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EDITORIAL

Re-thinking coral reef functional futures

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Summary

1. Tropical coral reefs currently face an unprecedented restructuring since their extant form and function emerged ~24 million years ago in the early Neogene. They have entered the Anthropocene – an epoch where humans have become the dominant force of planetary change. Human impacts on and interactions with coral reefs are escalating across multiple trophic levels and scales, but we have a rudimentary understanding of what this means for their functional ecology.

2. The overall goal of this special feature is to unpack what the Anthropocene means for the functional ecology of coral reefs, laying the foundations for new approaches and research directions in coral reef science. The collection describes the functional changes and novel dynamics that characterise Anthropocene reefs, from variations in their taxonomy and geology through to the resulting shifts in ecosystem services they provide to humanity.

3. Common changes to coral reefs are occurring that are challenging their historical functional role. These include reductions in benthic calcifiers and declining carbonate

production, and benthic assemblage shifts leading to a loss of structural complexity and flattening of reef seascapes. As reefs as we know them are lost from some locations, range extensions and the 'tropicalisation' of temperate locations present novel ecosystem configurations that are challenging ecological paradigms and our historical approach to ecosystem management.

4. Hindering our progress, however, is a "functionality crisis". Coral reef functional ecology to date has lacked a clear and universal definition of the term '*function*' and many assumed links between taxa and reef processes lack empirical evidence. Moving forward, we must establish causal links between functional traits, the species that possess them, and specific ecosystem processes if we are to successfully manage Anthropocene reefs. The functional space coral reefs occupy has arguably widened, presenting ethical challenges surrounding the increasingly interventionist management practices required to achieve particular functional endpoints.

5. For us to steer coral reefs towards a desirable functional future will require a more mechanistic understanding between ecosystem attributes and the provision of services, acknowledging that such services are co-produced by the ecosystem and society. Ultimately, this era in coral reef ecology requires a new approach to coral reef science, one that addresses the complex socio-ecological nature of coral reefs. These works outline a path ahead for defining and studying the functional ecology of coral reefs, drive debate as to what we want their functional future to look like, and call for ecosystem function to be at the heart of managing coral reef futures during this period of rapid transition.

Introduction

Early coral reefs lived among dinosaurs. These ancestral coral forms led to the emergence of scleractinian coral reefs ~65 million years ago (Ma) in the early Paleogene, that by the early Neogene (~24 Ma) had developed in to the functionally extant coral reefs we know today (Bellwood 2003; Bellwood, Goatley & Bellwood 2017) (Fig. 1). Between then and now, arguably little changed to the functionality of coral reefs, despite increases in species diversification (Bellwood, Goatley & Bellwood 2017). Recently, however, the globalisation of the human species has propelled coral reefs into an era of unprecedented change and coral reefs in the Anthropocene face an uncertain functional future (Fig. 1).

Over the past few decades, and guided by classic ecological theory and practice, we have learned a great deal about the structuring forces of coral reef ecosystems. Early on in the evolution of coral reef science, research focused on the role played by gradients in natural biophysical forcings such as wave energy, temperature, light, and primary production (Odum & Odum 1955; Glynn 1976; Dollar 1982). As interactions between people and coral reefs increased, so too did the study of the resulting changes to reef configurations. We began to study the role played by fisheries exploitation (McClanahan & Muthiga 1988; Russ & Alcala 1989) and nutrient enrichment due to coastal development (Grigg 1995; Hunter & Evans 1995), and the study of key ecosystem functions, such as herbivory, reef growth, and predation became commonplace (Hubbard & Scaturo 1985; Lewis 1986; McClanahan & Shafir 1990). From the late 1980s onwards, the threats presented by climate change-induced coral bleaching (Harriott 1985; Hoegh-Guldberg 1999) and disease outbreaks (Aronson & Precht 2001) became increasingly apparent, with documented changes in reef reconfigurations away from their historical baselines (Hughes 1994) and the deleterious effects this was likely to present to humanity (Done 1999).

