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Response and Effect Traits of Coral Reef Fish

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The response-and-effect framework is a trait-based approach that seeks to break down the mechanistic links between ecosystem disturbances, species' traits, and ecosystem processes. We apply this framework to a review of the literature on coral reef fish traits, in order to illustrate the research landscape and structure a path forward for the field. Traits were categorized into five broad groupings: behavioral, life history, morphological, diet, and physiological. Overall, there are fewer studies linking effect traits to ecosystem processes (number of papers on herbivory, $n = 14$; predation, $n = 12$; bioerosion, $n = 2$; nutrient cycling, $n = 0$) than there are linking response traits to disturbances (climate change, $n = 26$; fishing, $n = 20$; pollution, $n = 4$). Through a network analysis, we show that the size and diet of fish are two of the most common response and effect traits currently used in the literature, central to studies on both ecosystem disturbances and processes. Behavioral and life history traits are more commonly shown to respond to disturbances, while morphological traits tend to be used in capturing ecosystem processes. Pearson correlation coefficients quantifying the strength of the relationships between the most commonly studied process, herbivory, and key effect traits (size, gregariousness, and diel activity) are provided. We find that the most popular cluster of traits used in functional diversity metrics (e.g., functional richness, functional dispersion) is comprised of size, diet, space use/position in the water column, diel activity, gregariousness, and mobility, which encompass three of the broad trait categories. Our assessment of the literature highlights that more research is needed to support an evidence-based selection of traits to understand and predict ecosystem functioning. In synthesizing the literature, we identify research gaps and provide an avenue toward a more robust trait-selection process.

Keywords: ecosystem processes, environmental disturbances, functional diversity, coral reef ecology, ecosystem function, trait-based ecology, systematic review

INTRODUCTION

Trait-based approaches in ecology and conservation are increasingly applied as the fields shift toward prioritizing an understanding of ecosystem functioning and maintaining ecosystem services (Madin et al., 2016a; Kissling et al., 2018; Barnett et al., 2019). Such an approach allows for mechanistic insight into how species interact with, react to, and shape their habitats (Violle and Jiang, 2009; McLean et al., 2018). The application of trait-based functional ecology to coral reef ecosystems is still in its nascent stages (Bellwood et al., 2019). The launch of the Coral Trait Database in 2016 (Madin et al., 2016b) was a milestone to consolidate the use of coral traits, much

like the publication of the first terrestrial plant functional trait handbook (Pérez-Harguindeguy et al., 2013), or the terrestrial invertebrate functional trait handbook (Moretti et al., 2017). Similarly, for coral reef fish, several crucial review papers and projects have begun to provide direction and clarity around which traits could be measured consistently, what is meant by the term ecosystem functioning, and what a novel functional approach might look like (Kublicki, 2010; Villéger et al., 2017; Bellwood et al., 2019; Brandl et al., 2019; Woodhead et al., 2019; Quimbayo et al., 2021).

The “response-and-effect framework” posits that it is useful to determine which traits respond to environmental gradients (“response traits”) and which traits affect ecosystem processes (“effect traits”) (Diaz and Cabido, 2001; Loreau et al., 2001; Lavorel and Garnier, 2002; Grime, 2006; Suding et al., 2008). This concept runs parallel to that of the distinction between Eltonian and Grinnellian dimensions of a niche, where the Grinnellian dimension refers to the resource needs of a species, and the Eltonian dimension refers to the impact of a species on the environment (Devictor et al., 2010). The use of such a framework provides a practical way of addressing how disturbances are likely to affect population dynamics and ecosystem functioning as a whole (Díaz et al., 2013; Salguero-Gómez et al., 2018). The trait structure of a community not only affects its sensitivity to disturbance (McLean et al., 2019), but also its capacity to support long-term functioning (Debouk et al., 2015; Duffy et al., 2016). Response traits have also been proposed as a basis for building Essential Biodiversity Variables, allowing for the effective monitoring of biodiversity change over time (Kissling et al., 2018). By identifying traits that overlap as both response and effect traits, or correlated response and effect traits, predictions about how disturbances could affect ecosystem processes can be made (Gross et al., 2008; Suding et al., 2008).

Several studies have found that functional diversity metrics respond to disturbances but also determine potential ecosystem functioning (Diaz and Cabido, 2001; Mouillot et al., 2013; Sitters et al., 2016). The use of trait-based approaches to estimate the functional diversity of coral reef fishes has become common (e.g., Richardson et al., 2017; Floeter et al., 2018; Mbaru et al., 2019). Yet, the number and selection of traits used in functional indices may greatly influence the outcomes and conclusions that can be drawn from analyses. The creation of functional groups and the use of trait-based approaches to understanding ecological dynamics is only useful if the prior selection of traits and functional groups are ecologically relevant to the questions at hand. Therefore, when applying the response-and-effect framework, it is necessary to determine which traits should be used as response traits and which traits should be used as effect traits, and where there is sufficient evidence mechanistically linking these traits to disturbances and processes.

In this paper, we review the literature on coral reef fish response and effect traits. We do this by asking which fish traits have been investigated in relation to responding to disturbances (response traits) or affecting ecosystem processes (effect traits) and how many papers have studied each of these links. We also ask which traits are being used together and why. We then explore the consistency of the direction of

influence for comparable traits and extract quantitative data linking predominant traits with a commonly assessed ecosystem process. In synthesizing the literature, we provide guidance for an evidence-based selection of traits for functional research in coral reef ecology and conservation, and establish where future research and experimentation is needed to strengthen the field.

MATERIALS AND METHODS

We examined response traits in relation to three disturbances and effect traits in relation to four processes common on coral reefs. The disturbances were pollution, fishing, and climate change (Hughes et al., 2010, 2017). The processes were herbivory, bioerosion, predation, and nutrient recycling (Villéger et al., 2017; Brandl et al., 2019). These limits to inclusion of disturbances and processes were applied to structure the review through the response-and-effect framework.

A comprehensive search of the literature was conducted using the Web of Science database (1974–2018). An initial search on September 26, 2018 used the terms: Topic Sentence (TS) = ((fish* AND coral AND reef*) AND trait* AND (“functional diversity” OR “functional evenness” OR “functional richness” OR “functional dispersion” OR “functional divergence” OR “functional redundancy” OR “functional group*”) OR “functional complimentary”)) OR TS = (“coral reef” OR “coral reefs”) AND (fish OR fishes) AND (trait OR “life history”) AND (function OR functions OR functional OR process OR processes OR disturbance OR disturbances)). This search yielded 380 titles. Further search terms were used to find papers specifically related to relevant ecosystem processes and/or disturbances. For example: TS = ((fish* AND coral AND reef*) AND trait* AND “climate change”). A total of 227 papers were found with these follow up search terms. Furthermore, the reference lists of four review papers that appeared in the searches were “snowballed”. A total of 17 new references were added to the database using this method.

