

1 **Global gut content data synthesis and phylogeny delineate reef fish trophic**
2 **guilds**

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33

1 **Abstract**

2 The diversity of life on our planet has produced a remarkable variety of biological traits that
3 characterize different species. Such traits are widely employed instead of taxonomy to increase
4 our understanding of biodiversity and ecosystem functioning. However, for species' trophic
5 niches, one of the most critical aspects of organismal ecology, a paucity of empirical information
6 has led to inconsistent definitions of trophic guilds based on expert opinion. Using coral reef
7 fishes as a model, we show that experts often disagree on the assignment of trophic guilds for the
8 same species. Even when broad categories are assigned, 60% of the evaluated trait schemes
9 disagree on the attribution of trophic categories for at least 20% of the species. This
10 disagreement greatly hampers comparability across studies. Here, we introduce a quantitative,
11 unbiased, and fully reproducible framework to define species' trophic guilds based on empirical
12 data. First, we synthesize data from community-wide visual gut content analysis of tropical coral
13 reef fishes, resulting in trophic information from 13,961 individuals belonging to 615 reef fish
14 species across all ocean basins. We then use network analysis to cluster the resulting global
15 bipartite food web into distinct trophic guilds, resulting in eight trophic guilds, and employ a
16 Bayesian phylogenetic model to predict trophic guilds based on phylogeny and maximum body
17 size. Our model achieved a misclassification error of 5%, indicating that our approach results in
18 a quantitative and reproducible trophic categorization scheme, which can be updated as new
19 information becomes available. Although our case study is for reef fishes, the most diverse
20 vertebrate consumer group, our approach can be applied to other organismal groups to advance
21 reproducibility in trait-based ecology. As such, our work provides an empirical and conceptual
22 advancement for trait-based ecology and a viable approach to monitor ecosystem functioning in
23 our changing world.

1 **Introduction**

2 A fundamental goal in ecology is to understand the mechanisms behind the maintenance of
3 biodiversity and ecosystem functioning [1,2]. Understanding the ecological niches of species is
4 central to this endeavor [3,4]. In fact, the degree of niche overlap among species can be a major
5 determinant of the positive relationship among species richness [5], ecosystem productivity [6–
6 8], and ecosystem vulnerability [9] since limited functional redundancy can make ecosystems
7 more prone to lose entire energetic pathways [10–12]. With growing threats to biodiversity, the
8 need to quantify the impact of biodiversity loss has amplified the use of functional groups, which
9 are species groups that share common ecological characteristics and are often defined with
10 coarse, categorical descriptors of species traits [13–16].

11 Delineating the ecological niche with discrete categories has several operational
12 advantages. First, grouping species into categories helps decompose highly complex ecosystems
13 into comprehensible units, while traditional taxonomic analyses may be difficult to interpret in
14 highly diverse ecosystems. Second, ecological predictions tied to individual species are restricted
15 to the geographic range of the species, whereas predictions of functional groups can be globally
16 comparable. Third, the use of functional groups enables the quantification of functional metrics
17 (e.g. functional richness and functional redundancy) from a standard community data matrix
18 without complex experiments [17–19]. The promise of developing “user-friendly” metrics for
19 functional ecology has motivated the employment of trait-based data in community ecology;
20 even with a paucity of empirical information, it is often assumed that experts can achieve
21 accurate descriptions of the ecological niche of species [17,20,21].

22 Coral reefs, one of the most diverse marine ecosystem on Earth, have inspired a plethora
23 of trait-based ecological studies, with significant recent efforts to compile trait-based datasets for

1 two major components of this ecosystem: corals and fishes [22,23]. For some traits, such as
2 maximum body size in fishes, the compilation process is simple because unidimensional,
3 quantitative data (e.g. maximum total length) are compiled in publicly accessible databases;
4 however, when it comes to species' diet or behavior, obtaining consensual data is much more
5 difficult. For example, dietary data are multidimensional (i.e. various prey items can be recorded
6 across individuals), ontogenetically variable (i.e. diet differs between juveniles and adults),
7 spatially variable (i.e. species may show dietary plasticity across locations), and prone to
8 methodological differences and observer bias. Therefore, researchers that employ traits to
9 delineate trophic groups or behavioral characteristics commonly rely on expert opinion [19].
10 While there is some agreement among experts on which traits are relevant (e.g. diet, mobility,
11 body size, diel activity), there is often an implicit disagreement on the necessary categories to
12 describe these traits. For example, across the coral reef literature, the number and resolution of
13 reef fish trophic guilds substantially differs. Studies commonly define three [24] to eight [25]
14 trophic guilds, with particular ambivalence on the resolution at which to define herbivores and
15 invertivores [26–29].

16 Among all trait classification schemes for reef fishes, only a few are openly accessible.
17 Consequently, different research groups tend to employ proprietary functional classifications,
18 with little possibility to cross-check and compare assigned traits with previous classifications.
19 The classification of species into functional groups has advantages for our understanding of
20 ecological patterns [30,31]. However, the lack of agreement and the limited transparency of trait-
21 based datasets can conjure skepticism and inhibit the emergence of general patterns.

22 Here, we quantify expert disagreement in the definition of reef fish trophic guilds and
23 propose a novel, transparent, and quantitative framework to delineate trophic guilds. Using coral

1 reef fishes as a case study, we compiled all quantitative, community-wide dietary analyses from
2 several locations across the Pacific and Caribbean and used network analysis to define eight
3 modules that correspond to trophic guilds. We then examined phylogenetic niche conservatism
4 with a phylogenetic Bayesian multinomial model that predicted trophic guilds to the global pool
5 of coral reef fishes, including measures of uncertainty. Our framework is fully reproducible and
6 can be extended and updated as new data become available.

