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IN THE ANTHROPOCENE

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The meaning of the term 'function' in ecology: A coral reef perspective

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Abstract

1. The inherent complexity of high-diversity systems can make them particularly difficult to understand. The relatively recent introduction of functional approaches, which seek to infer ecosystem functioning based on species' ecological traits, has revolutionized our understanding of these high-diversity systems. Today, the functional structure of an assemblage is widely regarded as a key indicator of the status or resilience of an ecosystem. Indeed, functional evaluations have become a mainstay of monitoring and management approaches. But is the heavy focus on broad metrics of functional structure grounded in empirical research?

2. On tropical coral reefs, the ocean's most diverse ecosystems, remarkably few studies directly quantify ecosystem functions and the term 'function' is widely used but rarely defined, especially when applied to reef fishes. Our review suggests that most 'functional' studies do not study function as it relates to ecological processes. Rather, they look at easy-to-measure traits or proxies that are thought to have functional significance. However, these links are rarely tested empirically, severely limiting our capacity to extend results from community structure to the dynamic processes operating within high-diversity ecosystems such as coral reefs.

3. With rapid changes in global ecosystems, and in their capacity to deliver ecosystem services, there is an urgent need to understand and empirically measure the role of organisms in various ecosystem functions. We suggest that if we are to understand and manage transitioning coral reefs in the Anthropocene, a broad definition of the word 'function' is needed along with a focus on ecological processes and the empirical quantification of functional roles.

4. In this review, we propose a universal operational definition of the term 'function' that works from a cellular to a global level. Specifically, it is *the movement or storage of energy or material.* Within this broad definitional framework, all functions are part of a continuum that is tied together by the process-based unifier of material fluxes. With this universal definition at hand, we then present a path forward that will allow us to fully harness the power of functional approaches in understanding and managing high-diversity systems such as coral reefs.

KEYWORDS

anthropocene, coral reef fishes, ecosystem function, functional diversity, functional groups, trait-based ecology

1 | INTRODUCTION

Over the past few decades, the relationship between the ecological traits of species and ecosystem functioning has underpinned an expanding range of 'functional' studies (McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007), setting the stage for a new era of trait-based ecology. Recently, the rapid degradation of ecosystems has brought this functional approach into the arena of conservation biology, as the preservation of functionality (and the species that maintain this functionality) has become an increasingly urgent priority given the ongoing impacts of human development (Isbell et al., 2017).

Yet, our understanding of the term 'function' is far from clear; even a unified definition remains elusive (cf. Farnsworth, Albantakis, & Caruso, 2017; Jax, 2005). The goals of this review, therefore, were (a) to critically evaluate our understanding of the term 'function', (b) to explore the benefits and pitfalls of functional approaches in hyperdiverse ecosystems, by critically evaluating the utility of 'functional traits' and 'ecosystem functions', (c) to identify barriers to progress in functional studies and (d) to outline a blueprint for the future. In this future, the management, introduction and exploitation of organisms, based on their empirically derived functional roles, are going to shape human interactions with high-diversity systems. As the ocean's most diverse system, coral reefs are at the forefront of this new approach, with rapid anthropogenically driven transitions (Hughes, Barnes, et al., 2017a) underpinning an intense interest in describing and preserving coral reef 'functions' (Bellwood, Hughes, Folke, & Nyström, 2004; Kennedy et al., 2013). This review will therefore provide a critical evaluation of the concepts of function and functional traits, exploring their relevance for reef fishes and coral reefs.

2 | THE MEANING OF THE TERM 'FUNCTION'

2.1 | Is function just a term?

Despite attempts to provide clear definitions (Farnsworth et al., 2017; Jax, 2005), there is still considerable confusion over the term 'function'. Indeed, Jax (2005) identified four of the most important meanings of the term 'function' within ecology and the environmental sciences: 'function refers, in a descriptive sense, to processes and the causal relations that give rise to them, to the role of organisms within an ecological system, to the overall processes that sustain an ecological system (which together determine its "functioning") and finally to the services a system provides for humans or other organisms'. A universal definition for 'function' in the field of ecology, therefore, appears to be elusive.

The terms functional ecology, functional groups (FGs), ecosystem function, functional diversity, multifunctionality, functional morphology and functional traits all contain the word function or functional (see ESM Supporting Information Table S2 for a further 20 frequently used functional terms). But does the term function mean the same thing in each case? The term tends to carry connotations of increased value and ecological importance. For example, functional morphology is far more valuable than simple morphology because it infers a broader relevance for the individual or for an ecosystem (an important distinction); functional morphology is interactive, while morphology is descriptive. Non-functional often means broken so ipso facto, functional must be working. The Oxford English Dictionary describes 'function' as 'an activity that is natural to or the purpose of a person or thing'. Is this what we mean and, if so, does this justify the increased status of functional studies over mere descriptions?

This issue is particularly well exemplified when the term 'function' is applied to reef fishes (Villéger, Brosse, Mouchet, Mouillot, & Vanni, 2017). Although they are arguably the best-studied group of any reef organisms and frequently examined from a 'functional' perspective (Figure 1), the spectrum of studies invoking function has virtually no common denominator (cf. Bellwood & Choat, 1990; Floeter, Bender, Siqueira, & Cowman, 2018; Houk, Benavente, Iguel, Johnson, & Okano, 2014; Mouillot et al., 2014; Wainwright, 1988). 'Functionality' in reef fishes and their assemblage structure is, without a doubt, important; but what are we actually referring to?

The earliest use of the term function for reef fishes was in functional morphology (Motta, 1988; Wainwright, 1988), a field with wide-ranging significance for our understanding of functional links between morphology and ecology across multiple systems, organisms and processes (e.g. Ferry-Graham, Bolnick, & Wainwright, 2002). The pioneering work of early investigators has left a deep legacy of detailed information, particularly on the kinematics of fish feeding and locomotion (reviewed in Wainwright & Bellwood, 2002). It has also provided a rare, clear definition of function with Wainwright and Reilly (1994) stating that 'Functional morphology (and other functional sciences) provide an understanding of the *causal* relationship between phenotype and performance' which 'can play an important role in providing mechanistic explanations for ecological questions' (italics our emphasis). The key element that distinguishes 'functional' research is the causal link between the phenotype (be it morphology, physiology or behaviour) and ecological performance.

Although the earliest attempts to infer ecology from functional morphology set out to link morphology to prey use (i.e. 'what' species feed on), the association between phenotype and 'how' species feed turned out to be stronger. For example, Motta (1988) documented a clear relationship between the feeding apparatus of butterflyfishes and their foraging behaviour (but not their diet). Meanwhile, the study of fish-based herbivory resulted in a functional framework that causally linked parrotfish morphology and ecology. Extending beyond taxonomic boundaries, this framework separated parrotfishes into 'scrapers' (*Scarus s.s.*) and 'excavators' (*Chlorurus*) based on how species feed (Bellwood & Choat, 1990).

The establishment of these two FGs, scrapers and excavators, became a prime example of broad collections of taxa with measurably different contributions to coral reef ecosystems. Notably, groups were based on both morphological differences and empirically grounded quantifications of how feeding behaviour affected
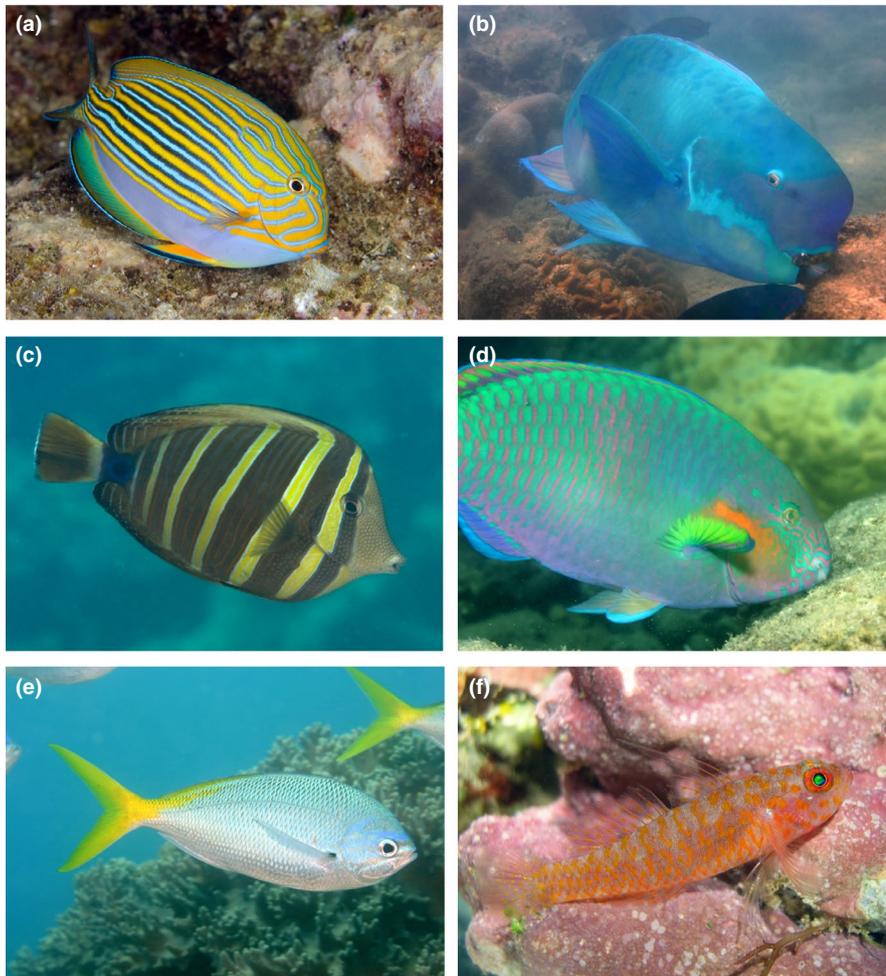
FIGURE 1 Fishes deliver a wide variety of ecosystem functions. Some species appear to fit easily into traditional, broad 'functional groups' like the (a) algal turf cropping *Acanthurus lineatus* or (b) the excavating parrotfish *Chlorurus microrhinos*, with its highly modified, coral-cracking jaws. However, through subtle differences in their ecology, other species have broken the mould of traditional groupings, such as (c) the crevice-feeding surgeonfish *Zebrasoma velifer* or (d) the sediment-removing parrotfishes, for example *Scarus rivulatus*. For other species, nothing but a coarse ecological classification exists (e.g. [e] the 'planktivore' *Caesio cunning* or (f) the 'cryptobenthic' *Trimma* sp.) which provides little evidence for their roles in ecosystem functions. (Photographs: J.P. Krajewski [a, b, c, d, e], A. González-Cabello [f])