Paper inclusion criteria were that (1) one or more of the processes or disturbances were being investigated in relation to (2) one or more traits of coral reef fish. Papers were excluded if (1) they were looking specifically at larval fish traits (e.g., pelagic larval duration), (2) the process or disturbance was not one that is being reviewed for this paper, (3) the paper was not accessible or not in English, and/or (4) the paper was a review article (although references were checked and snowballed). Papers were first filtered by titles, then abstracts, and finally full body texts. From a total of 624 papers accumulated with the three search strategies, 80 papers met the above criteria and were included in the systematic review (see PRISMA flow diagram, **Supplementary Figure 1**).

The traits, processes, and disturbances being studied in each paper were identified. Where possible, the direction of the relationship between the trait and process or disturbance was assessed. After a full list of traits had been accumulated, similar traits were grouped together to generate a succinct selection of relevant traits. For example, “size” was used as a way to group together traits such as “total length,” “maximum length,”

TABLE 1 | Broad groupings of traits, where blue corresponds to behavioral traits, yellow to life-history traits, red to morphological traits, purple to diet traits, and gray to physiological traits.

Behavioral traits	List history traits	Morphological traits	Diet traits	Physiological traits
Anti-predator response	Age/life-phase	Body morphology	Diet/trophic-level	Metabolic rate
Diel activity	Generation time	Eye morphology		
Feeding behavior	Growth rate	Fin morphology		
Gregariousness	Life span	Head morphology		
Habitat dependence	Natural mortality	Mouth/jaw morphology		
Habitat type	Reproductive turnover	Size		
Personality	Stage at maturity			
Space use	Survivorship			
Mobility				
Territoriality				

This color scheme is used throughout the paper.

and “body mass.” Traits were classified as either “behavioral,” “life history,” “morphological,” “diet and trophic level,” or “physiological” (Table 1).

In order to address the first question, “which traits have been investigated in relation to responding to disturbances (response traits) or affecting ecosystem processes (effect traits), and how many papers have studied each of these links?,” a weighted and directed tripartite network diagram was produced using the R package “igraph” (Csárdi, 2019). The diagram illustrates the number of papers, displayed as thickness of the lines (edges), linking traits to disturbances or processes (nodes).

To address the second research question, “which traits are being used together?,” the R packages “igraph” (Csárdi, 2019) and “CINNA” (Ashtiani et al., 2019) were used to produce an undirected, weighted network diagram. This diagram shows the links between traits used together in papers, where the size of the nodes shows the number of papers using the trait, and the size of the edges illustrates the frequency of trait combinations being included together in papers. The centrality of the nodes shows how commonly traits were used in combination with other traits. These centrality measures were quantified for the five most central traits. Centrality metrics used include degree centrality, subgraph centrality, and the topological coefficient. These metrics were selected as the top three most informative centrality measures, based on the output of a Principal Component Analysis (Ashtiani et al., 2018). Degree centrality can be defined as the number of nodes linked to a given node (Zhang et al., 2007), while subgraph centrality accounts for the participation of a node in the network’s sub graphs and deals with more complex networks (Estrada and Rodríguez-Velázquez, 2005), and the topological coefficient quantifies the extent to which neighbors share pairs of nodes (Doncheva et al., 2012). The median rank for the centrality metrics and the individual metric values were plotted using the R package “ggplot2” (Wickam, 2016).

To illustrate the traits being used together to generate functional diversity and related metrics, a Principal Coordinate Analysis (PCoA) (Kenkel, 2006) was carried out using the R package “ape” (Paradis et al., 2019). The analysis was conducted on a Jaccard’s dissimilarity matrix based on a presence/absence

matrix (Cheetham and Hazel, 1969) of traits within papers looking at functional diversity metrics. Two principal component axes, explaining 49% of the variation in the distance matrix, are illustrated. The number of clusters of traits within the plot was selected using the R package “NbClust.” This package determines the optimum number of clusters based on 30 indices (Charrad et al., 2014). Clusters were illustrated as convex hulls grouping traits together.

The type of evidence used in each paper to test/support disturbance-trait or trait-process links was then categorized as one of the following: *ex situ*, experiment; *ex situ*, measurement; *ex situ*, specimen measurement; *in situ* + *ex situ*, measurement; *in situ*, experiment; *in situ*, observation; modeling/theoretical approach; other. For example, if a paper assessed the effect of climate change-associated rises in temperature on reef fish boldness behavior in a controlled experimental lab environment, it would be counted in the “*ex situ*, experiment” category.

Next, we assessed the direction of the relationship between continuous or ordinal traits and processes/disturbances. Trait-process/disturbance linkages were assessed as either being positive, negative, or insignificant based on trends reported in the papers. For Bayesian analyses, where statistical significance is not relevant, only the direction of influence was recorded. For example, if a response trait, such as “generation time,” was shown to decrease in response to a disturbance such as “fishing,” it would be classified as a “negative” relationship. Similarly, if a process, such as “herbivory,” measured as the amount of algae removed in a given time/space, was shown to increase with the “size” (effect trait) of fish, the relationship would be classified as “positive.” Categorical trait relationships were excluded from this analysis, but paper result summaries are provided as a **Supplementary Table 1**.

To test the quantitative applicability of the framework to coral reef fish, we investigated the effect size of effect traits on the process of herbivory. Herbivory was selected as the ecosystem process for which to extract quantitative effect sizes, because (1) it was the most commonly studied process found in our search, and (2) herbivory was the process with the most consistent measurement in the literature (bite rate or impact). Three of