7

8 **Materials and Methods**

9 **Assessment of expert agreement**

10 We systematically searched Google Scholar, including papers since 2000, using the following
11 keywords: “coral reefs” AND “reef fish” AND (“fish community” OR “fish assemblage”) AND
12 “diet” AND (“functional group” OR “functional trait” OR “functional entity” OR “trophic guild”
13 OR “trophic group”). The results were individually assessed to find data on trophic guilds. We
14 only considered studies performed at the community level that targeted all trophic levels. Most
15 studies were excluded because they only included specific families or groups, or the data were
16 not provided with the publication. We often found redundant results, with groups publishing
17 several papers using the same classification scheme. In those cases, only the first reference was
18 retained. We contacted authors when trophic classifications were widely used across the
19 literature, but data were not provided with the publications.

20 Our search yielded a total of eight independent trophic classifications, including Mouillot
21 et al. [26] and Parravicini et al. [27] with 6,316 species, Brandl et al. [32] with 257 species,
22 Halpern and Floeter [33] with 1,046 species, Graham et al. [34] with 126 species, Morais and
23 Bellwood [35] with 515 species, Yeager et al. [36] with 480 species, Newman et al. [37] with 84

1 species, and Stuart-Smith et al. [29] with 3189 species. The classifications were not uniform in
2 terms of the number and nature of trophic guilds. To achieve comparability, we converted the
3 original classification to match five broad trophic guilds: *herbivores and detritivores*,
4 *invertivores, omnivores, planktivores, and piscivores*. All of the classifications could be
5 reattributed to these categories with the exception of Graham et al. [34], which did not include
6 the category *omnivores*. In this case, the comparison was made only across the four comparable
7 guilds.

8 In order to assess expert agreement, we compared each possible pair of classifications
9 that shared at least 30 species, generated a confusion matrix, and measured agreement as the
10 proportion of species with matching trophic guild assignments. We then calculated the average
11 agreement between classification pairs for each trophic guild.

12

13 **Data collection on fish gut contents**

14 To provide a quantitative definition of trophic guilds for reef fishes, we collected gut content
15 data across the literature at the individual or species level for Chondrichthyes (i.e. cartilaginous
16 fishes) and Osteichthyes (i.e. bony fishes). We obtained dietary information from six published
17 works: Hiatt & Strasburg (1960) for the Marshall Islands [38], Randall (1967) for Puerto Rico
18 and the Virgin Islands [39], Hobson (1974) for Hawaii [40], Harmelin-Vivien (1979) for
19 Madagascar [41], and Sano et al. (1984) for Okinawa [42]. In addition, we provide hitherto
20 unpublished data on the gut contents of 3,015 individuals collected in New Caledonia from 1984
21 to 2000.

22 All dietary information was based on visual gut content analysis where prey preference
23 was quantified as volumetric percentage or item frequency. The data were standardized and

1 analyzed as proportions. To our knowledge, the compiled dataset represents the first compilation
2 of detailed coral reef food webs across ocean basins. A total of 13,961 non-empty fish guts
3 belonging to 615 species were analyzed, and more than 1,200 different prey items were
4 described in the original datasets.

5 First, fish species and family names were taxonomically verified and corrected with the R
6 package *rfishbase* [43]. Only species with at least ten non-empty guts were kept for further
7 analysis. The taxonomic classification of each prey item was then obtained, and all poorly
8 informative (e.g. unidentified fragments, unknown species) and redundant items (e.g. “crustacea
9 fragments” when co-occurring with an item already identified to lower taxonomic level such as
10 “shrimp”) were discarded. Prey identification was highly heterogeneous across the six datasets,
11 differing in taxonomic level and the use of common or scientific names (e.g. crabs *versus*
12 Brachyura). In order to make the six datasets comparable, prey items were grouped into 38
13 ecologically informative prey groups (Table S1). Items were generally assigned to groups
14 corresponding to their phylum or class. Due to the high diversity and detailed descriptions of
15 crustaceans, they were assigned to the level of order or superorder. Most groups follow official
16 taxonomic classifications except for “detritus,” “inorganic,” and “zooplankton.” In the West
17 Indies dataset [39], items labelled as “Algae & Detritus” were assigned to both of the categories
18 “detritus” and “benthic autotroph,” and the percentage was equally divided in two. The category
19 “zooplankton” includes all eggs and larvae regardless of taxonomy.

20

21 **Definition of trophic guilds**

22 After data cleaning, we compiled dietary information for 615 species. Of those species, 516 were
23 present in only one location, 66 were collected in two locations, 25 in three locations, 7 in four

1 locations, and only 1 across five locations. Before running an analysis at the species level, we
2 tested whether there was a strong regional signal for species present across more than one
3 location. We created a quantitative bipartite network where fish species at each location were
4 linked to the 38 prey groups. This network was weighted so that edge weights represent the
5 proportional contribution of each prey group to the diet of a species at a given location.

6 In order to identify network modules that correspond to reef fish trophic guilds and their
7 preferred prey, we used the maximization of the weighted network modularity based on weighted
8 bipartite networks [44]. Since the modularity maximization algorithm has an initial random step,
9 it may converge to different (although similar) suboptimal solutions each time the analysis is
10 performed, which is common across several optimization algorithms, such as simulated
11 annealing [45]. To guarantee reproducibility and reduce the risk of basing our analysis on an
12 outlier, we performed the modularity maximization 500 times and retained the medoid solution,
13 which was identified as the solution with the highest similarity to the other 499 modules.
14 Similarity was assessed as the variation of information [46]. Overall, 68% of the site \times location
15 combinations for the same species belonged to the same module. Therefore, we considered the
16 regional effect to be minor and performed the analysis on the global network, ignoring regional
17 variability and increasing the number of individuals per species.

