounted for 17.52% of the variation. Each trophic level has been plotted in individual plots scaled to the complete morphospace to show the morphospace occupation at each trophic level. Colours for trophic levels in individual plots are the same as in the complete morphospace of all 1,545 reef acanthomorph species.

Table 1 | Rates of morphological evolution for 5 trophic levels of 1,545 species of coral reef fishes

Trait(s)	Herbivores	Omnivores	Low-level predators	Mid-level predators	Top-level predators	Lowest rate	P value
All traits	2.433	1.000	1.394	1.383	2.047	0.0002680	0.0001
Aspect ratio	4.982	1.031	1.184	1.000	1.208	0.0002560	0.0001
Body depth	1.344	1.000	1.797	1.042	3.044	0.0001290	0.0001
Orbit size	2.135	1.000	1.824	1.596	2.475	0.0001300	0.0001
Head length	1.952	1.390	1.297	1.000	1.303	0.0000602	0.0004
Lower jaw length	1.647	1.323	1.476	1.437	1.000	0.0002600	0.0119
Locomotor prey acquisition traits	3.154	1.091	1.459	1.000	2.045	0.0001750	0.0001
Peduncle depth	1.786	1.000	1.391	1.167	3.276	0.0001350	0.0001
Peduncle length	3.573	1.286	1.781	1.000	2.121	0.0002680	0.0001
Prey acquisition traits	1.961	1.000	1.442	1.630	2.191	0.0002810	0.0001
Maximum standard length	2.449	1.000	1.525	2.109	2.819	0.0007170	0.0001

Results are for 11 different sets of traits—1 for the entire dataset of 8 traits, 1 composed of 5 traits for prey acquisition performance, 1 for 5 traits important for the locomotion used in prey capture, and 1 for each of the 8 individual traits. The rates of each trophic level are presented as the ratio of the rate of evolution for that trophic level relative to the lowest calculated rate of evolution.

predators, low-level predators and omnivores, with diet breadths of 0.039, 0.072, 0.094 and 0.101, respectively (Fig. 3, Supplementary Table 10 and Supplementary Fig. 6). The results of the phylogenetic analysis of variance (ANOVA) ($F_{4,1540} = 46.18$, $P = 0.002$) recovered all pair-wise comparisons of diet breadth between trophic levels to be significantly different from each other except among top-level predators and herbivores ($P = 0.701$) and omnivores and low-level predators ($P = 0.203$) (Fig. 4). Phylogenetic ANOVA performed on the reduced Bellwood and Wainwright dataset and the dataset for

50% of extant taxa occurring on coral reefs yielded similar results to those of the full dataset, and are discussed in detail in Supplementary Figs. 2, 4 and 5 and Supplementary Tables 12 and 15.