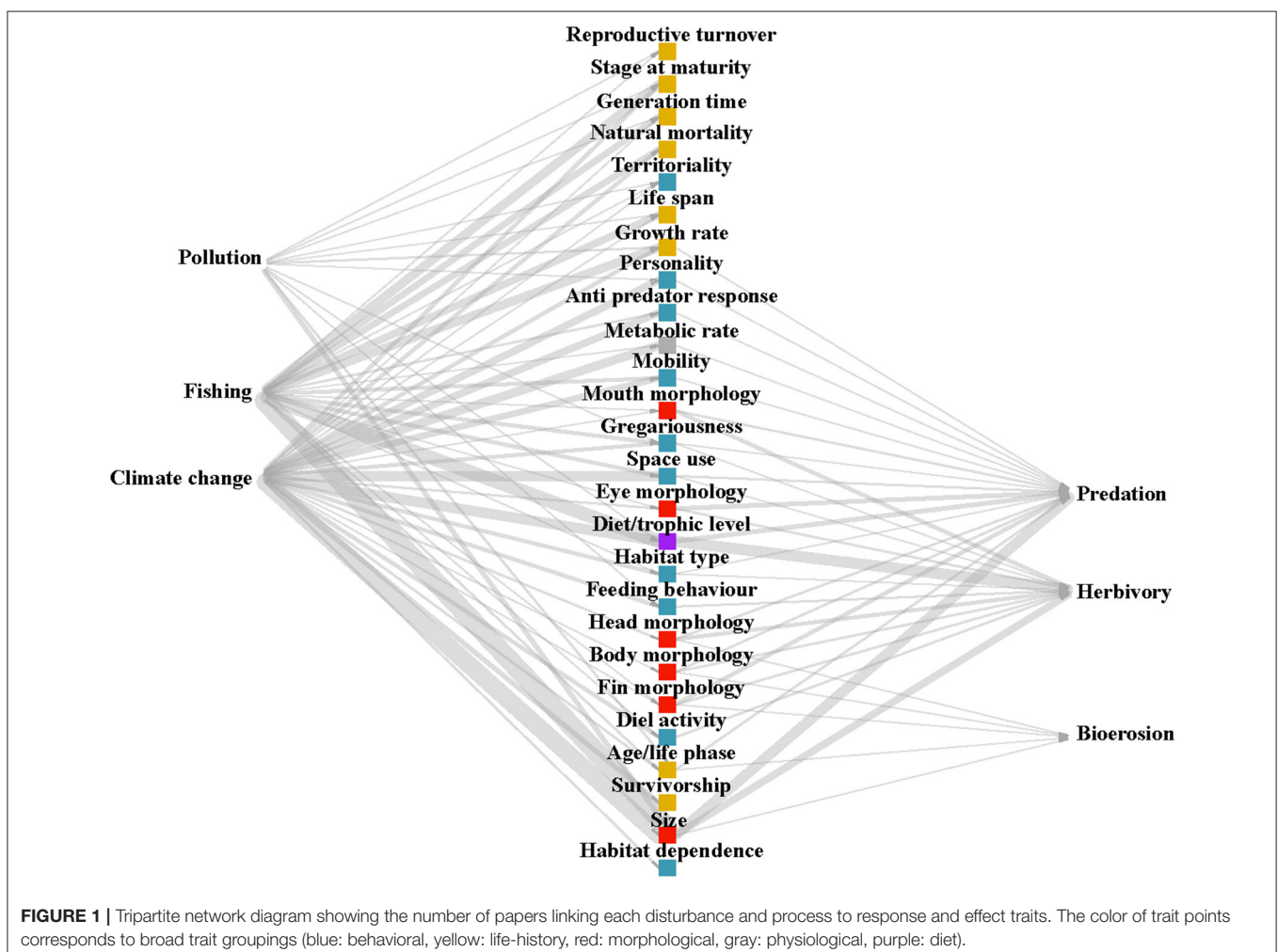
the most common traits related to herbivory in the literature—size, gregariousness and diel activity—were selected as effect traits to assess. Diet was excluded from the quantitative assessment because its relevance is in relation to diet categories which is implicit for herbivory. Because the initial search term limited papers to those using the term “trait,” whereas some papers use traits without explicitly naming them as such, an additional search was conducted to identify papers which may not have used the terms “trait” or “function” but had quantified herbivory. An additional four papers were found looking at the impact of traits on herbivory and directly measuring the process.

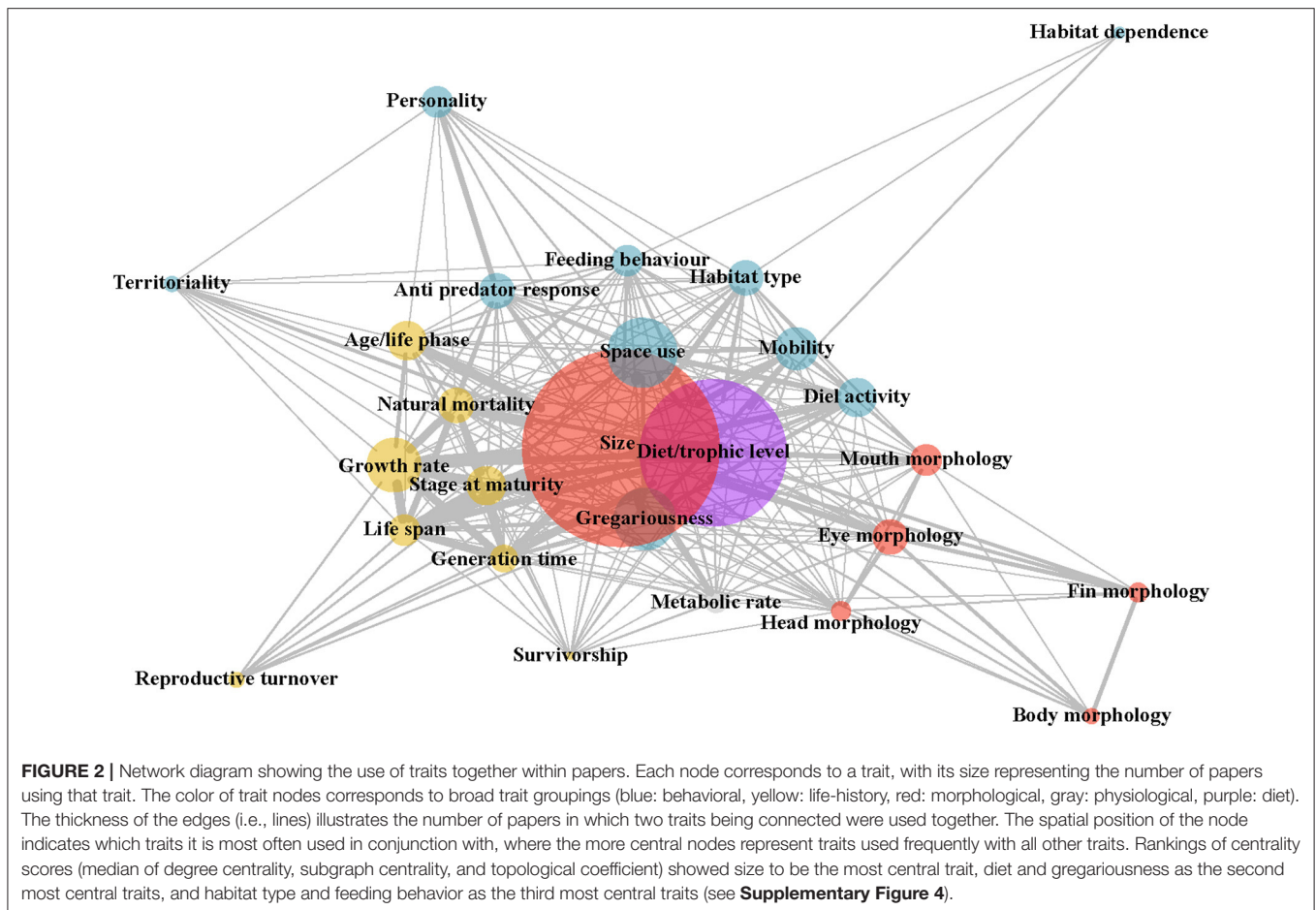
Where effect sizes were extracted from the literature, they were converted into Pearson r correlation coefficients according to Beltramini and Wolf (1987) and Friedman (1982). Pearson’s r was selected because it allows for contrasts between two or more groups without computational corrections and is easily interpreted as it sits on a limited scale from -1 to 1 (Rosenthal and DiMatteo, 2001). Relevant statistical information needed to compute the effect size was extracted where available. WebPlotDigitizer (Rohatgi, 2019) was used to extract raw data from figures. Where data was provided but not analyzed in