18

19 **Testing for phylogenetic conservatism and predicting trophic guilds**

20 We extracted the phylogenetic position of the 615 species used for the definition of trophic
21 guilds through the Fish Tree of Life [47]. 603 out of 615 species were available in the Fish Tree
22 of Life, but only 535 species had verified phylogenetic information. For the taxa available in the
23 Fish Tree of Life without verified phylogenetic information, we retrieved the pseudo-posterior

1 distribution of 100 synthetic stochastically-resolved phylogenies where missing taxa were placed
2 according to taxonomy using the function *fishtree_complete_phylogeny()* in the R package
3 *fishtree* [48].

4 We quantified the phylogenetic signal by calculating the phylogenetic statistic δ , which
5 uses a Bayesian approach for discrete variables [49]. The δ statistic can be arbitrarily large with a
6 high level of variation, depending on the number of species and trait levels. To evaluate the
7 significance of the δ statistic, we applied a bootstrapping approach where we quantified δ one
8 hundred times after randomly shuffling the trait values.

9 We then fitted a multinomial phylogenetic regression to predict fish trophic guild
10 according to phylogeny and body size with the R package *brms* [50]. We used a multinomial
11 logit link function. As such, the probability of a particular trophic guild is computed as follows:

12
13
$$Pr(k | \mu_1, \mu_2, \dots, \mu_k) = \frac{\mu_k}{\sum_1^k \exp(\mu_i)} \quad (1)$$

14 with μ_k defined as:

15
16
$$\mu_1 = 0, \mu_{k|2:8} = \beta_{0k} + \beta_{1k} \log(\text{sizemax}) + \gamma_{0phy \times k}, \quad (2)$$

17
18 where β_{0k} is the category-specific fixed-effect intercept, β_{1k} is the slope for the natural
19 transformed maximum body size for each category k , and $\gamma_{0phy \times k}$ is the matrix of random effect
20 coefficients that account for intercept variation based on relatedness as described by the
21 phylogeny for each diet category k . We used uninformative priors and ran the model for three
22 chains, each with 6,000 iterations and a warm-up of 1,000 iterations. We visualized the fitted
23 probabilities for each trophic guild with a phylogenetic tree, including the 535 species with
24 verified phylogenetic positions using the R package *ggtree* [49]. Next, we used our model to
25 predict the most likely trophic guild for the global pool of reef fish species. For the extrapolation,

1 we selected all species within reef fish families with more than one representative species (but
2 we also included *Zanclus cornutus*, which is the only species in the family Zanclidae), which
3 resulted in 50 families. Further, we only selected species with a maximum length greater than 3
4 cm, which was the maximum size of the smallest fish in our compiled database. This selection
5 process resulted in a list of 4,554 reef fish species.

6 Currently, no streamlined method exists to predict traits for new species from a
7 phylogenetic regression model. We circumvented this issue by extracting draws of the
8 phylogenetic effect ($\gamma_{0phy \times k}$) for each species included in the model. We subsequently predicted
9 the phylogenetic effects for missing species with the help of the function *phyEstimate* from the R
10 package *picante* [51]. This function uses phylogenetic ancestral state estimation to infer trait
11 values for new species on a phylogenetic tree by re-rooting the tree to the parent edge to predict
12 the node. We repeated this inference across 2,000 draws. Per draw, we randomly sampled one of
13 the one hundred trees. Then, we predicted the probability of each species to be assigned to each
14 diet category by combining the predicted phylogenetic effects with the global intercept and
15 slopes for maximum body size for each draw. Finally, we summarized all diet category
16 probabilities per species by taking the mean and standard deviation across all 2,000 draws.

17 We quantified the total standard deviation (i.e. the square root of the quadratic sum of the
18 standard deviations in each category) and the negentropy value, a measure of certainty calculated
19 by subtracting one from the entropy value (i.e. uncertainty). Thus, the negentropy value lies
20 between 0 and 1, and the higher the value, the higher the certainty for trophic guild assignment
21 (i.e. if a given species has a high probability of assignment to a dietary category, the negentropy
22 value will be high).

23

1 **Results**

2

3 **Assessment of expert agreement**

4 We evaluated the agreement among eight distinct and independent trophic guild classifications
5 by comparing the classification schemes in pairs. Considering the broadness of the expert-
6 assigned categories, we found remarkably low agreement. The median agreement between pairs,
7 expressed as the proportion of species with matching trophic group assignments, was 77% (Fig.
8 1). For 50% of the pairwise comparisons, at least a quarter of the species were attributed to
9 different trophic groups. In the most severe disagreement, the proportion of mismatched
10 assignments reached 39%. In addition, expert agreement differed depending on the trophic
11 group. Despite a few peaks of disagreement for *herbivores and detritivores* (~20%), overall,
12 there was high agreement among experts for this trophic guild, with an average agreement of
13 94% (Fig. 1b). On the contrary, *omnivores* showed the highest mismatch, with experts
14 disagreeing on an average of 30% of the species and peaks of disagreement higher than 60%
15 (Fig. 1b).

16 Expert agreement was variable and often homogeneously distributed around the mean for
17 all the trophic categories. Therefore, the high agreement between a few combinations of experts
18 did not necessarily exclude peaks of disagreement (Fig. 1b). The analysis of individual confusion
19 matrices between pairs of experts revealed high heterogeneity (Fig. 2). For example, Morais and
20 Bellwood [35] were generally in agreement with Mouillot et al. [26] (across 89% of the 515
21 species in common), while Mouillot et al. [26] agreed with Stuart-Smith et al. [29] across only
22 68% of the 2211 species in common.

23 Surprisingly, there was also a high heterogeneity in groups with high disagreement (i.e.
24 multiple alternative assignments for species not assigned to the same trophic group). Species

1 classified as *invertivores* according to one expert were considered *omnivores*, *piscivores*, or
2 *planktivores* according to other classification schemes (Fig. 2). Similarly, species considered
3 *omnivores* by one expert were alternatively considered *invertivores*, *herbivores* and *detritivores*,
4 or *planktivores* by another expert.