Multivariate functional diversity. We found that top-level predators had the greatest morphological dispersion, representing a higher amount of phenotypic functional diversity. Top-level predators had a dispersion value from the centroid of 3.115, while low-level predators, herbivores, mid-level predators and omnivores
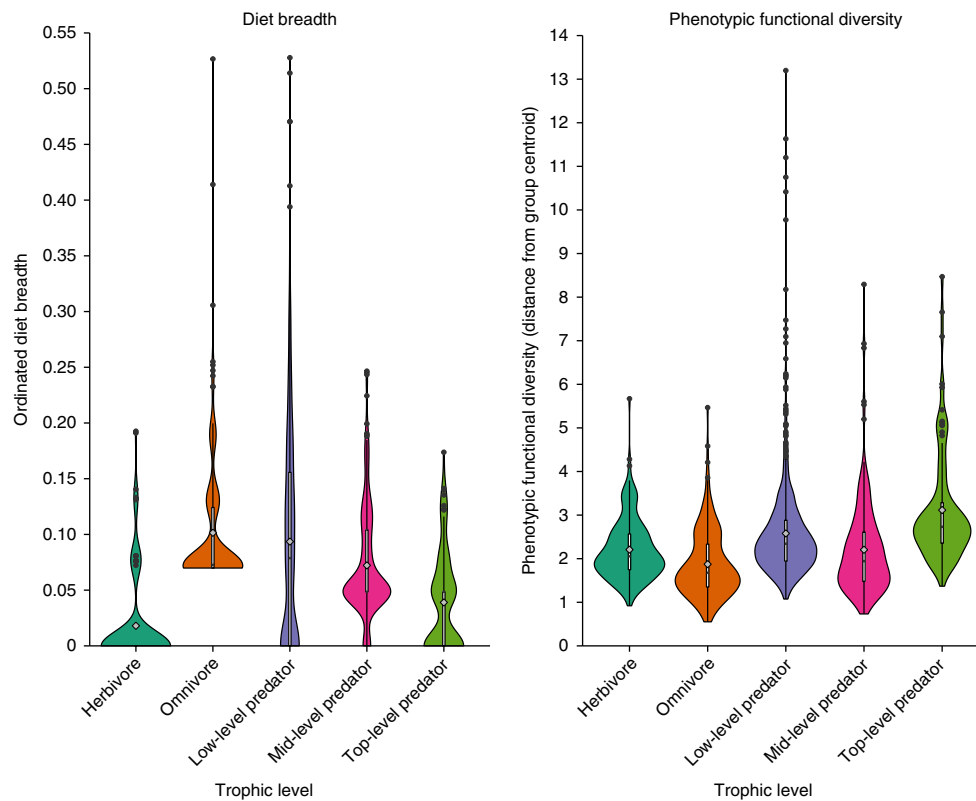
Fig. 3 | Violin plots of diet breadth and phenotypic functional diversity at each trophic level. Boxplots overlaid represent the quantile range, while grey diamonds are the means. Diet breadth was measured using the R package ordiBreadth for each trophic level. The results show that the extreme trophic levels have the narrowest diet breadths, while omnivores have the widest. Functional diversity values are distances from the centroid, measured using the betadisper function in vegan for eight ecomorphological traits. Phylogenetic ANOVA revealed that all trophic levels are significantly different from each other except for between mid-level predators and herbivores.

had multivariate dispersion values of 2.579, 2.207, 2.204 and 1.873, respectively (Fig. 3 and Supplementary Table 11). Phylogenetic ANOVA ($F_{4,1540} = 32.4$, $P = 0.005$) revealed that all trophic levels were significantly different from each other in morphological dispersion, except between herbivores and mid-level predators ($P = 0.99$; Fig. 4).

We found slightly different results for the reduced Bellwood and Wainwright dataset and the dataset for 50% of extant taxa occurring on coral reefs. While we consistently recovered top-level predators as having the highest functional diversity (and omnivores the lowest), the functional diversity values for herbivores approached those of omnivores in both datasets. Additionally, the estimated functional diversity values for top- and low-level predators were similar and not significantly different. We provide more detail on these results in Supplementary Figs. 2, 4 and 5 and Supplementary Tables 14 and 16.

There were significant differences in functional diversity in 18 families (Supplementary Tables 19 and 20), but these results were heavily driven by trophic levels occupied by only a single taxon, which produced a functional diversity value of zero (Supplementary Information).

Discussion

We find that species at trophic level extremes, which have reduced diet breadths relative to other trophic levels, have the fastest rates of morphological evolution and—for the top-level predators—more functional phenotypic diversity. This result is in contrast with what would be expected by the NVH. In addition, we consistently find that omnivores have the slowest rate of morphological evolution, as well as the lowest amount of phenotypic functional diversity. While

studies in other organisms find contrasting evidence for omnivory constraining morphological evolution[48,49], it is possible that functional constraints associated with feeding on functionally disparate prey sources limit morphospace to a generalized morphology to exploit a variety of prey[50].