relation to traits of interest (e.g., Humphries et al., 2014), a simple correlation was conducted using raw data. For size bins/categories, the average size was used. In papers presenting data on trait-bite-rate relationships for more than one species or more than one site, average effect sizes and 95% confidence intervals are calculated. Additionally, for each trait, an average Pearson’s r based on all the papers is presented with 95% confidence intervals. All statistical analyses were performed using R software version 3.5.2. (R Core Team, 2018).

RESULTS

Based on our search results (See PRISMA flow diagram, **Supplementary Figure 1**), the most studied disturbance affecting coral reef fish traits is climate change (number of papers, $n = 26$), followed by fishing ($n = 20$), and then pollution ($n = 4$). Climate change encompassed papers assessing the impacts of increasing temperatures, rising levels of CO_2 , extreme weather events and coral bleaching. Fewer papers investigated ecosystem processes using an explicit trait-based approach. The process most studied





was herbivory ($n = 14$), then predation ($n = 12$), bioerosion ($n = 2$), and finally no papers were identified through our search terms that quantified nutrient transfer through a trait-based approach ($n = 0$). “Predation” captured papers assessing prey traits, predator traits, or the interaction between both. The most studied disturbance-response trait links were between size and fishing ($n = 16$), size and climate change ($n = 15$), diet and fishing ($n = 11$), and diet and climate change ($n = 8$). The most studied effect trait-process links were diet and herbivory ($n = 9$), size and predation ($n = 8$), and size and herbivory ($n = 6$). Size and diet had the greatest number of papers that link the traits both to disturbances and processes, making them both well-studied response and effect traits (**Figure 1; Supplementary Figure 2**).

The network analysis plot, based on the traits of all papers included in the database, illustrates three key findings. Firstly, size and diet, followed by space use, gregariousness, and growth rate, are the most commonly used traits in the literature (**Figure 2**). Secondly, trait categories, for example, behavioral or morphological (depicted by color), tend to group together in network space. Size, a morphological trait, and gregariousness, a behavioral trait, are the exceptions to this, being situated in the middle of the plot (**Figure 2; Supplementary Figure 3**). Thirdly, size is almost consistently ranked as the most central trait, followed by diet, gregariousness, habitat type and feeding

behavior (**Supplementary Figure 4**). High centrality scores indicate that these traits as the ones most commonly used with combinations of other traits.

A total of 17 papers used traits to calculate functional diversity metrics for coral reef fish, or to derive functional entities. Functional diversity indices were most commonly calculated using size ($n = 15$), diet ($n = 14$), and space use ($n = 9$). The traits most commonly used together are size, diet, gregariousness, mobility, diel activity, and space use (e.g., position in the water column) ($n = 5$) (**Figure 3**). Two other groupings of traits were also apparent: age/life phase with reproductive turnover; and eye morphology with mouth morphology, feeding behavior, habitat type and territoriality. These groupings were based on Euclidean space in the PCoA axes and the traits encompassed were not necessarily used consistently all together in the literature. For example, habitat type was used in five papers; some of these papers also used traits located in the cluster of the most frequently applied six traits. In Brandl et al. (2016), habitat type is used along with diet, size, and territoriality to examine how coral reef fish functional diversity responds to a disturbance in the form of a tropical cyclone. Age/life phase and reproductive turnover represent a lesser studied cluster of traits, produced by papers that include broader life history strategies in functional analyses (e.g., Tuya et al., 2018).

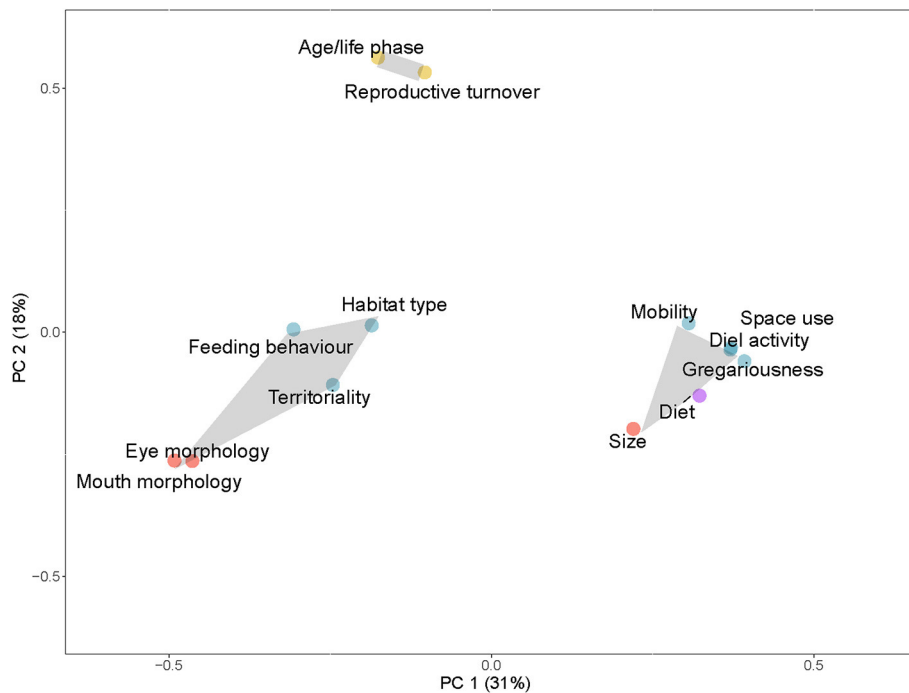


FIGURE 3 | PCoA plot of traits used to estimate functional diversity or to determine functional entities. Three clusters show traits commonly used together in functional diversity metrics. Color of trait points corresponds to broad trait groupings (blue: behavioral, yellow: life-history, red: morphological, gray: physiological, purple: diet).