6 **Definition of trophic guilds**

7 We defined trophic guilds by identifying modules (i.e. combinations of predators and prey) that
8 maximize the weighted modularity of the global network. Our analysis robustly identified eight
9 distinct modules that correspond to different trophic guilds (Fig. 3). We identified these trophic
10 guilds as:

- 11 (1) *Sessile invertivores*: species predominantly feeding on Asteroidea, Bryozoa, Cirripedia,
12 Porifera, and Tunicata;
- 13 (2) *Herbivores, microvores, and detritivores (HMD)*: species primarily feeding on
14 autotrophs, detritus, inorganic material, foraminifera, and phytoplankton;
- 15 (3) *Corallivores*: species primarily feeding on Anthozoa and Hydrozoa;
- 16 (4) *Piscivores*: species primarily feeding on Actinopterygii and Cephalopoda;
- 17 (5) *Microinvertivores*: species primarily feeding on Annelida, Arachnida, Hemichordata,
18 Nematoda, Peracarida, and Nemertea;
- 19 (6) *Macroinvertivores*: species primarily feeding on Mollusca and Echinodermata;
- 20 (7) *Crustacivores*: species primarily feeding on Decapoda and Stomatopoda;
- 21 (8) *Planktivores*: species mainly feeding on zooplankton and Harpacticoida.

22

1 **Phylogenetic signal**

2 To evaluate the significance of the phylogenetic statistic value ($\delta = 9.37$), we applied a
3 bootstrapping approach and quantified δ after randomly shuffling the trait values 100 times. The
4 median δ of these null models was 0.000199 (95% confidence interval [0.000196, 0.000204]),
5 indicating a strong phylogenetic signal associated with the eight trophic guilds.

6 Phylogeny and maximum body size were sufficient to correctly predict the trophic guild of
7 97% of the species in our dataset. For most families, there was strong phylogenetic conservatism,
8 which resulted in the high confidence of these predictions (Fig. 4). Within some families,
9 however, closely related species displayed distinct dietary preferences. The uncertainty around
10 these family-level predictions was higher, as showcased by high negentropy values for families
11 such as Balistidae, Diodontidae, and Labridae.

12 Given the high predictive performance of our Bayesian phylogenetic model, we used our
13 model to extrapolate the probability of all reef fish species belonging to the eight trophic guilds
14 and assigned the trophic guild with the highest probability. Using leave-one-out cross validation,
15 the final accuracy of this approach was 65%, which is comparable to other phylogenetically-
16 extrapolated traits applications, such as those involving microbial traits [52].

17 By inspecting the confusion matrix of the leave-one-out cross validation, we obtained
18 more detailed information on the accuracy of the trophic guild predictions (Fig. S1). Most
19 categories were well predicted with our extrapolation approach. In particular, the *sessile*
20 *invertivores*, *HMD*, and *piscivores* trophic guilds were predicted with high accuracy (77%, 75%,
21 and 73% correct predictions, respectively). The confusion matrix also provided information on
22 incorrectly assigned categories. For example, when *piscivores* were incorrectly assigned, they
23 were mostly classified as *crustacivores*. However, the network plot revealed that the fishes

1 classified as *piscivores* also fed on crustaceans (mostly decapods), so this “incorrect assignment”
2 was grounded in ecological reality and reflected uncertainty within the model. Additionally, the
3 *microinvertivores* trophic guild had the highest proportion of inaccurate predictions (52% correct
4 predictions). Here, species were often misclassified as *crustacivores* or *planktivores*.

6 **Discussion**

7 To harness the full strength of trait-based approaches, functional ecology requires
8 standardized and reproducible trait classification schemes across taxonomic groups [53–55].
9 Rather than rely on expert opinion for the assignment of trophic groups, which often results in
10 variable assignments, we demonstrate that the categorization of trophic guilds can be achieved
11 with a quantitative and reproducible framework that is grounded in empirical data across
12 biogeographic regions. We employed network analysis to partition 615 tropical coral reef fish
13 species into eight trophic guilds based on a synthesis of globally distributed, community-wide
14 fish dietary analyses. We then applied a Bayesian phylogenetic model that predicts trophic guilds
15 based on phylogeny and body size and attained a 5% misclassification error. Unlike traditional
16 trophic guilds based on expert opinion [26,27,29,32–37], our trophic classifications are
17 reproducible, provide uncertainty estimates, and can be updated and improved in the future with
18 additional dietary information. By making our trophic classification framework publicly
19 available, we aim to encourage a new, accessible benchmark for the definition of trophic guilds.
20 Given the growing number of trait-based studies that assign trophic guilds to understand and
21 monitor ecosystem functioning in our changing world, it is imperative that we establish
22 comparable and reproducible trophic classification frameworks.

1 Our findings highlight the discordance of expert opinion in the assignment of trophic
2 guilds and the necessity to develop a quantifiable, reproducible classification scheme that is
3 accessible to the wider scientific community (c.f. [56]). To address this issue, the framework
4 proposed herein represents the first implementation of a quantifiable classification scheme for
5 coral reef fishes, including measures of uncertainty around trophic guild assignments and
6 providing a new path forward to standardize the definition of traits. Despite broad similarities
7 between the trophic guilds reported in the literature and the groups identified by our analysis, our
8 classification scheme reveals a higher level of partitioning among invertebrate-feeding fishes as
9 compared to previously proposed trophic guilds. In the past, invertebrate-feeding fishes were
10 generally considered *sessile invertivores*, *mobile invertivores*, or *omnivores* (e.g. [27,28,36]), but
11 we identify five distinct invertebrate-feeding groups: *corallivores*, *sessile invertivores*,
12 *microinvertivores*, *macroinvertivores*, and *crustacivores*. Given the extreme numerical
13 dominance of invertebrates in coral reef environments [57], the collapse of all invertebrate-
14 feeders into two or three trophic groups was possibly an artefact of expert oversight, and the
15 expansion of invertebrate-feeding trophic guilds to five groups stands to improve ecological
16 resolution of fishes feeding on invertebrate prey.