the removal of algae or calcium carbonate. Equipped with these group classifications and detailed empirical examinations of the ecological roles of species in either group, ecologists could estimate ecosystem functions, such as herbivory and bioerosion, based on community structure alone (Bellwood, Hoey, & Hughes, 2012; Graham et al., 2018). The evidence from parrotfishes suggested that morphological and phylogenetic patterns had a strong match with realized ecosystem functions and that the two approaches segue seamlessly. Functional morphology underpinned ecosystem function. This neat association was illusionary.

While a relationship between morphology and function is frequently apparent, it soon became clear that, as in many other groups of organisms, there is more to a species' functional performance than a set of morphological or phylogenetically relevant characters (e.g. Nicholls & Racey, 2006; Tinoco, Graham, Aguilar, & Schleuning, 2017). Functional groups of coral reef herbivores as traditionally used, and derived from functional morphology, broadly classify species based on *how* material is removed (e.g. scraping or excavating), with relatively little concern for which resources are ultimately targeted, ingested and digested (cf. Clements, German, Piché, Tribollet, & Choat, 2017). By contrast, the identification of FGs from an ecosystem function perspective is quite different (Bellwood et al., 2004). They are concerned with *what* they do, regardless of how they do it.

Yet both have a common, unifying, element: the essence of the term 'function'. Extending the general approach of Done, Ogden, Weibe, and Rosen (1996), one may define a 'function' as pertaining to *the movement or storage of energy or material*. An 'ecosystem function' therefore, refers to *the movement or storage of energy or material within an ecosystem*. Following this definition, the terms 'ecosystem function' and 'ecosystem process' are effectively the same and can be used interchangeably (although we note that they may not have been considered in this way in the past). Working within this new definition, the defining characteristic of a functional group (from an ecosystem perspective) is the extent to which it modifies or facilitates the transfer or storage of energy or material within the system. In this respect, a scraping parrotfish, a sand-winnowing goby and a sticky-tentacled sea cucumber would all be classified as particulate removers. They are, in this context, a discrete functional group defined by what they do regardless of how they do it.

## 2.2 | Distinguishing 'how' and 'what' FGs

This highlights both differences in, and interdependence between, the two types of FGs: phenotype-based 'how' definitions and the ecosystem-based 'what' definitions. For grossly simplified groups (based on basic behaviour and/or a lack of understanding), the two

may be identical. 'Planktivores', for instance, can include such disparate groups as triggerfishes, butterflyfishes, surgeonfishes, damselfishes or gobies (Hobson, 1991). Yet, they are assumed by their behaviour (feeding in roughly the same location, i.e. in the water column) to be a single functional group. It is, of course, highly unlikely that all plankton-feeding reef fishes feed in the same way or on the same things but crude 'how' functional designations make for an easy segue to 'what' ecosystem functions.

With increasing knowledge of the realized ecological niches of species (with more data or by examining new niche axes), this null hypothesis of assumed similarity among 'what' functional group members is difficult to sustain (Brandl, Emslie, Ceccarelli, & Richards, 2016). This is grounded in both theoretical and mathematical reasoning (Rosenfeld, 2002) and can be seen in numerous groups across the tree of life (e.g. Nicholls & Racey, 2006; Cloyed &

Eason, 2017). It may therefore be beneficial to separate the more specific 'how' (including the 'why', 'where', and 'when') from the typically broader functional 'what' groups. This separation appears to be hierarchical and inter-related with morphology, physiology and/or behaviour separating smaller phenotype-based 'how' FGs (e.g. brushing surgeonfishes, sand-winnowing gobies, scraping parrotfishes) within broader ecosystem-level 'what' FGs (e.g. particulate removers; ESM Supporting Information Figure S1).

The impacts of these different approaches can be seen by comparing FGs of nominally herbivorous fish communities across three distinct biogeographic regions (Figure 2). In terms of 'how' FGs, the East Pacific has a small subset of the complex assemblages seen on Great Barrier Reef (GBR) or Caribbean reefs. Interestingly, the Caribbean and GBR differ little in terms of the number of individuals delivering each 'what' ecosystem function. For example, fishes
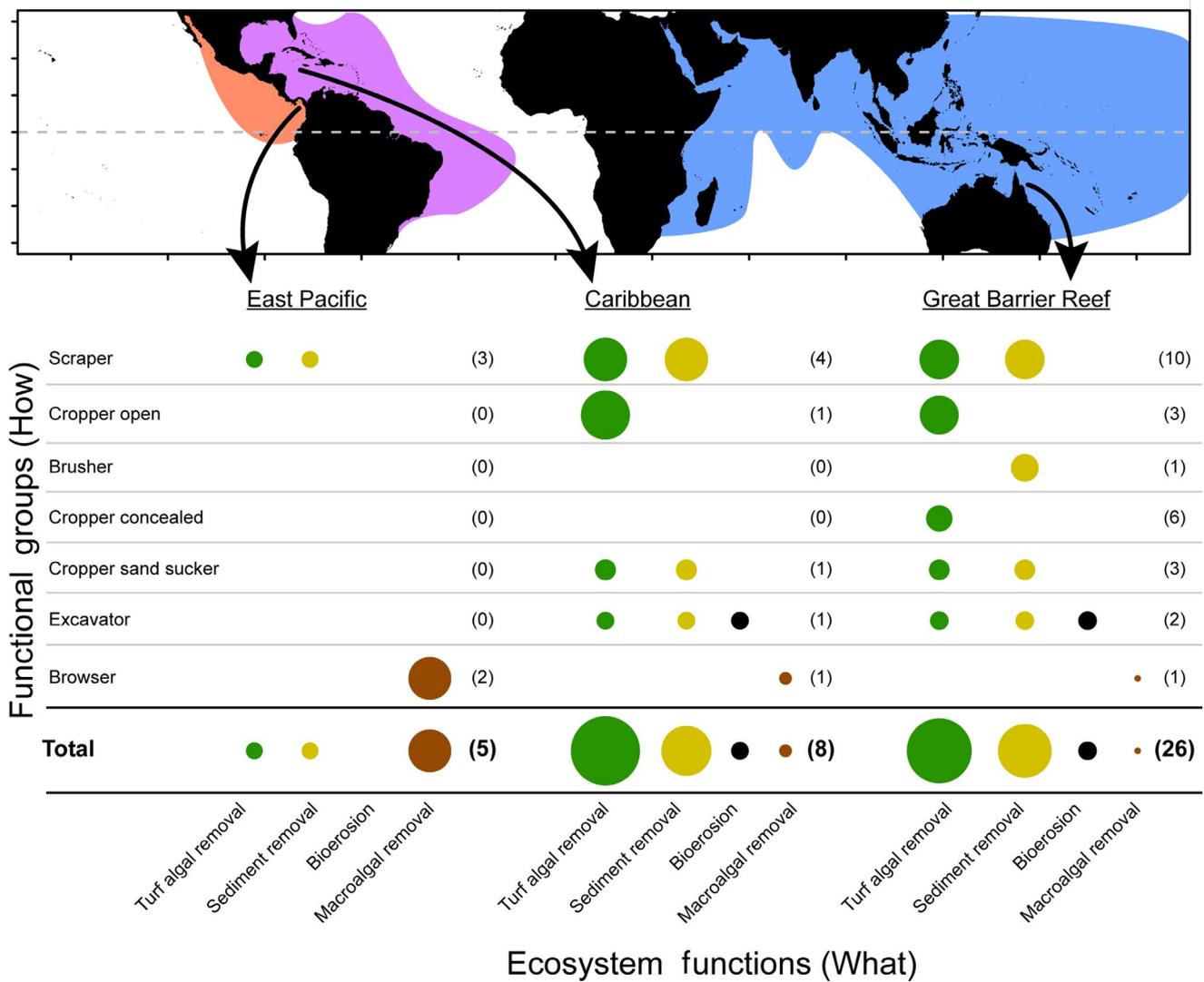
FIGURE 2 A comparison of herbivorous fish functional groups (FGs) in three biogeographic realms showing the relative contribution of phenotypic functional groups (defined by 'how' fishes feed) to ecosystem-level functional groups defined by 'what' fishes do. Bubble areas are proportional to the abundance of individual fish (>10 cm total length) in a given group; number of species in each realm in parentheses. An individual in a given FG can contribute to more than one ecosystem function. At an ecosystem level, there are remarkable parallels in the number of fish delivering ecosystem functions on the Great Barrier Reef and Caribbean despite major differences in species richness, functional group compositions and the relative contributions of functional groups. (Details and data in the ESM)

involved in turf algal removal. Yet, the two systems differ markedly in the composition of the 'how' FGs delivering this ecosystem function.