Our results differ from those found by previous HCH-supporting studies, which suggested that feeding at high trophic levels might constrain morphological evolution in fishes[17,19,51], as well as non-fish taxa[52]. One reason could be the broad phylogenetic sampling of our dataset in contrast with previous studies. Piscivores consistently have the slowest rate of lower jaw length evolution across all datasets. Lower jaw size is associated with gape size—a key factor governing suction feeding performance on large, elusive prey[53], as well as a constraint to the size of prey it is possible for an individual to ingest—and is probably under strong selection[33,54–56]. However, our data reveal that top predators exhibit extreme diversity in other traits. Rates of body depth and peduncle depth evolution in top-level predators also contribute significantly to them consistently being recovered as having the second-fastest rates of phenotypic evolution throughout all datasets. These two traits are directly related to feeding performance. Body depth is partly composed of the epaxial muscles on the dorsal portion of the fish. These muscles play a crucial role in suction feeding performance, with deeper-bodied species having a larger cross-sectional area[53,57,58]. Peduncle depth is thought to play a prominent role in the ability of cruising predators to sustain food searches over long distances. Lesser depth reduces the laterally directed drag incurred by the oscillating tail[59] and makes it easier to achieve the high acceleration required for a rapid strike towards an evasive prey item[60].
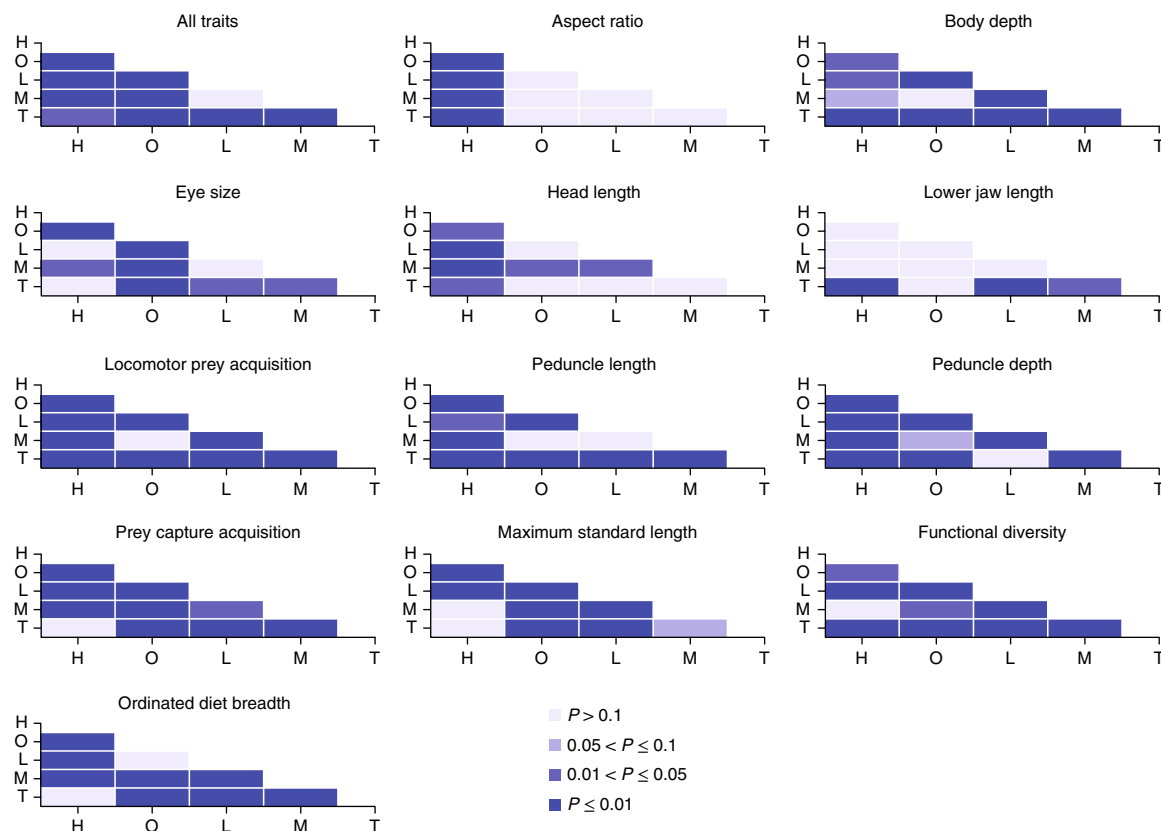
Fig. 4 | Summary of multiple pair-wise comparisons for rates of morphological evolution, functional diversity and diet breadth among trophic levels. Trophic levels are denoted by a single letter (H, herbivore; O, omnivore; L, low-level predator; M, mid-level predator; T, top-level predator). Significance for rates of phenotypic evolution was determined via phylogenetic simulation, while phylogenetic ANOVA was used to test for significant differences in functional diversity and diet breadth. Darker values represent lower *P* values and significant differences, while lighter values represent higher *P* values where comparisons are not significant.

Another explanation for the increased rate of evolution and morphological disparity in top-level predators is that the diversification of fish species at lower trophic levels, which form the prey base of top-level predators, may have driven ecological and phenotypic diversification in top-level predators—a pattern coined 'upward adaptive radiation cascades'[61]. While our study does not directly address this question, both theory[62] and empirical studies[63,64] suggest that such a pattern of co-evolution among trophic levels occurs, and we believe that it warrants future study, especially in reef systems, which—as biodiversity hotspots—harbour a wealth of prey items and have complex trophic interactions.