17 In contrast to the high resolution achieved within invertebrate-feeding groups, our
18 classification achieved limited resolution among the nominally herbivorous species, *herbivores*,
19 *microvores*, and *detritivores (HMD)*. Across the literature, past classification schemes often
20 separate macroalgal feeders, turf algae croppers, and detritivores (e.g. [26,27]). The lack of
21 precision in our framework is rooted in the difficulty in distinguishing algae, microbes, and
22 detritus within the alimentary tract of fishes, resulting in the pooling of these ingested items
23 during the visual assessment of fish gut contents. Consequently, species classified as *HMD* may

1 have fundamentally different foraging strategies, dietary preferences, and evolutionary histories
2 [58], which can greatly impact their functional role on coral reefs (e.g. [59]). Thus, while our
3 identified trophic guilds promise increased resolution for fishes that consume animal prey, our
4 identified groupings may not adequately capture consumer-producer dynamics on coral reefs.
5 Emerging techniques, such as gut content metabarcoding, may provide the additional resolution
6 needed to further discriminate prey items in this group [60,61]. Alternatively, coupling diet
7 categorization with other traits, such as feeding behavior, may help to pinpoint the variety of
8 feeding modes that exist within the *HMD* trophic guild.

9 Our results also highlight the necessity of integrating evolutionary history (i.e.
10 phylogenetics) in trait-based ecology (c.f. [62]). Recently, taxonomy and body size have been
11 revealed as important predictors of fish diet composition and size structure [63,64], and in the
12 highest resolution analyses of coral reef fish diet, taxonomic family was a better predictor of fish
13 diet than broad trophic guilds [60]. Given the exceedingly low rate of misclassification error in
14 our predictions of fish trophic guilds, we posit that phylogeny is a critical variable that should be
15 consistently considered in the assignment of trophic guilds. Across a plethora of organismal
16 groups (e.g. birds [65], reptiles [66], fishes [67,68], insects [69], parasites [70], plants [71], etc),
17 phylogenetic niche conservatism has been alternately supported and dismissed. In our case, when
18 examining fish trophic guilds using 38 prey categories, phylogenetic conservatism is readily
19 apparent at the family level, and therefore, it may allow us to extrapolate trophic assignments to
20 closely related consumer species. However, with increasing dietary resolution beyond what is
21 detailed in the present study, phylogenetic signals may weaken [72] since even closely related
22 species may exhibit dietary specialization [60,73]. In the future, with the availability of higher

1 resolution of dietary information, phylogenetic niche conservatism can be easily examined
2 within our framework.

3 With ongoing environmental and ecological change, a firm grasp on shifts in ecosystem
4 functioning will depend on the reliable assignment of organismal traits [15] and the
5 comparability of trait-based approaches across space, time, and independent studies [54].
6 Especially in complex, hyperdiverse environments such as coral reefs, it is imperative to
7 standardize how we measure and report these traits to prevent idiosyncratic results based on
8 subjective trait assignments [19,74]. Trophic guilds are among the most commonly applied traits
9 to assess ecosystem functioning because they directly relate to energy and nutrient fluxes across
10 trophic levels. Thus, our standardized framework to quantitatively assign trophic guilds across
11 coral reef fishes represents a major step forward for coral reef functional ecology, while heeding
12 the call for openly-accessible, reproducible trait databases [22,55,75]. As trait-based ecology
13 continues to be used to examine disturbances and implement management strategies, our
14 cohesive and accessible framework to predict reef fish trophic guilds can provide key insights
15 into the trajectory of coral reef communities. Coupling our trophic guild assignment framework
16 with predictive models could spur the emergence of an early detection system to forecast shifts
17 in ecosystem functioning [30].

18 Further, our results can serve as the foundation for an online platform that permits
19 researchers to collate, update, and utilize trait-based data on coral reef fishes. Similar to current
20 initiatives across the entire tree of life [55], we envision the creation of an online, user-
21 maintained dietary database to facilitate collaboration and traceability in trait-based reef fish
22 research. One challenge will lie in merging visual fish gut content analysis databases with
23 molecular data, such as gut content DNA metabarcoding (e.g. [60]), and biochemical data, such

1 as stable isotope analysis (e.g. [76]), and short-chain fatty acid profiles (e.g. [77]), which indicate
2 nutritional assimilation rather than the simple ingestion of prey items [58]. Despite this
3 challenge, accessibility to a large breadth of reef fish dietary information would improve our
4 framework. Our proposed trophic guilds are model predictions, so they are only as reliable as the
5 underlying dietary data. In addition, these predictions may suffer from extrapolation biases; for
6 example, if limited dietary information exists across species within a taxonomic group,
7 extrapolations to closely related species are more likely to be assigned erroneous trophic guilds.
8 Consequently, an ongoing, extensive compilation of dietary traits across coral reef fishes will
9 continuously improve our predicted trophic guild assignments.

10 Finally, our proposed framework is not limited to coral reef fishes; indeed, trophic guild
11 assignments can be quantifiable, reproducible, and transparent, with the inclusion of uncertainty
12 metrics, across many organismal groups. However, the standardization of trophic guilds is sorely
13 lacking across the ecological literature [56], especially based on quantitative data (e.g. [78]). We
14 posit that a similar approach can be readily applied across a multitude of organisms and
15 environments. In fact, given the paucity of dietary information available for coral reef fishes in
16 comparison to other organisms, particularly birds and mammals, building rigorous, global
17 trophic classification schemes for many other organisms should be readily achievable within our
18 framework. With a quantitative, transparent trophic classification scheme that can be augmented
19 over time and is applicable across ecological systems, our framework represents a significant
20 advancement for trait-based ecology and a viable approach to monitor ecosystem dynamics into
21 the future [55].