Importantly, it is the 'what' functions (i.e. the delivery of ecosystem functions) that are ultimately the key to the survival of reefs, making them a simple logical centrepiece for management or governance. When we remove an individual fish, we diminish a functional ('how') group but this may have little effect on the important ('what') ecosystem functions; other fish may be able to deliver the same ecosystem function in a different way. Pragmatically, it may not matter which species we remove or which 'how' FGs we protect if the required fluxes of energy or material are maintained. Within this framework, the logical priority is not to focus on the protection of species or FGs but ecosystem functions as a whole. Embracing the differences and interdependencies between the two functional approaches (how and what) helps clarify ambiguities in terminology and allows us to identify levels of redundancy or complementarity that may have been previously overlooked (e.g. across 'hows' and within 'whats'). Beyond aesthetic and/or ethical concerns, the key is not to prioritize the building blocks (i.e. species), while losing sight of the bigger picture: ecosystem functions.

It appears the term 'function' rightfully carries the connotation of increased ecological value. It provides connections from phenotype to ecosystem functions and facilitates an exploration of relationships among species that go beyond taxonomy. Despite their differences, phenotype-based FGs and ecosystem functions all have a common basis: *the movement or storage of energy or material*. This universal operational definition works from a cellular to a global level. It does not preclude finer-scale definitions (as noted above, cf. Wainwright & Reilly, 1994); rather, it provides a universal framework for all functional studies. For an individual of a given phenotype, functionality ranges from morphology (anatomical potential) and physiology (e.g. osmoregulation and the movement of ions) to behaviour (e.g. ingestion of prey). At an ecosystem or global level, functionality defines how communities interact with the environment (e.g. modifying the carbon cycle). Within this broad definitional framework, all aspects of functioning are part of a functional continuum, but invariably tied to the process-based unifier of material fluxes.

3 | FUNCTIONAL TRAITS AND ECOSYSTEM FUNCTIONS IN A CHANGING WORLD

Around the world, ecosystems are reconfiguring as they respond to direct human impacts and, more recently, global climate change (McGill, Dornelas, Gotelli, & Magurran, 2015). For many systems, including coral reefs, it is now recognized that maintaining ecosystem functions and services will require a focus on holistic ecosystem- or resilience-based management paradigms (e.g. Graham et al., 2013; Hughes, Barnes, et al., 2017a; Levin, Fogarty, Murawski, & Fluharty, 2009). However, the key to this approach is a well-grounded understanding of (a) intrinsic drivers of ecosystem functioning, (b) how to examine

and monitor functions on transitioning reefs and (c) if, and how, we can influence their performance. On coral reefs, fishes are an obvious component that are involved in a variety of biogeochemical fluxes on reefs (Allgeier, Layman, Mumby, & Rosemond, 2014; Barneche et al., 2014) and a key linkage between humans and marine ecosystems.

By the early 2000s, sufficient evidence was available to highlight the potential advantages of a functional approach for reef ecology and reef management (Bellwood et al., 2004). This was followed by an era of intense research on, and monitoring of, herbivore assemblages, seeking to define guidelines for the management of herbivorous reef fish assemblages across the globe (Edwards et al., 2014; Heenan & Williams, 2013; Mumby et al., 2007). However, the FGs suggested in 2004 (Bellwood et al., 2004), and still in use today, were all identified on pre-bleaching, 20th-century reefs. Furthermore, recent evaluations of these groups have discovered serious shortcomings in our ability to capture the complexity of the ecological processes under examination (e.g. Adam et al., 2018; Brandl & Bellwood, 2016; Kelly et al., 2016; Tebbett, Goatley, & Bellwood, 2017). It is clear that the basic FGs have significant limitations.

The problems with these traditional FGs highlight a 'functionality crisis'. Do we understand the breadth and depth of functions sufficiently to make informed recommendations for the management of ecosystem functioning? The answer to this question lies in our understanding of the performance of ecosystem functions and the contributions of specific species. This knowledge requires a strategy in which the examination of ecosystem functions has primacy. Yet, studies actually measuring in situ ecosystem functions on coral reefs are almost exclusively restricted to herbivores or corallivores (Figure 3; but see Allgeier et al., 2014; McClanahan, 2000). Other important ecosystem functions and the functional roles of the vast majority of reef fishes remain to be empirically determined (Figure 3).

Disentangling species-specific contributions to ecosystem functioning requires substantial empirical groundwork. However, coral reefs are at the forefront of studies of ecosystem transitions (Graham, Cinner, Norström, & Nyström, 2014; Harborne, Rogers, Bozec, & Mumby, 2017; Hughes, Barnes, et al., 2017a) and it is increasingly apparent that many severe disturbance events are at regional or global scales (Bruno & Valdivia, 2016; Hughes, Kerry, et al., 2017b). Accordingly, the call for evaluations of coral reef ecosystem functioning at these scales has likewise grown (Fisher et al., 2011; Hughes, Barnes, et al., 2017a; Kennedy et al., 2013). Established herbivore FGs have proven useful in understanding the functional structure of assemblages at both local and global biogeographic scales (e.g. Bellwood et al., 2004; Bonaldo, Hoey, & Bellwood, 2014; Edwards et al., 2014; Heenan, Hoey, Williams, & Williams, 2016), and in identifying the potential impacts of fishing and climate change (Edwards et al., 2014; Heenan et al., 2016). However, the lack of high-resolution global-scale data on species' functional roles, comparable to herbivores, has long curbed the extension of these studies to other ecosystem functions.

To fill this void, there has recently been a rapid increase in the use of 'functional traits' (Brandl et al., 2016; D'Agata et al., 2016;
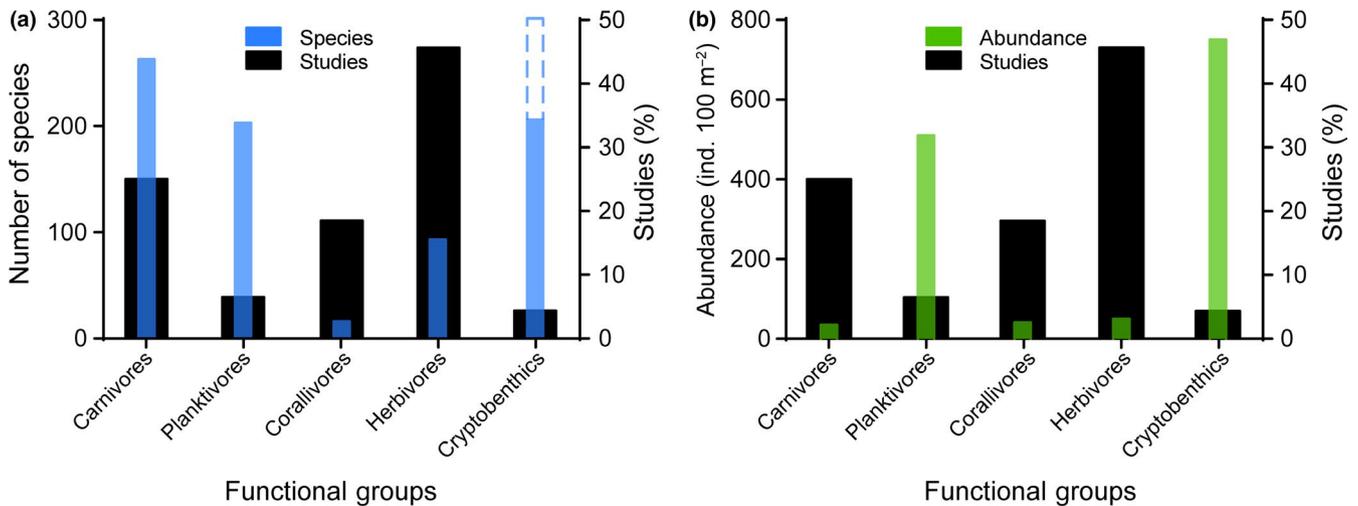
FIGURE 3 The focus on a few functional groups, for example herbivores and corallivores, may reflect perceived importance. However, as reefs change, functional importance is likely to be highly dynamic. Given the (a) diversity and (b) abundance of non-herbivore groups, there is considerable scope for novel functional discoveries. The lack of functional studies may be because groups have been overlooked (due to difficulty of observations (e.g. planktivores) or small size (cryptobenthic fishes)) rather than rejected based on a knowledge of their limited importance. (Details in the ESM)

McWilliam et al., 2018; Mouillot et al., 2014; Stuart-Smith et al., 2013). For plants, these functional traits have been defined as 'any biological attribute of an individual that impacts organism performance and thus fitness' (Violle et al., 2007). Such traits, as proxies for functions, have been widely used in the terrestrial plant literature (Cornwell et al., 2008; Lavorel & Garnier, 2002; Shipley et al., 2016; Violle et al., 2007), using attributes that are easy to measure and thought to be tightly linked to ecological performance. With the ever-increasing refinement of analytical approaches (e.g. Villéger, Novack-Gottshall, & Mouillot, 2011), such trait-based approaches have opened up exciting new areas of investigation (especially at large, biogeographic scales; e.g. D'Agata et al., 2016; McWilliam et al., 2018; Mouillot et al., 2014; Stuart-Smith et al., 2013) and can surpass species identity in the prediction of ecosystem functioning across ecosystems (Gagic et al., 2015).