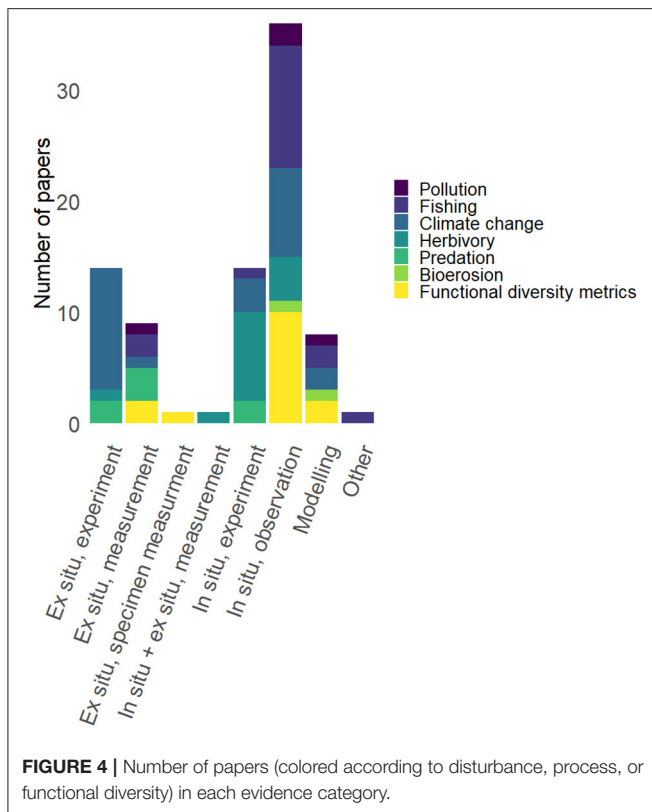
Overall, the evidence for the majority of functional diversity papers is based on *in situ* observational evidence ($n = 10$; total *in situ* observational $n = 36$). The number of papers based on this type of evidence is more than double the number of papers based on *ex situ* experimental ($n = 14$) and *in situ* experimental ($n = 14$) evidence. Trait-relationships based on *ex situ* measurements ($n = 9$) and purely theoretical or modeling-based papers ($n = 8$) were less common. *Ex situ* specimen trait measurements ($n = 1$) and a combination of *in situ* and *ex situ* measurements ($n = 1$) were each only represented by one paper (Figure 4).

The direction of influence of disturbances on response traits and effect traits on ecosystem processes shows the consistency of findings across the limited set of papers identified in the review (Figure 5). Most papers found a negative influence of pollution on the size of fish ($n = 3$). There was an even split between the number of papers finding an insignificant and positive effect of pollution on the trophic level of coral reef fish ($n = 2$). There was 100% agreement on the negative relationship between fishing and the life history traits of life span ($n = 3$) and generation time ($n = 3$), showing that all papers framed as trait-based and/or functional in the literature identified, found that high fishing pressure results in short life spans and generation times. Fishing had a negative impact on gape size ($n = 1$), a mostly negative impact on the size ($n = 10$) and trophic level ($n = 5$) of fish, but a positive influence on natural mortality ($n = 3$), and a mostly positive impact on growth rate ($n = 4$). All papers assessing the impact of climate change on anti-predator responses ($n = 4$) found a negative relationship. On the other hand, climate change was found to have a positive relationship with metabolic rate ($n = 4$).

There was a mixed effect of climate change on fish size and the growth rate of fish. Climate change was either found to insignificantly affect fish trophic level or have a negative impact on trophic level ($n = 2$) (Figure 5).

The small sample size of papers looking at continuous traits linking to measured ecosystem processes showed that there was a positive impact of time of day on herbivory ($n = 1$), and a mostly positive impact of size on herbivory ($n = 5$). Gregariousness was found to either have an insignificant or positive impact on herbivory ($n = 2$). Few papers quantified the process of predation in trait-based terms. However, of those that did, there was a negative effect of the size of prey on the rate of predation ($n = 2$) and a positive effect of the growth rate of prey on the extent of predation ($n = 2$) (Figure 6).

The initial search results highlighted that herbivory was the most consistently quantified ecosystem process and was typically measured as bite rate (e.g., bites/minute) or bite impact (e.g., $\text{kg} \times \text{bites/minute}$). A Pearson correlation coefficient was calculated for each paper quantifying the relationship between effect traits and this measure of herbivory. There was a negative correlation between fish size and bite rate, as shown by the average of papers above the red dotted line in Figure 6A. However, papers looking at fish size and measures of bite impact (below the red line in Figure 6A) tended to find a positive correlation. A strong average positive, correlation between gregariousness and herbivory was identified, but note, this is based on only two studies. A positive relationship between diel activity and herbivory was also found. Diel activity was sometimes measured as a categorical trait [e.g., nocturnal and diurnal in Hoey and Bellwood (2009)] or



on different time-scales [e.g., minutes after sunrise in Goatley and Bellwood (2010)], and the correlation coefficient reflects the strong magnitude of influence rather than the direction of influence (Figure 6).

DISCUSSION

Our review highlights four main findings: (1) size and diet are used as both response and effect traits with a relatively large number of studies investigating their importance to the range of different disturbances and processes explored in this paper; (2) nutrient cycling and bioerosion are understudied processes in the trait-based coral reef fish literature; (3) there is a distinct clustering of trait types (e.g., morphological traits, life history traits, etc.) in functional diversity studies, in addition to a cluster of six mixed trait types frequently used together (size, diet, position in the water column, gregariousness, mobility, diel activity); (4) because traits are not consistently coded across the literature, amassing an informative sample size to quantify the effect size of disturbance-trait or trait-process relationships is a challenge. Nevertheless, using a small sample size of papers measuring the relationship between key traits and the process of herbivory, we highlight variation in even the most seemingly well-known interactions. We reflect on these findings and propose a way forward for trait-based approaches in coral reef fish ecology and conservation.