22

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6 results of our extrapolation will be made available once the manuscript is published in a
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10 **Conceptualization:** Valeriano Parravicini, Jordan M. Casey, Nina M. D. Schiettekatte

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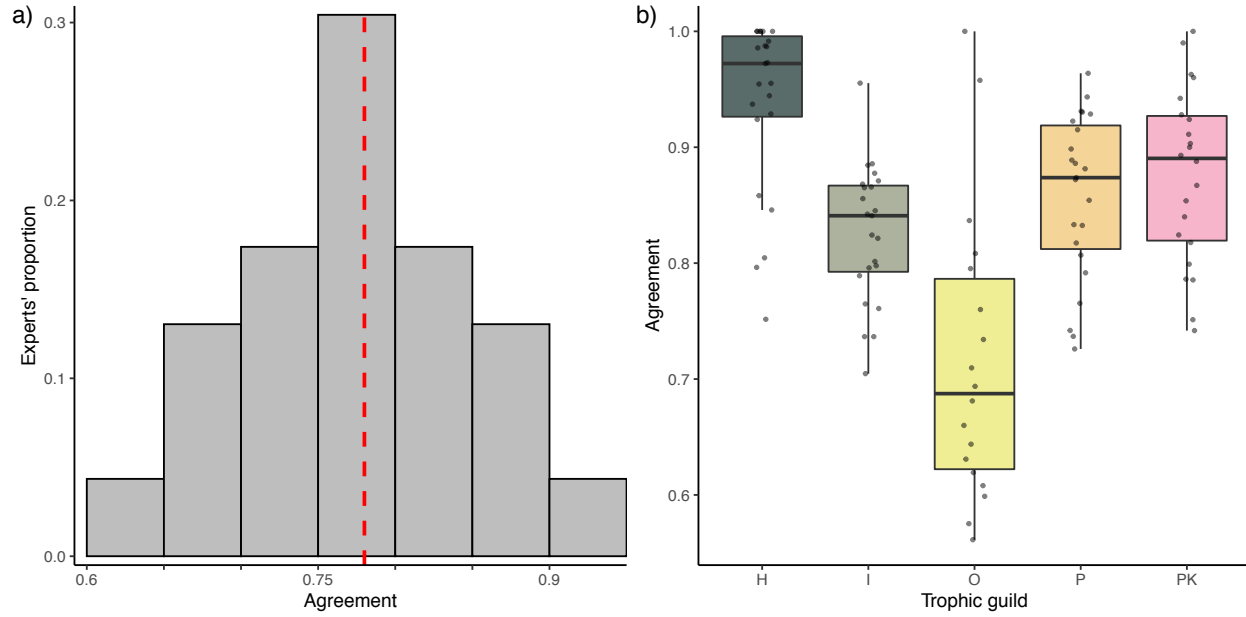
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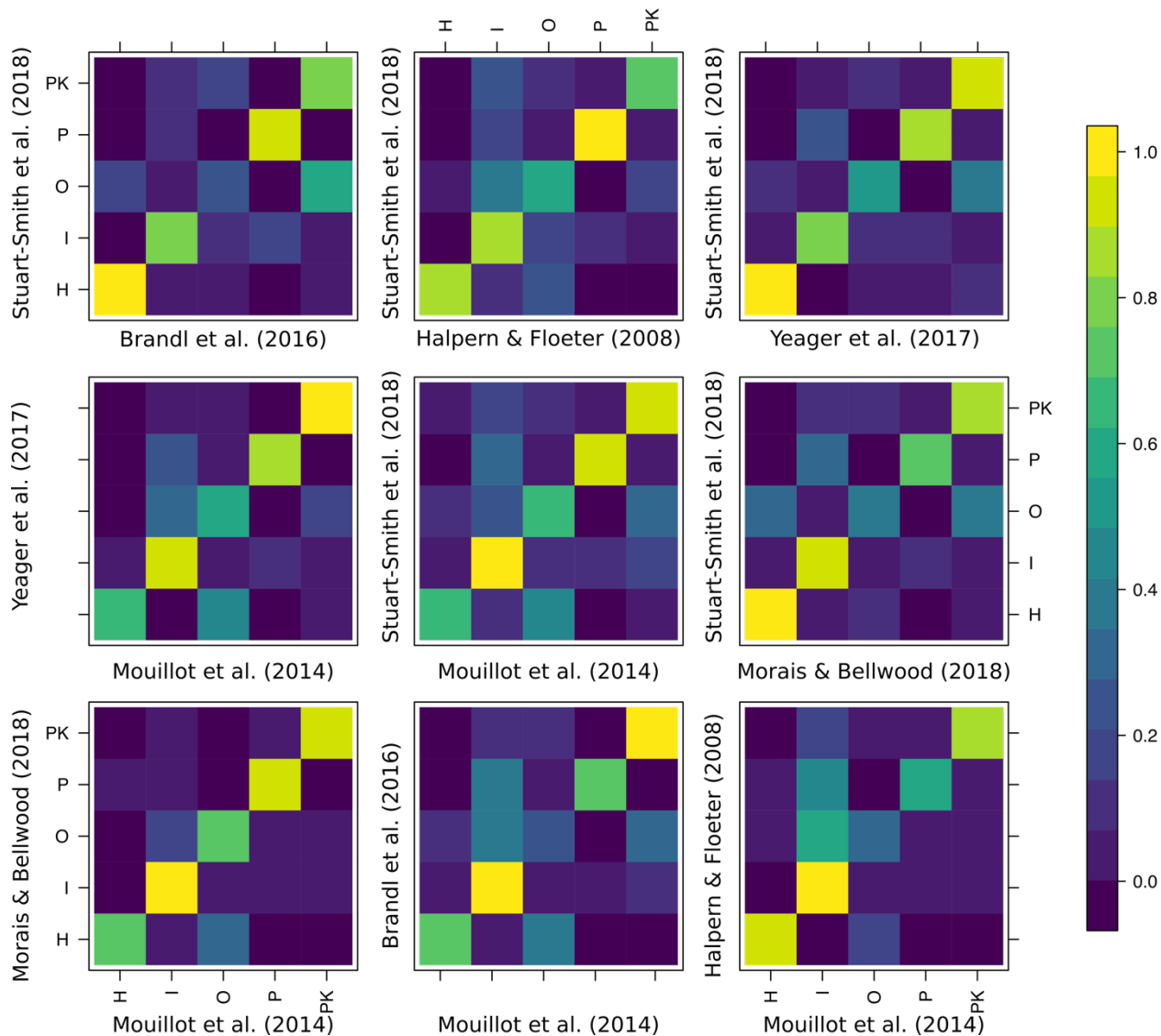