Over the last two decades, an informal shortlist of fish traits has arisen that (a) are easy to obtain for numerous species (e.g. derived from FishBase) and (b) are believed to be functionally informative. The main traits on this list are as follows: size (usually maximum size of a species), trophic group (in broad categories, e.g. carnivore), schooling behaviour (solitary, pairing, schooling), mobility (sedentary, mobile), position in water column (benthic or pelagic) and activity patterns (nocturnal/diurnal). These traits have revealed useful insights from global distributions of trait combinations (Mouillot et al., 2014; Stuart-Smith et al., 2013) to local changes in community composition (Brandl et al., 2016; Richardson, Graham, Pratchett, Eurich, & Hoey, 2018).

Despite limitations (addressed below), traits and their presumed functions offer a potential avenue to overcome the complexity that is inevitable in high-diversity systems such as coral reefs. Furthermore, they can operate in the absence of functional knowledge, avoiding the need to empirically measure each species' contribution to

a variety of ecological processes (with appropriate caveats, e.g. if we are simply looking at patterns and correlations). Such correlations offer fertile ground for further investigation of causality. Traits therefore offer a first step in the evaluation of broad-scale trends that may be functionally relevant.

Furthermore, we are at a watershed moment in the study and management of the world's coral reefs. Reefs are changing fast as they reconfigure in response to direct human disturbance (predominantly overfishing and terrestrial inputs) and the impacts of climate change (especially bleaching and subsequent coral mortality). A functional approach offers one of the most promising solutions for the management of resilience in such dynamic ecosystems. We do not have time to describe the functional characteristics of all 6,000 + reef fish species, although any effort to assemble such databases should be encouraged and continued (cf. Winemiller, Fitzgerald, Bower, & Pianka, 2015). Decisions based on ecosystem function have to be made now. Traits, and functional traits in particular, offer an invaluable tool in this endeavour. Yet, a thorough understanding of both the strengths and weaknesses of traits, and the meaning of the term function, is required if we are to fully exploit this powerful approach to inferring ecosystem functioning from fish assemblage structures on coral reefs.

4 | A CRITICAL EVALUATION OF FUNCTIONAL TRAITS: IMPLICATIONS FOR CORAL REEFS

4.1 | Assessing the value of traits versus functional traits

Given an operational definition of a function, one can explore the extent to which functional studies examine functions. Unfortunately, the vast majority do not. Most studies look at phenotypic traits as

proxies for functions. In terrestrial plant studies, based on strong links between traits (e.g. leaf area) and different strategies of resource acquisition (determined a priori), the use of functional traits has revolutionized our understanding of how plant communities relate to ecosystem functioning world-wide (Cornwell et al., 2008; Lavorel & Garnier, 2002). In fishes, a similarly strong relationship may be described between fin shape and locomotion (Wainwright, Bellwood, & Westneat, 2002) or between jaw strength and prey hardness (Wainwright, 1988). The morphological traits serve as proxies for where, how or why a given type of prey is used. However, how, and if, these relationships ultimately translate into ecosystem functioning is poorly quantified. As noted by Violle et al. (2007), progress in functional studies is dependent on consistent definitions, and in coral reef taxa, including fishes, there is a clear need to understand the differences between *traits* and demonstrably *functional traits*.

To meet the requirements for the latter, a functional trait has to be embedded in biological knowledge of the organism and have a *causal* relationship with a *clearly specified* function (or multiple functions). For reef fishes, a good example is the size of the *levator posterior* muscle which directly influences the capacity of *Halichoeres* fishes to consume hard-shelled prey (Wainwright, 1988). However, such causal relationships are often hard to establish outside the field of biomechanics, and further links to realized ecosystem functions are rare. And even in these cases, ecological complexity can dampen the linearity and strength of causal relationships in the field (e.g. Bellwood, Wainwright, Fulton, & Hoey, 2006). Establishing *causal* links between traits and *clearly defined ecosystem functions* is perhaps the greatest challenge for future functional studies.

In lieu of clear mechanistic knowledge, presumed linkages are usually based on correlations. Even supertraits (sensu Madin et al., 2016), that is traits that explain a lot of variation across diverse assemblages and in more than one function, are often just high-performing correlations, while causation still remains to be demonstrated. For reef fishes, the commonly used categorical traits (size, schooling, diet, etc.) have all been related to presumed functions, which may affect a given ecosystem function. However, trait selection is often based on ease of measurement, or estimation, not functional value. Few traits have been shown to have a *causal* relationship with associated ecosystem functions. The inferred 'function' frequently consists of retrofitting functionality to pre-existing traits. If traits cannot be causally linked to a specific function, any resultant groupings or patterns cannot be directly related to ecosystem function.

4.2 | Linking traits, FGs and ecosystem functions

If most functional trait-based studies do not clearly articulate the linkages between traits and specific functions or cannot establish empirically based causality, then this changes how the results of trait-based studies can be interpreted. Thus, when considering trait-based multivariate analyses, we are looking at trait space that

may have functional implications, not 'functional space'. Likewise functional diversity metrics actually measure trait diversity. Most traits are likely to have some significance at an individual level (in terms of individual fitness), but their ecosystem effects are almost impossible to infer or quantify. Thus, while patterns of traits are undoubtedly interesting (especially from a biogeographic perspective), the suggestion that variation in reef fish traits can directly inform management approaches, by informing us about the fluxes of energy or material on reefs, is, at present, unjustifiable. We suggest that it may be better to simply refer to traits and trait space (rather than functionality), followed by cautious functional interpretations; unless causal relationships for all traits are established in advance.

The problem of making strong inferences on ecosystem functioning from traits may be further exacerbated when we scale up the presumed functional abilities of an individual, population or species to ecosystem-level functions. In many studies, the contribution of a species to an ecosystem function is estimated indirectly. This is usually based on the product of local species abundances and typical rates of functional activity (e.g. consumption rate per individual), to provide an overall estimate of the magnitude of a function over a unit area (e.g. rates of grazing on reefs or bioerosion m^{-2}) (Bellwood et al., 2012; Graham et al., 2018; Perry & Alvarez-Filip, 2018). The advantage of this approach is that functional impacts can be estimated at an individual, population, species, functional group or community level and can be expressed as a rate-based process in terms of its spatial impact (function per unit area). However, if there are problems accurately quantifying an individual's functional impact, the resultant estimates of ecosystem function are likely to be grossly inaccurate. For example, recent debate over the surgeonfish *Ctenochaetus striatus* has highlighted the dangers of functional misidentifications. *Ctenochaetus* has been known as a particulate feeder for over 50 years, but it is often misclassified as a grazing herbivore (see discussion in Tebbett et al., 2017). As the most abundant surgeonfish on Indo-Pacific reefs (Cheal, Emslie, Miller, & Sweatman, 2012), a basic error of functional identification would impinge on every model constructed using these functional designations and would undermine our understanding of a key ecosystem function on coral reefs.

There are also issues when separating the direct versus indirect consequences of a function. For example, fish may remove sediment (a direct ecological function), but this action has far-reaching implications for other processes (e.g. competition between corals and algae). Thus, a species' contribution may directly or indirectly influence functions or processes of interest. Indeed, some of the most important ecosystem processes may be underpinned by multiple ecological functions. Simple, direct links may be the exception rather than the rule.

Establishing causal links between species traits and ecosystem functions is challenging. It is even more daunting when multiple ecological functions are considered (i.e. ecosystem multifunctionality). Multifunctionality frameworks are also sensitive to the number of species and functions considered (Gamfeldt & Roger, 2017), and any inference drawn from species traits for a range of different functions appears risky. Phylogenetic frameworks that

ascribe functional differences based on phylogenetic relatedness are likewise unlikely to remedy these issues; phylogenetic richness may be a useful surrogate for functional richness but unless validated, it just represents a proxy by proxy. Finally, multidimensional trait spaces (quantified using convex hull volumes) are sensitive to outliers, especially when categorical traits are used, enhancing the influence of traits that create increased volumes (i.e. outliers in multidimensional space), whether they are functionally important in the ecosystem or not. Thus, the challenge of establishing empirical linkages between functional traits and ecosystem functions remains a salient one, even for some of the most common and promising approaches used to quantify ecosystem functioning.

4.3 | The overriding impact of body size

One of the largest problems in the interpretation of the relationship between commonly used traits and ecosystem functioning is the overwhelming impact of body size. Body size as a trait is disproportionally impactful as both a driver and a response variable. As a response variable, body size is hypersensitive to human exploitation (due to human selectivity for large sizes (Olden, Hogan, & Zanden, 2007)). As such, size decreases are often the predominant responses in various local, regional or global comparisons that seek to determine anthropogenic effects on functional composition (Bellwood et al., 2012; D'Agata et al., 2016). Similarly, body size also acts as a primary driver of ecological processes. It directly impacts almost all basic anatomical, physiological and behavioural parameters (Barneche et al., 2014; Brandl, Goatley, Bellwood, & Tornabene, 2018). On reefs, for example, fish size has been closely tied to ecosystem functions such as nutrient cycling (Allgeier et al., 2014), bioerosion (Bonaldo et al., 2014) or growth (Morais & Bellwood, 2018). Indeed, size is a *universal trait* in that it is related to every known organismal function, incorporating all metabolic, ontogenetic, allometric and ecological attributes. Thus, body size almost invariably affects ecosystem functioning, while being disproportionally strongly affected by anthropogenic stressors – it is a highly reactive and predictive universal trait.