Trends in the Literature

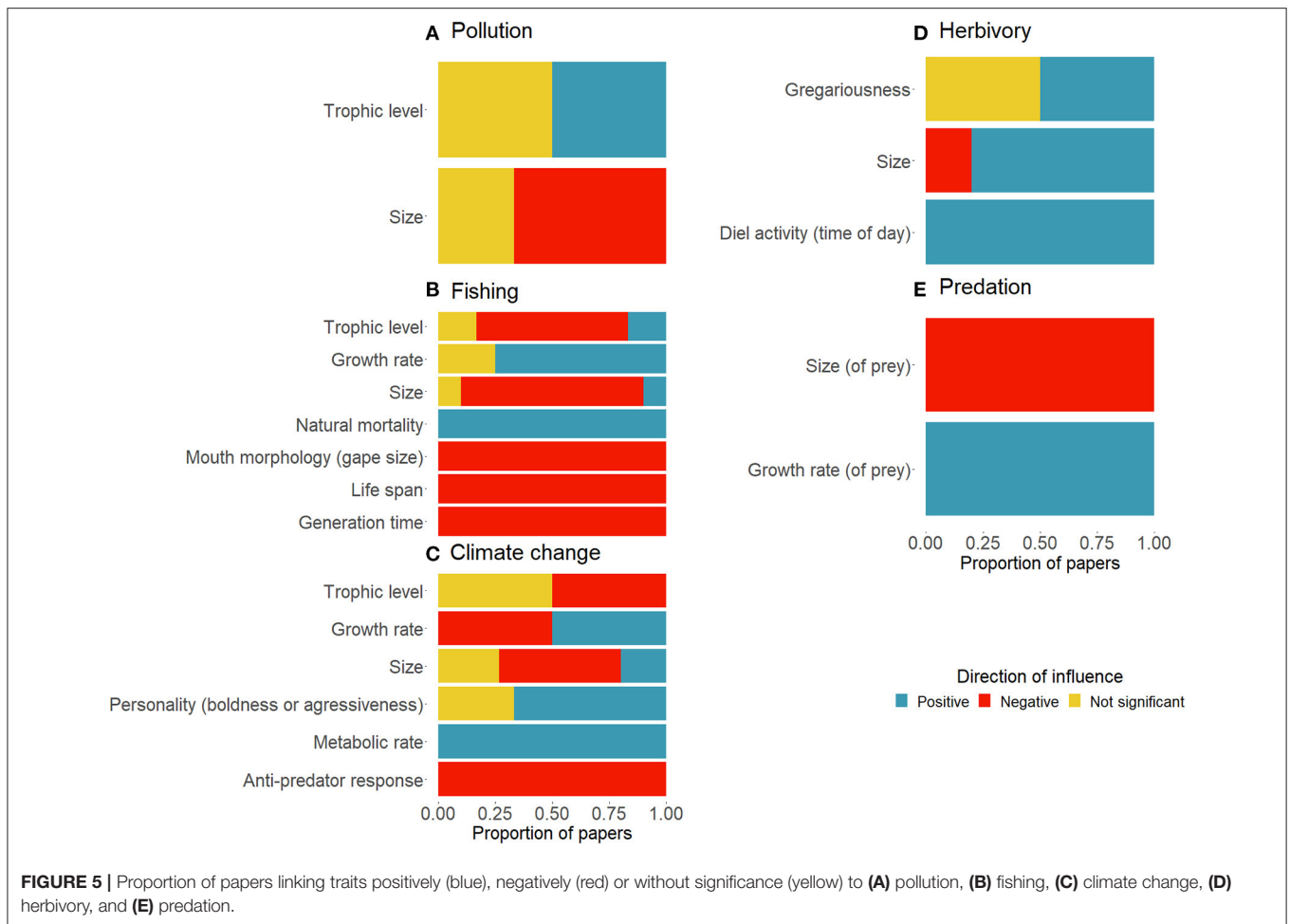
Size and diet were identified as both response and effect traits (Figure 1). As illustrated in the network diagram, both traits are centrally located, with size having a median centrality ranking as the top trait, and diet ranking alongside gregariousness as the second most central trait, indicating their use in conjunction with a range of other traits within papers (Figure 2; Supplementary Figure 4). Size is also demonstrated to have a consistent relationship with herbivory, whereby bite rate is negatively correlated with size and bite impact is positively correlated with size (Figure 6). These findings support the view that size acts as a super-trait, as it scales with, and therefore shapes, a range of other functional traits (Jacob et al., 2011). However, the relationship between size and diet or trophic level is not linear, but rather, it is mediated by traits such as body depth, tooth shape, and mouth width (Keppeler et al., 2020).

In comparison to ecosystem processes, trait-based approaches to studying the effects of disturbances on coral reef fish (response) traits were more numerous. Specifically, fishing and climate change were both studied in 20 or more papers, whereas only four papers focused on pollution (Figure 1). Disturbances can interact additively or synergistically to affect the coral reef environment at a number of different levels ranging from microbial to large fish (Darling et al., 2010; Ban et al., 2014; Zaneveld et al., 2016). While fishing pressure and pollution could involve, in some cases, local solutions, climate change is likely to necessitate urgent global cooperation and decision making (Mumby et al., 2013; Hughes et al., 2017). The level of uncertainty associated with global decision making has led scientists to consider the consequences of different possible climate change scenarios (Hoegh-Guldberg et al., 2007; Pandolfi, 2015). A trait-based approach could be particularly useful to understand what novel ecosystem configurations might arise under these different scenarios (Graham et al., 2014; McClure et al., 2019).

The most commonly studied ecosystem processes were herbivory and predation. This focus in the literature is likely due to the emphasis of herbivory as a key process that prevents phase shifts to non-coral benthic communities (Hughes, 1994; Bozec et al., 2016; Cramer et al., 2017). Unlike herbivory, where only consumer traits were being studied, predation was often researched in terms of both consumer (predator) and prey traits. Studying the interactions of predators and prey contributes to an understanding of community dynamics that support ecosystem functioning (Schmitz, 2017). Although this review was limited to investigating fish traits, the interaction of fish traits with coral traits or algal traits represents a similar avenue to exploring the relationship between community producer-consumer dynamics (Rasher et al., 2013).

Gaps in the Literature

Few papers explored relationships between effect traits and bioerosion and nutrient cycling. While bioerosion is a widely recognized process on coral reefs (Lokrantz et al., 2008; Bellwood et al., 2012), only two papers were identified that measured it using an *explicit* trait-based approach. Such gaps in the literature highlight the need for further research quantifying such ecosystem processes, so that they can be more confidently