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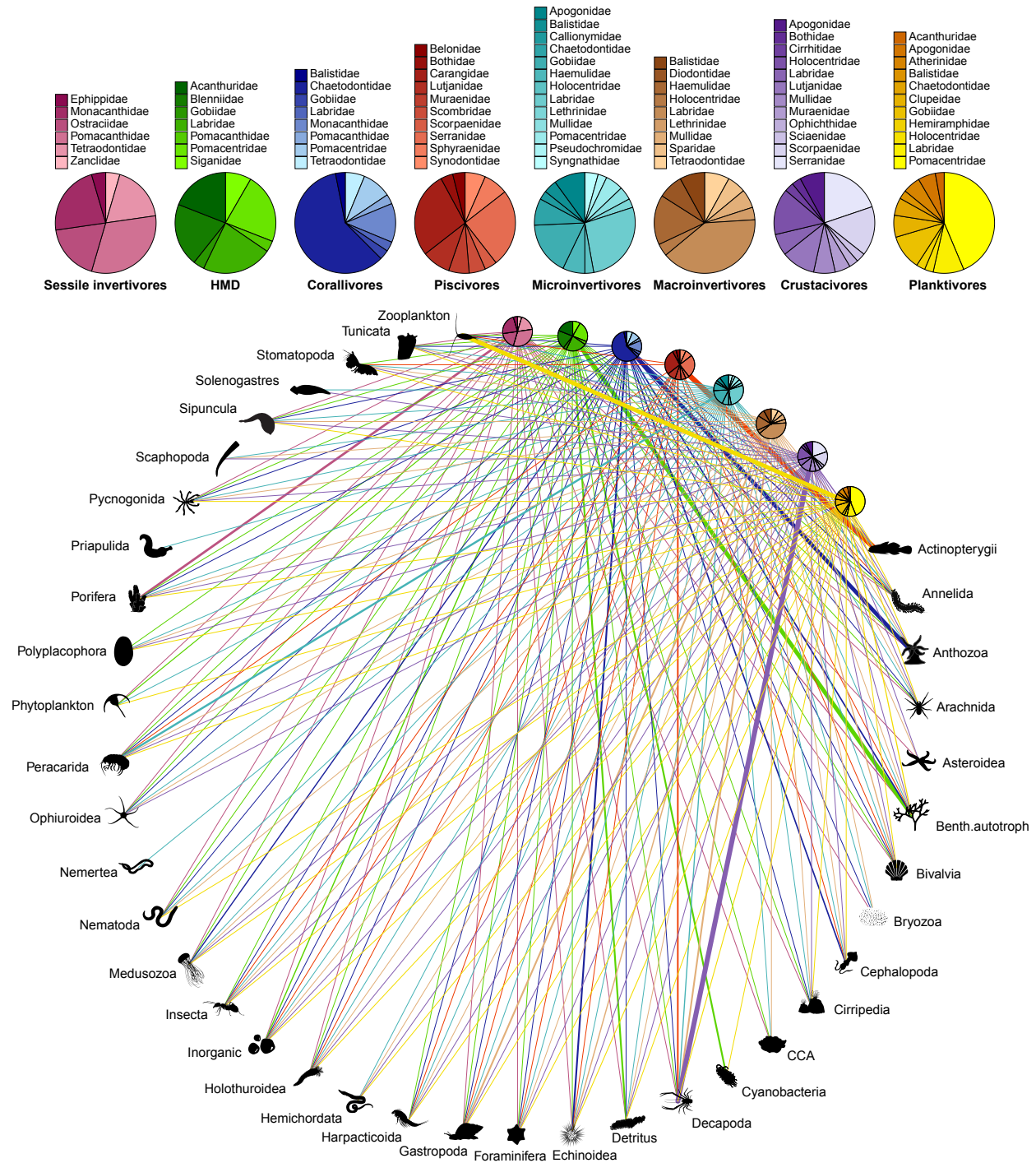
1
2 **Figure 1.** Expert agreement on trophic guild assignment. (a) The distribution of the agreement
3 (i.e. proportion of species assigned to the same trophic category) across the 32 comparisons
4 between pairs of experts. The red dotted line represents the median. (b) Agreement between pairs
5 of experts by trophic category (H=herbivores and detritivores, I=invertivores, O=omnivores,
6 P=piscivores, PK=planktivores).