Furthermore, while body size may seem like a well-documented trait, it is surprisingly difficult to capture. Firstly, in situ species-specific body sizes can vary markedly among locations based on a variety of human-mediated (D'Agata et al., 2016) or environmental (Taylor et al., 2018) factors. Secondly, this variation is not captured in studies that use maximum body size as a static trait that belies location-specific variation in ecosystem functioning. Maximum body size, the most commonly used trait, may not reflect reality; in this scenario, *Homo sapiens* is a 2.7-m-high mammal. Finally, and most importantly, size is uninformative in terms of functions as it is non-discriminating. Size is *causally* related to *all* functions and is poorly captured by the most commonly used proxy. As a result, size will emerge as the driving factor of functional patterns in many analyses, but it is particularly difficult to determine which function or functions it impacts most.

4.4 | The universal modifier: Behaviour

An additional issue with traits, especially in motile organisms, is that their functional links are easily modified by behaviour (i.e. the difference between fundamental and realized niches). We see this in ontogenetic shifts in morphologically similar individual fish (browsing to planktivory in *Naso brevirostris*) or mismatches of fundamental and realized niche volumes across multiple ecological axes (Brandl, Robbins, & Bellwood, 2015). Thus, behaviour, in terms of movement, position or social context are all potentially major determinants of an organism's functional role, a state that is not easily inferred based on static, broad trait categories (e.g. mobility, sociality) or morphology. This was demonstrated in an analysis of the diet of coral reef wrasses (Bellwood et al., 2006) where 10 morphological traits with direct, causal, links to the performance of the feeding apparatus revealed only weak links to ecosystem function, with no clear relationship between feeding apparatus specialization and dietary specialization. The traits all appear to have been overwhelmed by behaviour and/or ecological opportunism.

4.5 | Linking presence to ecosystem function: Was Schrödinger's cat functional?

Although trait distributions, based on presence–absence data, may be particularly useful in large-scale biogeographic studies (e.g. Mouillot et al., 2014), early recognition of the value of abundances in functional studies has led to the development of indices that incorporate local abundances (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). However, even if abundances are used, the influence of species' abundances on trait-based metrics can be weak, even at local scales (McPherson, Yeager, & Baum, 2018), and functional links may still be open to question. On coral reefs, most studies assume that if a fish is present in an area, and if we know its functional attributes, we can estimate local ecosystem function. There are very few studies that have demonstrated that fishes do deliver functions in this manner. This mismatch was eloquently expressed by Steneck (1983) who stated that 'The 'apples and oranges' involved here result from trying to force units and techniques which are designed to determine *patterns* in herbivore abundance on the *process* of herbivory. [...] It is generally assumed that the abundance of herbivores corresponds with their impact on algae. This assumption has never been tested'.

This statement was correct in 1983 and since then only a few studies have successfully linked presence/abundance to function in a spatial context (e.g. Bejarano et al., 2017; and even in this case, the function is in terms of the number of bites taken from algal turfs, a proxy for algal removal). However, numerous studies have shown that there is frequently a disconnect between presence and presumed function. This is most notable in terms of algal removal by species that are not observed on visual counts but do occur in videos (Vergés, Bennett, & Bellwood, 2012). This problem brings to the fore questions over the widespread use of visual transects to estimate function on coral reefs. Studies have indicated that there

is a significant diver effect in visual censuses, especially when estimating large fishes, with common methods underestimating fish abundances by up to 73% (Emslie, Cheal, MacNeil, Miller, & Sweatman, 2018). As these larger fishes can have a disproportionately large effect on ecosystem functions (Bonaldo et al., 2014), ecosystem functions are likely to be significantly underestimated using visual censuses. Meanwhile, the contribution of the other 50% of reef fishes (the cryptobenthic fishes) is completely overlooked (Brandl et al., 2018). Thus, visual censuses count a small, biased subset of fish species and individuals for which actual functional impact is rarely measured, while other functions are often delivered by species that are not visually apparent. In other words, although species with a given suite of coarse traits may be present on a given reef, this reef may or may not maintain critical ecological processes, a functional analogue to Schrödingers famous feline thought experiment (Schrödinger, 1935).

5 | A BLUEPRINT FOR THE FUTURE OF FUNCTIONAL STUDIES

How do we manage ecosystems so that they persist and continue to deliver the goods and services that we value? The answer begins with understanding ecosystem functions and ends with the suite of species that represent the minimum necessary to support critical functions. The former need to be safeguarded from human disturbances, while the latter serve as the agents via which management strategies can be implemented most efficiently (ideally, such strategies will be embedded within the application of diverse social solutions that address local governance and compliance [see Hughes, Barnes, et al., 2017a]). In these endeavours, there are three key steps. First, if we wish to understand ecosystem functions, we need to think about the context of the system in question, that is what goods and services do we wish to sustain. Second, with this in mind, we need to recognize that all ecosystem functions are not equal – some are more important than others; but this is invariably context-specific. Just as we can no longer afford to protect all species, we need to recognize the need for 'functional triage' to determine which functions should be protected first and why. Finally, we must embrace change and recognize the inevitability and magnitude of changes we are now facing. These aspects will be considered below.

5.1 | A new hierarchy of functionality and its application to coral reefs

Some researchers argue that all biodiversity should be protected, others that some species are more important than others. This latter perspective, where a single species dominate a certain process within a system, was crystalized in the term 'keystone species' (Paine, 1969). On coral reefs, there was likewise an early recognition that some FGs, especially herbivores, were important in mediating benthic community structure and facilitating coral growth. They were recognized as 'critical FGs' (Bellwood et al., 2004). The difference between keystone species and critical FGs is that the former looks at the functional importance of one species, while the latter recognizes the importance of the *function* – regardless of the species involved.

While not all functions are equally important for the maintenance of whole-system resilience, the ranking of functions is highly context-dependent, making it difficult to generalize. There is also an issue that arises from our motivations to preserve function. Whether it is protection or management for societal, aesthetic or nutritional purposes, ultimately we commonly have an anthropocentric basis for our actions. This may dictate the relative importance of different functions. Furthermore, to be effective, we must be able to take actions to influence functions; wave exposure regimes may be important determinants of organismal life history, species assemblages and, ultimately, ecosystem functioning (Taylor et al., 2018), but we cannot realistically attempt to manage ocean hydrography. The identification of critical functions must address clearly specified needs and offer some basis for human intervention. We must think about the context of the system in question, and which goods or services we wish to conserve. Only then can we discern which functions are critical.

From the beginning, there has been some confusion over the identification of critical ecosystem functions versus the critical FGs that mediate them. The most important step is to recognize that the ecosystem function is paramount, not the providers. We posit that there are four essential steps, in the order of decreasing importance: (a) identify the critical ecosystem function(s), (e.g. removal of sediment) at the appropriate spatial and temporal scale for the system of interest, (b) at a matching scale, identify the traits that are important for mediating this function (e.g. scraping teeth to remove sediments from turfs), (c) identify the species that possess the requisite traits and deliver the required functions (e.g. parrotfishes, urchins etc). Finally, (d) identify and quantify critical FGs, that is collections of species with appropriate traits that deliver the required ecosystem function.

Since 2004, despite calls to identify critical functions on reefs, few have been recognized as such. Most research has focused on finer divisions within recognized critical FGs, for example browsers, grazers, scrapers, excavators and brushers within nominal herbivores (Brandl & Bellwood, 2016; Tebbett et al., 2017) (Figures 2 and 3). These groups have facilitated a burgeoning social-ecological literature, where these classical FGs underpin proposed management and governance approaches (e.g. Graham et al., 2013; Hughes, Barnes, et al., 2017a). However, this is all based on functional groups established in the early 1990s, and since then coral reefs have changed profoundly. Importantly, the relative importance of 'critical' functional groups may also be changing (Figure 4).