We find mixed evidence for the TEH. While we recover herbivores and top-level predators as having faster rates of phenotypic evolution relative to other trophic levels, supporting the TEH, we find that only top-level predators display high phenotypic functional diversity. While herbivores have the fastest rate of phenotypic evolution in our analyses, we do not recover them as having high functional phenotypic diversity. This result is stronger in the two sub-datasets due to the exclusion of some rather extreme herbivores, such as halfbeaks (family Hemiramphidae), that do not meet the criteria for the Bellwood and Wainwright dataset or the dataset for 50% of extant taxa occurring on coral reefs. This suggests that there are certain constraints on herbivores in relation to possible morphospace occupation.

One contributor to the elevated rates of evolution found in both herbivore and top-level predators is body size. Consistently, we recover the trophic extremes as having the fastest rates of body size evolution across all datasets. While there is conflicting evidence looking at broad-scale patterns among body sizes and trophic levels in fish[65,66],

we believe the elevated rate of body size evolution at the extreme trophic levels is best described by microhabitat partitioning among the reef in which large reef-cruising phenotypes and smaller phenotypes associating with high levels of reef structure and interstitial spaces are both successful[67].

Our results suggest that there are multiple ways to be a successful top-level predator. While our study does not specifically test many-to-one mapping of morphology to trophic level, a many-to-one mapping of morphology to trophic ecology may explain why top-level predators occupy a large area of morphospace, and warrants future research[68,69]. While we find that low-level predators have the second-highest value for phenotypic variation and are significantly different from all other trophic levels, this result is not surprising due to the sheer number of taxa that fall into this group (nearly four times as many than any other trophic level). While the distribution of taxa in each trophic level roughly follows the known distribution for global fish diversity[70], the low-level predators encompass a large amount of diversity in terms of ecomorphology and prey use, including some of the most enigmatic and extreme species in our dataset, such as pipefish. The high rates of phenotypic evolution in herbivores, yet low amounts of functional diversity, suggest that there are a limited number of ways to consume algae and other plant matter—at least with our measured functional traits. We would expect that incorporation of other functional morphological traits, such as tooth shape[71,72], the shape and size of the digestive tract[72–74], and the presence of intramandibular joints[73,75,76], would probably elevate the level of functional diversity measured within this group as it relates to partitioning of trophic resources within herbivores[77]. Another possible explanation for the high rates of morphological evolution

yet low functional phenotypic diversity in herbivores is that herbivory and detritivory are often relatively recent evolutionary transitions among reef acanthomorphs[78,79]. Under a Brownian motion model of trait evolution, trait variance is expected to increase over evolutionary time. Therefore, recent transitions to herbivory may have led to the fast rates of phenotypic evolution we observed, yet limit possible dispersion into more extreme phenotypes, leading to limited functional phenotypic diversity. Transitions to diets low in protein and fat have also been linked to increased diversification rates, probably due to ecological opportunity and exploitation of such resources[80,81], and integrating diversification with phenotypic and trophic evolutionary patterns would prove fruitful in elucidating the macroevolutionary factors governing reef diversity.

One criticism of the NVH is that it is generally tied to morphological variation, while the hypothesis could pertain to any phenotypic trait, including behavioural traits[23]. While we have discussed some possible factors influencing the elevated rates of morphological evolution at extreme trophic levels, foraging behaviour probably has a role in shaping the evolution of these traits. For example, one component of the elevated morphological rates measured in herbivorous species might be divergence between strategies of active browsing for algae and plants[82] versus the strategy of algal gardening, in which territorial species defend a patch of reef from other herbivores, and forage algae from within this territory[83]. This might explain the elevated rates of caudal peduncle length and caudal fin aspect ratio observed in herbivorous species relating to their foraging strategy. Many browsers are typically active swimmers over reefs or in turbulent reef zones, while the more territorial algal gardeners are far more sedentary, where a lower aspect ratio is better suited for protecting their algal garden and renders them capable of quick short bursts for chasing intruders away[84]. Differences in foraging strategies are also apparent for top predators, which hunt using stalking, ambush or pursuit strategies[85–87]. Even within these hunting strategy categories, there is considerable variation in body forms. For example, two piscivorous predators (fishes of the families Aulostomidae and Antennariidae) both employ ambush hunting methods despite being on opposite extremes of the morphospace[88–90].