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Figure 2. Confusion matrices of the agreement between pairs of experts that share at least 200 species in common. Colors represent proportions of species in each trophic guild as classified by experts (H=herbivores and detritivores, I=invertivores, O=omnivores, P=piscivores, PK=planktivores).



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3 **Figure 3.** Bipartite network including 615 fish species (grouped into eight trophic guilds; HMD

4 = *herbivores, microvores, and detritivores*) and their prey items (grouped into 38 categories; see

5 Table S1). The relative proportion of each prey category consumed by each trophic guild

- 1 corresponds with the width of each interaction bar. The pie charts show the relative proportion of
- 2 fish families within each trophic guild.

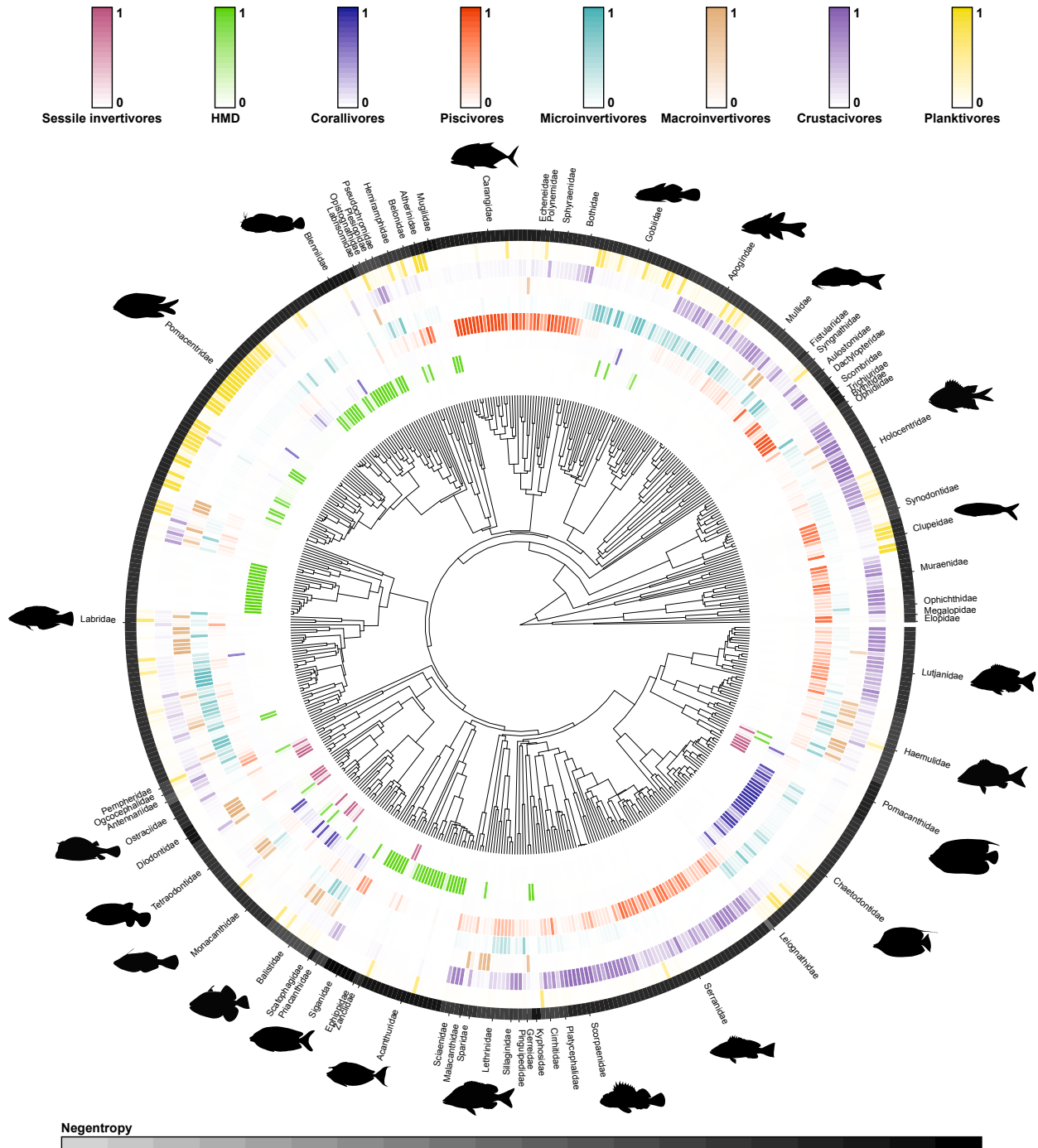


Figure 4. Phylogenetic tree of 535 reef fish species with fitted trophic guild assignments based on empirical dietary data. Trophic guild predictions were made with a Bayesian multinomial phylogenetic regression. The probability of trophic guild assignments for each species is visualized with color scales (depicted above the phylogenetic tree), with darker colors indicating

1 a higher probability of assignment. In the outer black ring, each distinct segment represents a fish
2 family (with silhouettes included for the most speciose families). Uncertainty of overarching
3 trophic guild assignment for each fish family is visualized with negentropy values (i.e. reverse
4 entropy); thus, darker shades indicate a higher degree of certainty of trophic guild assignment.
5

1 **Supporting Information**

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3

4 **Table S1.** List of prey categories used to define the trophic preferences of coral reef fishes.

5

| Prey categories |
|------------------------|
| Actinopterygii |
| Annelida |
| Anthozoa |
| Arachnida |
| Asteroidea |
| Benthic autotroph |
| Bivalvia |
| Bryozoa |
| Cephalopoda |
| Cirripedia |
| Coralline algae |
| Cyanobacteria |
| Decapoda |
| Detritus |
| Echinoidea |
| Foraminifera |
| Gastropoda |
| Harpacticoida |
| Hemichordata |
| Holothuroidea |
| Inorganic |
| Insecta |
| Medusozoa |
| Nematoda |
| Nemertea |
| Ophiuroidea |
| Peracarida |
| Phytoplankton |
| Polyplacophora |
| Porifera |
| Priapulida |
| Pycnogonida |
| Scaphopoda |
| Sipuncula |
| Solenogastres |
| Stomatopoda |
| Tunicata |
| Zooplankton |

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2 **Figure S1.** Confusion matrix showcasing the accuracy of the eight trophic guild predictions from
3 the leave-one-out cross validation based on the extrapolation of the Bayesian phylogenetic
4 model. Trophic guilds include: (1) *sessile invertivores*, (2) *herbivores, microvores, and*
5 *detritivores*, (3) *corallivores*, (4) *piscivores*, (5) *microinvertivores*, (6) *macroinvertivores*, (7)
6 *crustacivores*, and (8) *planktivores*.