For example, despite early concerns about macroalgal dominance on coral reefs, there is increasing evidence that many Anthropocene reefs will be dominated by thick mats of turf algae and sediments (Bellwood et al., 2018; Goatley, Bonaldo, Fox, & Bellwood, 2016; Jouffray et al., 2014). The nature of these mats will be critical for the persistence of coral-dominated reefs and their utility to humanity. Recent work has identified two extreme alternate conditions in algal

FIGURE 4 (a) North Reef, Lizard Island on the Great Barrier Reef in 1984, as an example of a 20th-century scleractinian coral-dominated reef system. (b) The same site in 2018 after cyclones and back-to-back coral bleaching reflects the appearance of many Anthropocene reefs. (c) and (d) display how, in maintaining the status quo, different functions would be considered critical through time. For example, the removal of structural carbonates may be of critical importance in systems dominated by plating *Acropora* (c), but as fast-growing, branching and plating corals are lost, this function is reduced in importance (d). By contrast, the removal of sediments from algal turfs is of low importance where systems are dominated by corals (c); however, in systems with high algal turf cover, sediment removal can maintain high algal turf productivity and facilitate algal turf removal (d)
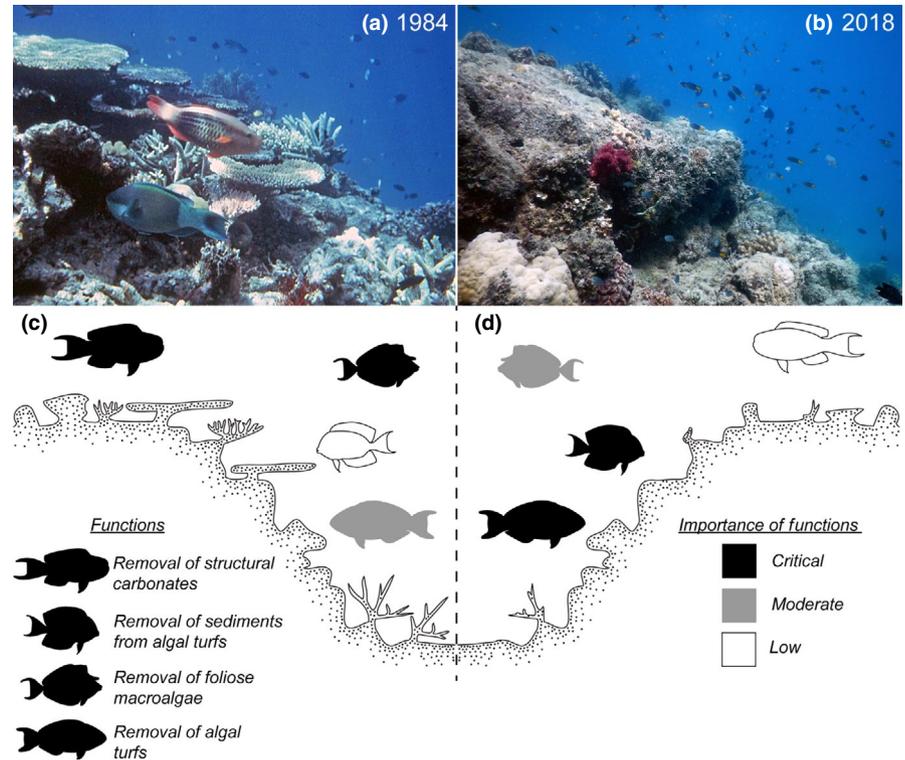
turfs: long sediment-laden algal turfs (LSATs) and short productive algal turfs (SPATs; Goatley et al., 2016). LSATs have been implicated in reductions in coral settlement, coral survival, fish feeding, reef productivity and fish growth (Arnold, Steneck, & Mumby, 2010; Bellwood et al., 2018; Goatley et al., 2016). SPATs, by contrast, have been associated with high productivity and herbivory rates, thus underpinning key reef functions (Bellwood et al., 2018; Goatley et al., 2016).

Given shifting benthic configurations on Anthropocene reefs towards LSATs (Goatley et al., 2016), sediment removal and modification of algal turfs as well as other processes, yet to be identified, may be emerging as new critical functions. Foremost among these is a conceptual shift from factors that shape static biomass, to a deeper understanding of factors that underpin productivity (Bellwood et al., 2018). For example, functional groups that underpin trophic networks such as cryptobenthic fishes (Brandl et al., 2018) or functional groups that favour SPATs over LSATs, thus boosting local algal productivity yields to fishes (Tebbett, Bellwood, & Purcell, 2018). To remain ecologically relevant, research has to embrace the possibility of ecosystem states becoming more ephemeral and has to be able to respond to changing critical ecosystem functions (Figure 4).

5.2 | Reconciling complexity and practicality through functional groups

Our understanding of ecosystem functions that involve consumer species, such as fishes, is almost always indirect, via proxies or traits that almost invariably hold only weak empirically demonstrated links with associated ecosystem functions. Naturally, it is impossible to

empirically examine links to specific functions for all traits held by all species; yet each link we do establish is an invaluable step forward, which highlights the profound importance of basic, organismal research in high-diversity ecosystems. Likewise, it is clear that a lack of resolution in traits can prevent meaningful functional interpretations. There is a trade-off between ecological resolution and practicality for both ecologists and managers. Functional groups may represent an acceptable compromise. Combining morphological and/or behavioural traits, they can offer broad insights into ecosystem functions. Furthermore, functional groups are the level of functional identification that permits practical interactions in a human context. When we fish on a reef, we often impact fishes that are easily identified as members of important functional groups that underpin critical ecosystem functions. Functional groups have the potential to incorporate the empirically determined causal links between traits and functions and offer a convenient unit for management purposes.

In the scheme proposed, looking at first functions, then traits and finally species, functional groups act as a collective term that draws groups of traits and species into a manageable unit. Excavating parrotfishes, for example, have perhaps 20 known morphological traits that facilitate or indicate their capacity to excavate the substratum; by combining species in a group that share many of these features, we can offer a functional shorthand for a complex group that may be phylogenetically and ecologically disparate but share the key common feature: their function.

However, the use of functional groups to reconcile complexity and manage functions comes with necessary caveats. First, the linkages between the group and the presumed function must be

ground-truthed. One way forward may be to combine estimates of function based on proxies with direct measures of functions, for example measuring actual erosion from blocks that replicate real reef substrata alongside inferences of bioerosion from fish abundances. Count-based approaches may offer an extrapolated estimate of functions, but care is needed to ensure they reflect the actual rate of functions and that the organisms responsible are all documented and described in sufficient ecological detail. This type of linkage is clearly a priority for future research. Second, groupings need to be adaptive. Functional groups of herbivores proposed in 2004 (Bellwood et al., 2004) are now known to be a coarse representation of the ecological complexity across species within each group, limiting their utility for inferring functions (Brandl & Bellwood, 2016). 'Adaptive functional groups' of the future need to be continuously scrutinized for their ecological relevance and, as such, repeatedly re-adopted into functional studies rather than simply recycling previous trait schemes.

5.3 | Embracing change: Functions on coral reefs in the past, present and future

The fossil record and phylogenetic reconstructions show how taxa have changed over time (Bellwood, Goatley, & Bellwood, 2017; Floeter et al., 2018). These insights help us to understand global patterns of biodiversity, biogeography and evolutionary processes. By combining functions, we can also reconstruct ecosystem functions over time (e.g. Cramer, O'Dea, Clark, Zhao, & Norris, 2017). Indeed, reconstructing functional changes over the past 50 My may help us to understand the consequences of functional changes in ecosystems and enable us to forecast the implications of changes in the future (Bellwood et al., 2018). Recent bleaching events have foreshadowed the future of coral reefs over the next few centuries where it is likely that we will be facing a period of rapid transition as recurrent bleaching events change the ability of reefs to sustain coral cover. The loss of acroporid corals, in particular, is likely to have a major effect as they provide much of the 3D structure on reefs and presumably numerous ancillary functions for fishes (Pratchett, Thompson, Hoey, Cowman, & Wilson, 2018). However, these new Anthropocene reefs are also reminiscent of reefs in the geological past. The evidence to date suggests that this loss of corals will impact local fish biodiversity and biomass (Pratchett et al., 2018; cf. Wismer, Tebbett, Streit, & Bellwood, 2019)) but the impact on ecosystem functions remains to be determined. Some functions may be robust to changes in coral biodiversity, or fish biodiversity, with some major functions such as herbivory appearing to operate at high levels even in low-coral cover locations (Bellwood et al., 2018; Brandl et al., 2016). This resilience to change may not be permanent or apply to other functions. It is important to recognize that these responses will be occurring in a changing fitness landscape, with unknown consequences for population selection over both ecological and evolutionary time-scales.

The profound impacts of climate change on reefs have challenged the status quo for reef ecosystems, scientific approaches and management practices. The recent bleaching events have been a clarion call to establish a new understanding of functions on reefs, their relative importance, and their capacity to change. It is also clear that new management practices and governance structures will be needed. But at this stage, the key question remains unanswered: what do we need to protect on Anthropocene reefs? From the evidence amassed herein, the main conclusion is that we do not need to protect biodiversity, functional groups or a single keystone species, but critical ecosystem functions – and the traits, species and groups that support them. To monitor and protect these functions, empirical linkages will be indispensable.

We are entering a new era for coral reefs. Of all conceptual breakthroughs in the last five decades, one of the most pervasive and compelling has been the widespread recognition of the importance and value of 'functional' studies. But exactly what we meant by function varied. With a more rigorous definition and an understanding of the various functional approaches, our ability to understand and then manage reefs of the future is looking increasingly feasible. Climate change remains humankind's greatest intellectual and practical challenge, yet, for reefs, we finally have a conceptual framework within which we can hope to steer reefs through the period of rapid transition that we now face. At the heart of this endeavour is one word: function.

AUTHORS' CONTRIBUTION

D.R.B. and S.B.T. conceived the research idea. All authors contributed vigorously to the discussion and writing of this paper.

DATA ACCESSIBILITY

All data are contained within the manuscript or in the Supporting Information.

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REFERENCES

Adam, T. C., Duran, A., Fuchs, C. E., Roycroft, M. V., Rojas, M. C., Ruttenberg, B. I., & Burkepile, D. E. (2018). Comparative analysis of foraging behaviour and bite mechanics reveals complex functional diversity among Caribbean parrotfishes. *Marine Ecology Progress Series*, *597*, 207–220.