The trophic levels experiencing the fastest rates of functional evolution—top-level predators and herbivores—are also heavily targeted by reef fisheries. Many reef fisheries focus on top-level predators, leading to widespread overfishing of iconic coral reef predators such as groupers[91]. Substantial fishing pressure also affects herbivores (especially large grazers such as parrotfish and rabbitfish), and overfishing of these species can substantially affect algal biomass and coral cover[41,92,93]. Unfortunately, because many reef fisheries are at subsistence level and many reef species occur on wide geographic scales, it can be challenging to assess fishing pressures in an integrated way[94]. We suggest that a focus on trophic position and functional traits can provide a key avenue for integrating evolutionary ecology with sustainability and conservation, particularly in relation to traditional single species-focused approaches.

It is important to note that our study does not address non-trophic selective pressures that may be important in shaping the morphological diversity of reef assemblages. While our main axis of diversification revolves around the depth or elongation of the body, which we have discussed above as being important for prey capture, it is also important for defence from predators[31,95]. Modes of locomotion are quite diverse in reef fishes, involving various uses of fins, which are thought to have consequences for swimming performance, body form and fin design[96,97]. Additionally, our study does not contain data on myriad other morphological and physiological aspects that play a role in shaping the trophic ecology of species, and we welcome the addition of increasingly sophisticated sets of functional traits in future studies. At the deep phylogenetic scale of our analysis, interspecific variation is probably far more prevalent

than intraspecific variation. However, as our study was performed on a single representative photograph of a species, it does not capture possible intraspecific variation due to factors such as sexual dimorphism or body condition. It is also possible that using more complex models, such as Ornstein–Uhlenbeck processes[98,99], might reveal other aspects of the trait evolution process. We also note that, while they control for phylogeny, methods for examining rates of continuous trait evolution may be subject to the issues identified by Maddison and FitzJohn[100]: a rate increase in one clade of top-level predators and no rate change in any other top-level predator clade would still be significant under the tests used here. Our results at the family level highlight the utility of large-scale comparative analyses to adequately account for transitions and understand broad macroevolutionary patterns.

Our results suggest limited diet breadth, and the extremes of trophic level do not constrain functional diversity and phenotypic evolution in reef fishes. This result is in contrast with that predicted by the NVH, indicating that limited niche breadth does not constrain evolutionary rates and phenotypic diversity. Our results provide the most support for the TEH, as species at trophic level extremes have the fastest rates of morphological evolution. We suggest that trophic ecology plays a critical role in assemblage functional trait evolution on macroevolutionary timescales.

Methods

Trophic level data acquisition. We used the R interface to FishBase, rfishbase (refs [101,102] and http://www.fishbase.org/) to identify species of reef-associated acanthomorph fishes for which diet data were available. For the reef-associated acanthomorphs identified, we obtained volumetric diet data and food item data using the rfishbase diet and ecology functions. To avoid bias in ontogenetic changes in trophic ecology through development, diet data were filtered to remove entries that were entirely based on recruits and juveniles. Trophic levels based on volumetric diet data and from food items were calculated following the routines described by Froese and Pauly[103]. Preference was given to records where the trophic level could be calculated from volumetric stomach contents, as opposed to estimates based on food items, although estimates based on food items have been shown to be a rough estimator of trophic level[103,104]. Species were placed in 5 discrete trophic categories following Froese[70], with trophic levels less than 2.20 being classified as herbivores, 2.21–2.80 as omnivores, 2.81–3.80 as low-level predators, 3.81–4.20 as mid-level predators and greater than 4.2 as top-level predators (Supplementary Table 1). We provide more detail on trophic level data acquisition in the Supplementary Information.

Phylogenetic reconstruction. DNA alignments were obtained for 3 mitochondrial and 12 nuclear genes for the 1,545 species of reef acanthomorphs from 92 families for which trophic level data were obtained, and an outgroup taxa, *Megalops atlanticus*, using the Phylogeny Assembly with Databases pipeline[105]. Additional sequences were extracted from whole mitochondrial genomes using the R package AnnotationBustR[106,107] to supplement sequences obtained using the Phylogeny Assembly with Databases pipeline (Supplementary Table 2 and Supplementary File 1). Phylogenetic analyses were performed using RAxML 8.2.8 (ref. [108]) under the GTR + gamma model of sequence evolution partitioned by gene and codon position. For use in comparative analyses, we converted the phylogeny to an ultrametric tree using treePL with 12 fossil calibrations[109] (Supplementary Table 5). We provide more detail on the phylogenetic reconstruction methods used in this study in the Supplementary Methods.