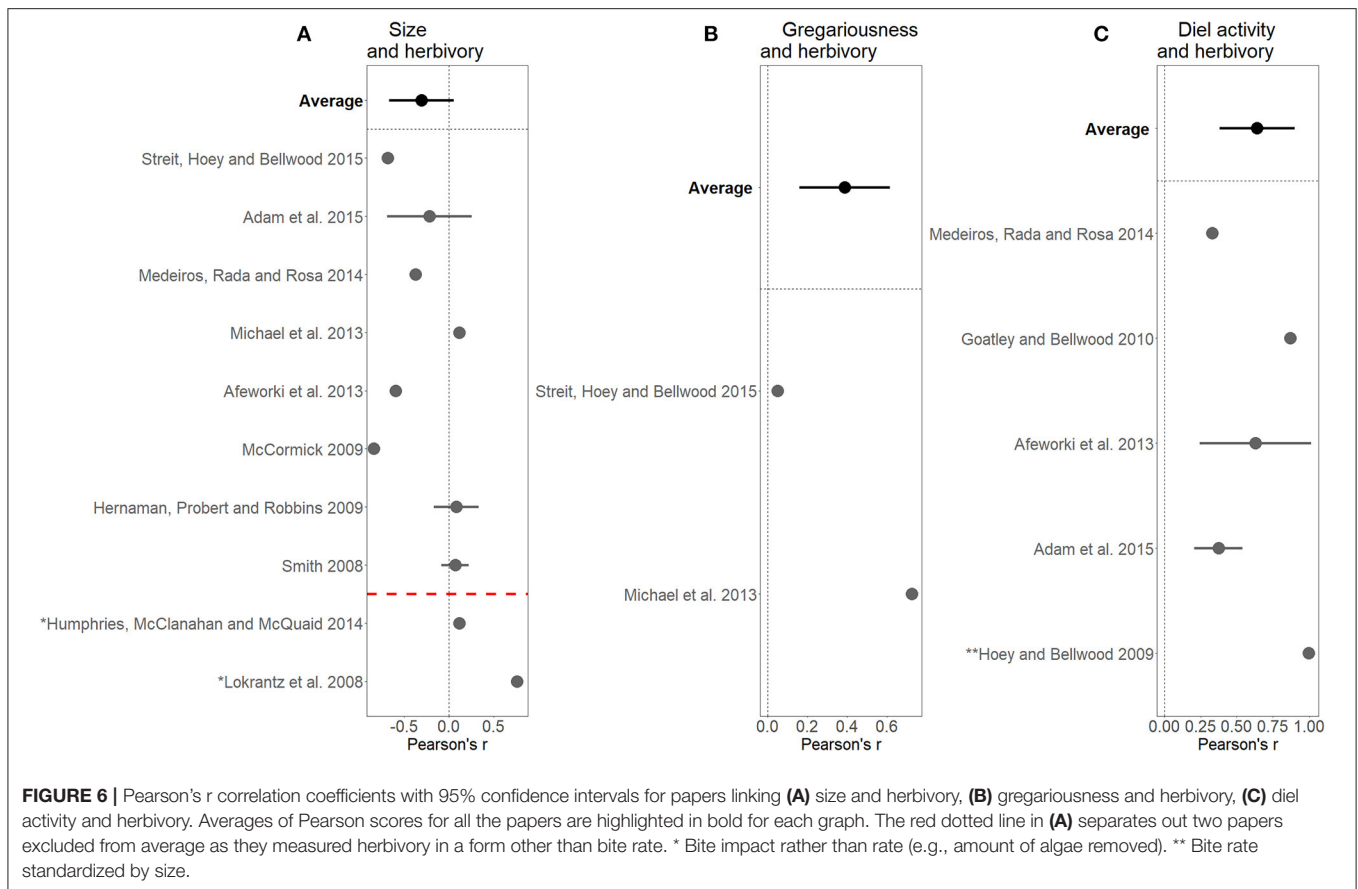


linked to coral reef fish traits. However, since conducting the review (September 2018), there have already been strides taken to fill in research gaps and drive forward the application of trait-based approaches to estimate important functions and processes on coral reefs. For example, when this review was conducted, no papers were found linking traits to nutrient cycling, even though the process of nutrient cycling is important to the productivity of the ecosystem (Allgeier et al., 2016). A notable addition to the literature addressing this gap is a paper and companion R package proposing a trait-based approach to model nutrient cycling (Schiettekatte et al., 2020). The authors use traits such as body size, life stage, and diet to model fish ingestion and excretion rates, and accurately predict these rates for three species. Similarly, another notable publication in the field proposes a trait-based methodology and R package to facilitate the estimation of reef fish productivity (Morais and Bellwood, 2020). While productivity was not considered as a process in this review, it is an essential indicator of ecosystem functioning. The productivity of consumers on the reef (process) is demonstrated to respond to habitat degradation (disturbance) through a trait-mediated pathway (Morais et al., 2020). Thus, while the approach is not explicitly framed in the response-and-effect framework, it applies the logic of overlapping response and effect traits

to demonstrate the value of traits in detailing the mechanisms through which disturbances affect ecosystem functioning.

Trait Centrality and Clustering

The results of the network and centrality analyses highlight which traits are most commonly being used together. Amongst the evidence base, there is a distinct clustering by trait type (Figure 2). Results from the ordination plot also show that the six traits popularized in Mouillot et al. (2014) (size, diet, space use/position in the water column, diel activity, gregariousness, and mobility) are frequently grouped together to compute functional diversity metrics (Figure 3). These traits cover all broad trait categories except for life history traits and physiological traits. Physiological traits, such as metabolic rate, are often difficult to obtain and vary regionally (Killen et al., 2017). Conversely, life history traits are easily obtainable (Thorson et al., 2017). However, we found that they are not commonly used in functional diversity studies and form their own cluster in the PCoA analysis (Figure 3). This is also partly attributable to the conservative definition we used for the term “life history” traits; in this paper, “life history” traits are restricted to those directly associated with survival and reproduction, as outlined in the seminal work by Stearns (1976). Such traits might



complement the selected six traits to better reflect the response diversity of coral reef fish, as such traits are frequently used to measure the response of coral reef fish to disturbances (Figure 1; Supplementary Figure 3). Nevertheless, the six traits capture a broad range of response and effect traits that have been linked to both ecosystem processes and disturbances. Three of the six traits were assessed quantitatively with respect to their impact on the process of herbivory; several studies show the importance of size, gregariousness, and diel activity in influencing the bite rates and algal removal rates of fish (Figure 6). Furthermore, the six traits have been used to effectively elucidate both global and small-scale ecosystem changes (Stuart-Smith et al., 2013; Brandl et al., 2016) and the ease at which they are obtainable likely means they have great potential for further use in functional studies (Bellwood et al., 2019).

Conversely, morphological traits, which form a cluster driven by ecosystem processes (Supplementary Figure 3), and are sometimes used as stand-alone traits in studies looking at functional morphospace (e.g., Goatley et al., 2010; Quimbayo et al., 2021) (Figure 3), are not as easily available, and as such have typically been used in studies conducted on historical records, at a small geographical scale, or for few species (e.g., Munday et al., 2011; Fox and Bellwood, 2013; Streit et al., 2015). Thus, there is scope to build upon morphological trait databases, so that ecosystem functioning can be better

understood at a larger scale (Kiørboe et al., 2018). If such traits become more readily available, they might start being used in conjunction with behavioral and life history traits to bridge together research being conducted on the impact of disturbances and ecosystem functioning.

Although this review provides a broad overview of coral reef fish traits through a response-and-effect framework, it should be noted that it does not extensively cover all of the literature dealing with traits. This is partly because the term “trait” is extremely broad and partly because systematic reviews are always somewhat biased through search terms and database algorithms (Pullin and Stewart, 2006; Drucker et al., 2016). Nevertheless, one of the purposes in this paper was to bring some structure to the coral reef fish trait literature through the response-and-effect framework.

Toward a Trait-Based Approach for Coral Reef Fish Ecology

Identify Overlapping or Correlated Response and Effect Traits

A dichotomy does not exist between response and effect traits. On the contrary, many traits, especially those related to resource use, both respond to disturbances and affect ecosystem processes (Diaz and Cabido, 2001). In our review of the literature, both

size and diet were found to be extensively used as response and effect traits (Figure 1). Identifying traits that are both response and effect, as well as response/effect traits that are strongly correlated, allows for a parsimonious prediction of the impacts of disturbances on ecosystem functioning (Suding et al., 2008). Correlated traits can be identified through multivariate ordination techniques. For example, Beukhof et al. (2019) demonstrate how traits positioned in close proximity in a PCA of trait-space (e.g., length and fecundity) follow similar temporal trends when exposed to environmental disturbances.