Allgeier, J. E., Layman, C. A., Mumby, P. J., & Rosemond, A. D. (2014). Consistent nutrient storage and supply mediated by diverse fish

communities in coral reef ecosystems. *Global Change Biology*, *20*, 2459–2472. https://doi.org/10.1111/gcb.12566

Arnold, S. N., Steneck, R. S., & Mumby, P. J. (2010). Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology Progress Series*, *414*, 91–105. https://doi.org/10.3354/meps08724

Barneche, D. R., Kulbicki, M., Floeter, S. R., Friedlander, A. M., Maina, J., & Allen, A. P. (2014). Scaling metabolism from individuals to reef-fish communities at broad spatial scales. *Ecology Letters*, *17*, 1067–1076. https://doi.org/10.1111/ele.12309

Bejarano, S., Jouffray, J.-B., Chollett, I., Allen, R., Roff, G., Marshell, A., … Mumby, P. J. (2017). The shape of success in a turbulent world: Wave exposure filtering of coral reef herbivory. *Functional Ecology*, *6*, 1312–1324. https://doi.org/10.1111/1365-2435.12828

Bellwood, D. R., & Choat, J. H. (1990). A functional analysis of grazing in parrotfishes (family Scaridae): The ecological implications. *Environmental Biology of Fishes*, *28*, 189–214. https://doi.org/10.1007/BF00751035

Bellwood, D. R., Goatley, C. H. R., & Bellwood, O. (2017). The evolution of fishes and corals on reefs: Form, function and interdependence. *Biological Reviews*, *92*, 878–901. https://doi.org/10.1111/brv.12259

Bellwood, D. R., Hoey, A. S., & Hughes, T. P. (2012). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1621–1629. https://doi.org/10.1098/rspb.2011.1906

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*, 827–833. https://doi.org/10.1038/nature02691

Bellwood, D. R., Tebbett, S. B., Bellwood, O., Mihalitsis, M., Morais, R. A., Streit, R. P., & Fulton, C. J. (2018). The role of the reef flat in coral reef trophodynamics: Past, present, and future. *Ecology and Evolution*, *8*, 4108–4119. https://doi.org/10.1002/ece3.3967

Bellwood, D. R., Wainwright, P. C., Fulton, C. J., & Hoey, A. S. (2006). Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 101–107. https://doi.org/10.1098/rspb.2005.3276

Bonaldo, R. M., Hoey, A. S., & Bellwood, D. R. (2014). The ecosystem roles of parrotfishes on tropical reefs. *Oceanography and Marine Biology: an Annual Review*, *52*, 81–132.

Brandl, S. J., & Bellwood, D. R. (2016). Microtopographic refuges shape consumer-producer dynamics by mediating consumer functional diversity. *Oecologia*, *182*, 203–217. https://doi.org/10.1007/s00442-016-3643-0

Brandl, S. J., Emslie, M. J., Ceccarelli, D. M., & Richards, Z. T. (2016). Habitat degradation increases functional originality in highly diverse coral reef fish assemblages. *Ecosphere*, *7*, e01557. https://doi.org/10.1002/ecs2.1557

Brandl, S. J., Goatley, C. H. R., Bellwood, D. R., & Tornabene, L. (2018). The hidden half: Ecology and evolution of cryptobenthic fishes on coral reefs. *Biological Reviews*, *93*(4), 1846–1873. https://doi.org/10.1111/brv.12423

Brandl, S. J., Robbins, W. D., & Bellwood, D. R. (2015). Exploring the nature of ecological specialization in a coral reef fish community: Morphology, diet and foraging microhabitat use. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20151147.

Bruno, J. F., & Valdivia, A. (2016). Coral reef degradation is not correlated with local human population density. *Scientific Reports*, *6*, 29778. https://doi.org/10.1038/srep29778

Cheal, A. J., Emslie, M., Miller, I., & Sweatman, H. (2012). The distribution of herbivorous fishes on the Great Barrier Reef. *Marine Biology*, *159*, 1143–1154. https://doi.org/10.1007/s00227-012-1893-x

Clements, K. D., German, D. P., Piché, J., Tribollet, A. D., & Choat, J. H. (2017). Integrating ecological roles and trophic resources on coral reefs: Multiple lines of evidence identify parrotfishes as microphages. *Biological Journal of the Linnean Society*, *120*, 729–751.

Cloyed, C. S., & Eason, P. K. (2017). Niche partitioning and the role of intraspecific niche variation in structuring a guild of generalist anurans. *Royal Society Open Science*, *4*, 170060. https://doi.org/10.1098/rsos.170060

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., … Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, *11*, 1065–1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x

Cramer, K. L., O'Dea, A., Clark, T. R., Zhao, J. X., & Norris, R. D. (2017). Prehistorical and historical declines in Caribbean coral reef accretion rates driven by loss of parrotfish. *Nature Communications*, *8*, 14160. https://doi.org/10.1038/ncomms14160

D'Agata, S., Mouillot, D., Wantiez, L., Friedlander, A. M., Kulbicki, M., & Vigliola, L. (2016). Marine reserves lag behind wilderness in the conservation of key functional roles. *Nature Communications*, *7*, 12000. https://doi.org/10.1038/ncomms12000

Done, T., Ogden, J., Weibe, W., & Rosen, B. (1996). Biodiversity and ecosystem function of coral reefs. In H. Mooney, J. Cushman, E. Medina, O. Sala, & E. Schulze (Eds.), *Functional roles of biodiversity: A global perspective* (pp. 393–429). New York, NY: John Wiley & Sons.

Edwards, C. B., Friedlander, A. M., Green, A. G., Hardt, M. J., Sala, E., Sweatman, H. P., … Smith, J. E. (2014). Global assessment of the status of coral reef herbivorous fishes: Evidence for fishing effects. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20131835.

Emslie, M. J., Cheal, A. J., MacNeil, M. A., Miller, I. R., & Sweatman, H. P. A. (2018). Reef fish communities are spooked by scuba surveys and may take hours to recover. *PeerJ*, *6*, e4886. https://doi.org/10.7717/peerj.4886

Farnsworth, K. D., Albantakis, L., & Caruso, T. (2017). Unifying concepts of biological function from molecules to ecosystems. *Oikos*, *126*, 1367–1376. https://doi.org/10.1111/oik.04171

Ferry-Graham, L. A., Bolnick, D. L., & Wainwright, P. C. (2002). Using functional morphology to examine the ecology and evolution of specialization. *Integrative and Comparative Biology*, *42*, 265–277. https://doi.org/10.1093/icb/42.2.265

Fisher, R., Radford, B. T., Knowlton, N., Brainard, R. E., Michaelis, F. B., & Caley, M. J. (2011). Global mismatch between research effort and conservation needs of tropical coral reefs. *Conservation Letters*, *4*, 64–72. https://doi.org/10.1111/j.1755-263X.2010.00146.x

Floeter, S. R., Bender, M. G., Siqueira, A. C., & Cowman, P. F. (2018). Phylogenetic perspectives on reef fish functional traits. *Biological Reviews*, *93*, 131–151. https://doi.org/10.1111/brv.12336

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., … Bommarco, R. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20142620. https://doi.org/10.1098/rspb.2014.2620

Gamfeldt, L., & Roger, F. (2017). Revisiting the biodiversity-ecosystem multifunctionality relationship. *Nature Ecology and Evolution*, *1*, 0168. https://doi.org/10.1038/s41559-017-0168

Goatley, C. H. R., Bonaldo, R. M., Fox, R. J., & Bellwood, D. R. (2016). Sediments and herbivory as sensitive indicators of coral reef degradation. *Ecology and Society*, *21*, 29. https://doi.org/10.5751/ES-08334-210129

Graham, N. A. J., Bellwood, D. R., Cinner, J. E., Hughes, T. P., Norstrom, A. V., & Nyström, M. (2013). Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment*, *11*, 541–548. https://doi.org/10.1890/120305

Graham, N. A. J., Cinner, J. E., Norström, A. V., & Nyström, M. (2014). Coral reefs as novel ecosystems: Embracing new futures. *Current Opinion in Environmental Sustainability*, *7*, 9–14. https://doi.org/10.1016/j.cosust.2013.11.023

Graham, N. A. J., Wilson, S. K., Carr, P., Hoey, A. S., Jennings, S., & MacNeil, M. A. (2018). Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature*, *559*, 250–253.

Harborne, A. R., Rogers, A., Bozec, Y.-M., & Mumby, P. J. (2017). Multiple stressors and the functioning of coral reefs. *Annual Review of Marine Science*, 9, 445–468. https://doi.org/10.1146/annurev-marine-010816-060551

Heenan, A., Hoey, A. S., Williams, G. J., & Williams, I. D. (2016). Natural bounds on herbivorous coral reef fishes. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20161716. https://doi.org/10.1098/rspb.2016.1716

Heenan, A., & Williams, I. D. (2013). Monitoring herbivorous fishes as indicators of coral reef resilience in American Samoa. *PLoS ONE*, 8, e79604. https://doi.org/10.1371/journal.pone.0079604

Hobson, E. S. (1991). Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In P. F. Sale (Ed.), *The ecology of fishes on coral reefs* (pp. 69–95). San Diego, CA: Academic Press.