Morphological data acquisition. We obtained a representative lateral image of each species in our diet dataset from online fish image databases or other available resources (Supplementary Table 1). A set of 13 landmarks were digitized on each image using tpsDIG 2.26 (ref. [110]) to measure 7 functional traits: head length, orbit size, lower jaw length, body depth, caudal peduncle length, caudal peduncle depth and the caudal fin aspect ratio (Supplementary Fig. 1 and Supplementary Table 3). All functional traits except the caudal fin aspect ratio were size-corrected to account for allometry by taking the residuals from a $\log_{10}$–$\log_{10}$ regression on standard length. In addition to the six size-corrected $\log_{10}$-transformed functional traits and $\log_{10}$-transformed caudal fin aspect ratio, we included the $\log_{10}$-transformed maximum standard length of each species for our analysis obtained using the rfishbase species function. These traits are important ecomorphological traits for feeding performance as they relate to the trophic apparatus, prey detection and locomotion associated with prey capture[54,60,111,112]. These eight $\log_{10}$-transformed traits were subjected to PCA using the prcomp function in R to generate a morphospace. We provide a detailed description of the digitization process for generating our phenotypic dataset in the Supplementary Methods.

Measuring rates of trait evolution. We used the R package geomorph to measure the multivariate rate of morphological evolution for each trophic level for the 8 measured traits using the compare.evol.rates function under 10,000 simulations to assess significance[113]. We also ran the compare.evol.rates function on two subsets of traits: one set for prey acquisition morphology, which was composed of head length, lower jaw length, eye diameter, body depth and maximum standard length; and another for traits important for locomotion associated with prey capture, which was composed of head length, body depth, caudal peduncle length, caudal peduncle depth and the caudal fin aspect ratio. In addition to the multivariate models described above, we ran each of the eight traits individually to measure the rate of evolution for each trait. As the definition of what constitutes a reef fish is debatable[114,115], we also ran the above models on a subset of 1,306 taxa from 57 families that are found on, and characteristic of, coral reefs, according to Bellwood and Wainwright[47], as well as on a dataset of 1,038 taxa from 32 families where at least 50% of extant taxa occur on coral reefs, to limit potential biases in the results caused by the inclusion of fishes from families not typically associated with reef environments. To assess whether similar patterns occur in smaller clades, we also measured rates of trait evolution in all families containing more than one trophic level category and more than five species ($n = 29$).

Diet breadth analysis. We measured diet breadth for each species using the R package ordiBreadth[116]. This method calculates ordinated diet breadth by subjecting a dissimilarity matrix (in our case a Jaccard dissimilarity matrix) of dietary items to principal coordinates analysis and, after ordination, measures ordinated diet breadth as the sum of the distances of a given consumer's multivariate centroid to its consumed prey items. This method has advantages over taxonomic and phylogenetic measures of diet breadth as it tends to group shared suites of prey that have functionally similar demands[116].

For easier interpretability, we report the scaled diet breadth, which is the scaled measure of occupation a species has in relative diet space. This value is bounded between 0 and 1, representing specialist species with diets consisting solely of one prey type to a hypothetical generalist consumer feeding on all prey items, respectively. For consistency among food records, we used the 'FoodII' column in the FishBase diet records to generate a binary matrix of 18 prey items. For species that had volumetric diet data, we removed prey items that comprised less than 5% of the diet to remove prey items that were probably incidentally consumed or play a minor role in the overall diet of the species. The analysis was also repeated with a 1% cut-off (Supplementary Information).

To test whether certain trophic levels had narrower diet breadths, we performed a phylogenetic ANOVA using the R package geiger[117], and performed Tukey's honest significant difference test to determine whether there were significant differences in diet breadth among trophic levels. We would expect that taxa at the extremes of trophic levels would have significantly lower diet breadths compared with taxa at intermediate trophic levels, as to reach the extremes of trophic levels the diets of herbivores and top-level predators must be composed predominantly of plant and nekton prey items, respectively, while intermediate trophic levels can be obtained by feeding on a variety of prey types, some of which are highly disparate in processing requirements. We also measured ordinated diet breadth as described above for the subset of taxa consisting of reef families according to Bellwood and Wainwright and 50% of extant taxa occurring on coral reefs datasets.