In cases where two traits are known to correlate, and one of those traits is known to respond to an ecosystem disturbance, while the other is known to affect an ecosystem process, they can be used together to harness predictive capacity. Working with microbial communities, Amend et al. (2016) found that response traits affected by drought that were strongly correlated with traits responsible for ecosystem processes allowed for the effective prediction of shifts in the functioning of microbial communities with disturbances characteristic of global change. Similarly, this review determined that the traits metabolic rate (positive relationship) and anti-predator responses (negative relationship) are linked to climate change (Figure 5). However, both traits have also been linked to the process of predation (White et al., 2013; Ferrari et al., 2015) (Figure 1). Therefore, such traits provide an opportunity for determining the pathways through which disturbances can affect ecosystem processes.

Establish Causation and Build the Predictive Abilities of Trait-Based Approaches

One concern with the response-and-effect framework could be the implied causation in the relationships between disturbances and response traits and effect traits and ecosystem processes. While the framework does attempt to structure the direction of correlations by explaining mechanisms, causation is a notoriously hard concept to prove within science (Anjum and Mumford, 2018). However, it is generally accepted that if hypothesized causal relationships have supporting data that can be theoretically justified, used, and applied, directionality in such relationships can be recognized. Such justifications underlie the processes of mechanistic and causal modeling (Connolly et al., 2017). In this review, the effect traits demonstrated to impact the process of herbivory (Figure 6) were able to be identified as effect traits, because there was a plausible causal pathway. Considering another example: size-selective fishing is proposed as the mechanism underlying a shift in the size structure of fish communities. The clear causal pathway and breadth of observational evidence supporting this disturbance-response trait link, in addition to the predictive power that comes with assuming this causal relationship, illustrates the value and purpose of structuring traits according to the response-and-effect framework. Like many of the tools applied decades ago to understand ecosystem functioning, the response-and-effect framework originates in the terrestrial plant ecology field. One of the central goals of the approach is to enable the prediction of changes in community composition and ecosystem functioning (Lavorel and Garnier, 2002).

Body size is somewhat of an anomalous trait, as it is easily recorded and has great functional importance. For other traits with less well-known causal pathways, building up an evidence base of observations under a range of conditions is important. Moreover, experimentation could be used as a controlled method of assessing causality. While this approach may not always be feasible or appropriate, small-scale controlled experiments can further test or corroborate relationships observed on a large scale (Figure 4). For example, disturbances associated with climate change provide natural experiments on a global scale (e.g., Keith et al., 2018; Richardson et al., 2018). Observations following such events offer useful information about response traits to form hypotheses that can be further tested through experimentation (e.g., Biro et al., 2010).

Favor Continuous Traits or Standardized Trait Categories, and Consider Intraspecific Variation

This review demonstrates the centrality of size in the literature (Figure 2) and its versatility as a response and effect trait (Figure 1). Moreover, size can be measured on a continuous scale. In order to model the overall direction of a response or effect trait across a number of studies, consistency in measurement is essential. With categorical data, a range of potential errors get introduced in the effort to standardize (Nakagawa and Cuthill, 2007). Categorical traits have also been shown to decrease the quality of functional space (Maire et al., 2015). Maintaining consistency of categories and/or using continuous traits allows for useful meta-analyses to be compiled for a range of disturbance-trait-process relationships.

In addition to being a super-trait, size provides an avenue for investigating the importance of intraspecific variation. Intraspecific variation is a burgeoning field of research within functional ecology (Albert et al., 2011; Allgeier et al., 2017; Des Roches et al., 2018). Where substantial variability exists within species, it may no longer be sufficient to use species-level trait data (Bolnick et al., 2011). One example of the importance of intraspecific variability is illustrated in a paper by Barneche et al. (2018). The authors show that there is hyperallometric scaling in reproductive output; larger coral reef fish mothers, within the same species, have a far greater reproductive output than smaller mothers. The functional trait of an individual fish might also depend on its sex, age, or size at which it was sampled. For example, many species undergo ontogenetic shifts in their diet; it has been found that some piscivores are able to expand their diet breadth as they grow older and bigger, and their gape size can accommodate larger prey (Dunic and Baum, 2017). This diversity of size amongst individuals of a species, can be easily recorded. The size and species identity of fish is often collected using routine visual surveying techniques (Caldwell et al., 2016). Indeed, total length is a relatively simple trait to measure observationally and non-invasively *in situ* (Villéger et al., 2017).

Diet, on the other hand, is not typically measured for each fish during a survey, unless it is one of the explicit aims of the research. Rather, species are assigned a diet category post data collection using expert knowledge, published literature, or databases such as Fishbase (e.g., MacNeil et al.,

2015). More recently, Parravicini et al. (2020) highlight the disagreement in the literature about broad reef fish trophic guilds, and provide a standardized set of diet classifications using phylogeny and maximum body size to predict trophic guild with high accuracy. However, improvements can still be made by accounting for intraspecific variation. Intraspecific variation linked to ontogenetic shifts in diet could be accounted for by assigning diet to an individual fish count based both on species information and size, where that species-level data exists. Further, technological developments such as video surveys coupled with deep learning may allow the automated estimation of diet and other individual fish characteristics beyond size (Villon et al., 2018; Li et al., 2020). Progress has also been made using gut content DNA metabarcoding to rapidly and confidently estimate diet across diverse food webs. With DNA barcode libraries expanding, there is the potential to estimate high resolution diet across large scales (Casey et al., 2019). The incorporation of between-individual variation to a trait-based approach, with traits such as size and diet, would allow for a more dynamic view of environment~trait~function relationships—a dynamism which is essential to scaling up to population dynamics, whereby such dynamics ultimately shape multiple interacting ecosystem processes (Salguero-Gómez et al., 2018).

CONCLUSIONS

This review demonstrates the ability of the response-and-effect framework to guide future research directions based on the understanding that environmental changes will undoubtedly produce functional changes. Evidence suggests that some traits provide a crucial link between fish responses to disturbances and effects on ecosystem processes. However, the evidence base is thin for linking effect traits to many processes. Thus, if

an emphasis on the conservation of ecosystem functioning on coral reefs is to be made, there is much scope to develop a more concrete understanding of how traits link to individual processes and eventually the multifunctionality of the reef. Identifying overlapping traits, causation, and improving our ability to capture intra-species trait information will greatly advance this endeavor.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

JH-H collected data, did the data analysis, and wrote the first draft of the manuscript. NG and DM helped to conceive the project, provided supervision, data analysis suggestions, and editorial comments. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.640619/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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