Houk, P., Benavente, D., Iguel, J., Johnson, S., & Okano, R. (2014). Coral reef disturbance and recovery dynamics differ across gradients of localized stressors in the Mariana Islands. *PLoS ONE*, 9, e105731. https://doi.org/10.1371/journal.pone.0105731

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., ... Scheffer, M. (2017a). Coral reefs in the Anthropocene. *Nature*, 546, 82–90.

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., ... Wilson, S. K. (2017b). Global warming and recurrent mass bleaching of corals. *Nature*, 543, 373–377.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., ... Larigauderie, A. (2017). Linking the influence and dependence of people on biodiversity across scales. *Nature*, 546, 65–72. https://doi.org/10.1038/nature22899

Jax, K. (2005). Function and "functioning" in ecology: What does it mean? *Oikos*, 111, 641–648.

Jouffray, J.-B., Nyström, M., Norstrom, A. V., Williams, I. D., Wedding, L. M., Kittinger, J. N., & Williams, G. J. (2014). Identifying multiple coral reef regimes and their drivers across the Hawaiian archipelago. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, 20130268. https://doi.org/10.1098/rstb.2013.0268

Kelly, E. L. A., Eynaud, Y., Clements, S. M., Gleason, M., Sparks, R. T., Williams, I. D., & Smith, J. E. (2016). Investigating functional redundancy versus complementarity in Hawaiian herbivorous coral reef fishes. *Oecologia*, 182, 1151–1163. https://doi.org/10.1007/s00442-016-3724-0

Kennedy, E. V., Perry, C. T., Halloran, P. R., Iglesias-Prieto, R., Schönberg, C. H. L., Wisshak, M., ... Mumby, P. J. (2013). Avoiding coral reef functional collapse requires local and global action. *Current Biology*, 23, 912–918. https://doi.org/10.1016/j.cub.2013.04.020

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Levin, P. S., Fogarty, M. J., Murawski, S. A., & Fluharty, D. (2009). Integrated ecosystem assessments: Developing the scientific basis for ecosystem-based management of the ocean. *PLoS Biology*, 7, e1000014. https://doi.org/10.1371/journal.pbio.1000014

Madin, J. S., Hoogenboom, M. O., Connolly, S. R., Darling, E. S., Falster, D. S., Huang, D., ... Baird, A. H. (2016). A trait-based approach to advance coral reef science. *Trends in Ecology and Evolution*, 31, 419–428. https://doi.org/10.1016/j.tree.2016.02.012

Mcclanahan, T. R. (2000). Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biological Conservation*, 94, 191–198. https://doi.org/10.1016/S0006-3207(99)00176-7

McGill, B. J., Dornelas, M., Gotelli, N. J., & Magurran, A. E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Evolution*, 30, 104–113. https://doi.org/10.1016/j.tree.2014.11.006

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

McPherson, J. M., Yeager, L. A., & Baum, J. K. (2018). A simulation tool to scrutinise the behaviour of functional diversity metrics. *Methods in Ecology and Evolution*, 9, 200–206. https://doi.org/10.1111/2041-210X.12855

McWilliam, M., Hoogenboom, M. O., Baird, A. H., Kuo, C.-Y., Madin, J. S., & Hughes, T. P. (2018). Biogeographical disparity in the functional diversity and redundancy of corals. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 3084–3089. https://doi.org/10.1073/pnas.1716643115

Morais, R. A., & Bellwood, D. R. (2018). Global drivers of reef fish growth. *Fish and Fisheries*, 19(5), 874–889. https://doi.org/10.1111/faf.12297

Motta, P. J. (1988). Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): An ecomorphological approach. *Environmental Biology of Fishes*, 22, 39–67. https://doi.org/10.1007/BF00000543

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, 28, 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Mouillot, D., Villeger, S., Parravicini, V., Kulbicki, M., Arias-Gonzalez, J. E., Bender, M., ... Friedlander, A., Vigliola, L., Bellwood, D. R. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13757–13762. https://doi.org/10.1073/pnas.1317625111

Mumby, P. J., Harborne, A. R., Williams, J., Kappel, C. V., Brumbaugh, D. R., Micheli, F., ... Blackwell, P. G. (2007). Trophic cascade facilitates coral recruitment in a marine reserve. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 8362–8367. https://doi.org/10.1073/pnas.0702602104

Nicholls, B., & Racey, P. A. (2006). Habitat selection as a mechanism of resource partitioning in two cryptic bat species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. *Ecography*, 29, 697–708.

Olden, J. D., Hogan, Z. S., & Zanden, M. J. V. (2007). Small fish, big fish, red fish, blue fish: Size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography*, 16, 694–701. https://doi.org/10.1111/j.1466-8238.2007.00337.x

Paine, R. T. (1969). A note on trophic complexity and community stability. *The American Naturalist*, 103, 91–93. https://doi.org/10.1086/282586

Perry, C., & Alvarez-Filip, L. (2018). Changing geo-ecological functions of coral reefs in the Anthropocene. *Functional Ecology*, 33, 976–988. https://doi.org/10.1111/1365-2435.13247

Pratchett, M. S., Thompson, C. A., Hoey, A. S., Cowman, P. F., & Wilson, S. K. (2018). Effects of coral bleaching and coral loss on the structure and function of reef fish assemblages. In M. J. H. van Oppen, & J. Lough (Eds.), *Coral bleaching: Patterns, processes, causes and consequences* (pp. 265–293). Basel, Switzerland: Springer.

Richardson, L. E., Graham, N. A. J., Pratchett, M. S., Eurich, J. G., & Hoey, A. S. (2018). Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Global Change Biology*, 24, 3117–3129. https://doi.org/10.1111/gcb.14119

Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. *Oikos*, 98, 156–162. https://doi.org/10.1034/j.1600-0706.2002.980116.x

Schrödinger, E. (1935). Die gegenwärtige situation in der Quantenmechanik. *Naturwissenschaften*, 23, 823–828.

Shipley, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180, 923–931. https://doi.org/10.1007/s00442-016-3549-x

Steneck, R. S. (1983). Quantifying herbivory on coral reefs: Just scratching the surface and still biting off more than we can chew. In L. Reaka (Ed.), *The ecology of deep and shallow coral reefs*. Symposia series for undersea research (Vol. 1, pp. 103–111). Rockville, MD: National Oceanic and Atmospheric Administration.

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., … Edgar, G. J. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, *501*, 539–542. https://doi.org/10.1038/nature12529

Taylor, B. M., Brandl, S. J., Kapur, M., Robbins, W. D., Johnson, G., Huveneers, C., … Choat, J. H. (2018). Bottom-up processes mediated by social systems drive demographic traits of coral-reef fishes. *Ecology*, *99*, 642–651. https://doi.org/10.1002/ecy.2127

Tebbett, S. B., Bellwood, D. R., & Purcell, S. W. (2018). Sediment addition drives declines in algal turf yield to herbivorous coral reef fishes: Implications for reefs and reef fisheries. *Coral Reefs*, *37*, 929–937. https://doi.org/10.1007/s00338-018-1718-6

Tebbett, S. B., Goatley, C. H. R., & Bellwood, D. R. (2017). Clarifying functional roles: Algal removal by the surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus* on coral reefs. *Coral Reefs*, *36*, 803–813. https://doi.org/10.1007/s00338-017-1571-z

Tinoco, B. A., Graham, C. H., Aguilar, J. M., & Schleuning, M. (2017). Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. *Oikos*, *126*, 52–60. https://doi.org/10.1111/oik.02998

Vergés, A., Bennett, S., & Bellwood, D. R. (2012). Diversity among macroalgae-consuming fishes on coral reefs: A transcontinental comparison. *PLoS ONE*, *7*, e45543. https://doi.org/10.1371/journal.pone.0045543

Villéger, S., Brosse, S., Mouchet, M., Mouillot, D., & Vanni, M. J. (2017). Functional ecology of fish: Current approaches and future challenges. *Aquatic Sciences*, *79*, 783–801. https://doi.org/10.1007/s00027-017-0546-z

Villéger, S., Novack-Gottshall, P. M., & Mouillot, D. (2011). The multi-dimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecology Letters*, *14*, 561–568. https://doi.org/10.1111/j.1461-0248.2011.01618.x

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892.

Wainwright, P. C. (1988). Morphology and ecology: Functional basis of feeding constraints in Caribbean labrid fishes. *Ecology*, *69*, 635–645. https://doi.org/10.2307/1941012

Wainwright, P. C., & Bellwood, D. R. (2002). Ecomorphology of feeding in coral reef fishes. In P. F. Sale (Ed.), *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (pp. 33–55). San Diego, CA: Academic Press.

Wainwright, P. C., Bellwood, D. R., & Westneat, M. W. (2002). Ecomorphology of locomotion in labrid fishes. *Environmental Biology of Fishes*, *65*, 47–62.

Wainwright, P. C., & Reilly, S. M. (1994). *Ecological morphology*. Chicago, IL: The University of Chicago Press.

Winemiller, K. O., Fitzgerald, D. B., Bower, L. M., & Pianka, E. R. (2015). Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters*, *18*, 737–751. https://doi.org/10.1111/ele.12462

Wismer, S., Tebbett, S. B., Streit, R. P., & Bellwood, D. R. (2019). Spatial mismatch in fish and coral loss following 2016 mass coral bleaching. *Science of the Total Environment*, *650*, 1487–1498. https://doi.org/10.1016/j.scitotenv.2018.09.114

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