Functional diversity analysis. To determine whether certain trophic levels had more phenotypic functional diversity than other trophic levels, we measured the multivariate dispersion at each trophic level, following Anderson et al.[118]. We measured the mean multivariate dispersion of each trophic level from its centroid in multivariate trait space using the betadisper function on the morphospace described above using the R package vegan[119], while correcting for sample size biases following Stier et al.[120]. This measure of dispersion has been recommended as a functional diversity index[121]. We then performed a phylogenetic ANOVA[122] in geiger[117] and performed Tukey's honest significant difference test to determine whether there were significant differences in functional diversity among trophic levels. We would expect that trophic levels with wider overall diet breadths would have greater multivariate phenotypic dispersion relative to trophic levels with narrower diet breadths following the NVH, and that trophic extremes would have reduced multivariate functional dispersion following the HCH. We also measured functional phenotypic diversity as described above for the subset of taxa consisting of reef families according to Bellwood and Wainwright and 50% of extant taxa occurring on coral reefs datasets. To assess whether similar patterns occur in smaller clades, we also measured functional diversity in all families containing more than one trophic level category and more than five species ($n = 29$).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data and scripts used in this study are stored in the Dryad Digital Repository (https://doi.org/10.5061/dryad.7t3d30c), which is open access.

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Author contributions

S.R.B. and M.D.M. designed the study. S.R.B. and J.A.F. performed the analyses. S.R.B., J.A.F. and M.D.M. wrote the manuscript with substantial comments from B.C.O. and P.C.W.

Competing interests

The authors declare no competing interests.

Additional information

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☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated
☐	☒	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on [statistics for biologists](#) may be useful.

Software and code

Policy information about [availability of computer code](#)

Data collection	All data originated from publicly available datasets Sequence data was obtained from GenBank. Fish diet data were obtained through FishBase. We obtained lateral images of fishes for digitization of morphology from a variety of publicly available online resources and primary literature.
Data analysis	Diet data for reef Acanthomorph fishes was obtained through the R interface to FishBase, rfishbase. We used custom R scripts we include in our supplemental material to calculate trophic level by implement the sampling routine described in TrophLab. We used PHLAWD to obtain and align sequence Data from GenBank. RAxML was used for phylogenetic reconstruction. Phylogenies were fossil calibrated using treePL. A variety of R packages were used to analyze the data. All software other than the custom R scripts are open source and freely available and we include the custom R scripts as supplemental files.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

Data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

> Data and scripts used in this study are stored in the Dryad Digital Repository (https://doi.org/10.5061/dryad.7t3d30c), an open-access repository.

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☒ Life sciences ☐ Behavioural & social sciences ☐ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	As we performed phylogenetic comparative analyses, our sample sizes were limited to species means. In cases where species had more than one diet study record on FishBase, we calculated the average trophic level. Our morphological dataset was limited to a single representative for each species due to the difficulty of finding high quality lateral images of adult non-preserved fishes. At the deep scale of this phylogenetic study, we expect far more inter-specific variation than intra-specific variation.
Data exclusions	Three species were included in our phylogenetic reconstruction and later excluded from the phenotypic evolution analyses as they lacked a caudal fin and caused homology issues in relation to digitizing morphological traits relative to the other species in our data set. All 993 diet records obtained through R fishbase were inspected for quality by the authors and we eliminated 10 records that deviated substantially from known ecologies of these species. These records all came from a single study in which unidentified food was listed as detritus. Inclusion of these records would have substantially biased trophic level estimations for these species, and were therefore removed.
Replication	We report all accession numbers we used from GenBank for the generation of the phylogeny and provide the data and code used to perform this study as supplemental files.
Randomization	We performed phylogenetic comparative methods and randomization is not relevant to this study.
Blinding	We performed phylogenetic comparative methods and blinding is not relevant to this study.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	Unique biological materials
☒	Antibodies
☒	Eukaryotic cell lines
☒	Palaeontology
☐	☒ Animals and other organisms
☒	Human research participants

Methods

n/a	Involved in the study
☒	ChIP-seq
☒	Flow cytometry
☒	MRI-based neuroimaging

Animals and other organisms

Laboratory animals	No live animals were involved in this study.
Wild animals	No animals were collected for this study.

Field-collected samples

No collections were made as part of this study. All data used in this study was obtained through published databases and literature and not directly collected by the authors.