As our knowledge grew, so too did our realisation that coral reefs represent tightly coupled social-ecological systems (Kittinger *et al.* 2012), whose complex states and dynamics (Jouffray *et al.* 2015; Donovan *et al.* 2018) are governed by interacting cross-scale human socioeconomic, cultural (Cinner *et al.* 2016; Hicks *et al.* 2016a) and biophysical processes (Williams *et al.* 2015; Jouffray *et al.* 2019). Under such contexts, classic ecological theory and paradigms can break down (Williams *et al. this issue*). In recent years, it has become evident that climate change-induced ocean warming driven by rising CO_2 emissions is leading to an increase in the frequency of mass coral bleaching events across the planet (Hughes *et al.* 2018a). These events are often overwhelming local management and environmental variability to cause mass coral mortality at unprecedented scales (Hughes *et al.* 2017a) and reconfiguring entire reef assemblages (Hughes *et al.* 2018b; Stuart-Smith *et al.* 2018). Despite the potential for recovery between bleaching events (Sheppard, Harris & Sheppard 2008; Gilmour *et al.* 2013; Graham *et al.* 2015), global climate change model projections predict a continued diminishing return time of coral bleaching events in the coming decades (van Hooidonk *et al.* 2016) that will severely challenge the capacity for reef recovery (Osborne *et al.* 2017). It is unequivocal that coral reefs have entered the Anthropocene (Norström *et al.* 2016; Hughes *et al.* 2017b), an epoch where humans are the dominant force of planetary change. However, we have a rudimentary understanding of what this might entail for the functional ecology of coral reefs.

Unravelling the Anthropocene for coral reefs from a functional perspective

Functional ecology aims to understand how core ecosystem functions, such as carbonate accretion, herbivory, and nutrient cycling in the case of coral reefs (Brandl *et al.* In Press), govern ecosystem dynamics, how certain species shape the system, and how this understanding informs responses to disturbances (Bellwood *et al.* this issue). The field of functional ecology draws heavily on trait-based approaches. Traits of organisms (for example, elements of morphology or behaviour) attempt to capture their role in ecosystem function (McGill *et al.* 2006; Mouillot *et al.* 2013). The greater the evidence for a given trait or trait combination capturing an ecosystem function, the more likely a trait-based approach will yield insights into the behaviour of that ecosystem.

A functional approach offers the opportunity to study how coral reefs are responding to the complex network of socioeconomic, cultural and biophysical processes that now dictate their dynamics (Williams *et al. this issue*). This special feature unravels the Anthropocene for coral reefs from a functional perspective, outlining a path ahead by which we can steer them towards a desirable functional future, characterised by diverse calcifying coral reefs that continue to co-produce services for society. The collection describes the functional changes and novel dynamics that characterise coral reefs in the Anthropocene. The papers discuss the functional implications of assemblage shifts across trophic levels, changes to reef geological processes and seascapes, range extensions of tropical species, and the knock-on effects these changes are having on the ecosystem services reefs provide. The collection also provides a definitional framework for the study of '*function*' and calls for a new approach to coral reef science in this era of rapid change.

The works highlight some common changes occurring to coral reefs in the Anthropocene that are challenging their historical functional role. Under intense bleaching-induced coral mortality, coral assemblages are becoming morphologically less diverse and dominated by taxa with a higher morphological '*compactness*' (Zwada *et al. this issue*). Concurrently, reductions in carbonate production and reef accretion are occurring that, in combination with bio-erosion, are resulting in net-erosional states and the flattening of reef seascapes (Perry & Alvarez-Filip *this issue*).

In some locations, coral reefs as we know them are transitioning to novel configurations with novel functions (Fulton *et al. this issue*) that provide us with new opportunities to derive benefits from ecosystem services (Woodhead *et al. this issue*) (Fig. 2). For example, fleshy macroalgae are classically viewed as the functional endpoint to the coral-algal regime shift that results from cumulative human stressors (Hughes 1994). However, "algae" are a diverse group and a natural part of many coral reef seascapes (Vroom *et al.* 2006). These complex macroalgal reef habitats contribute to coral reef ecosystem function, including providing nursery habitats for juvenile reef fish, and boosting secondary productivity as they detach, float and become a food source for browsing herbivorous fishes (Fulton *et al. this issue*). Some of these fishes, such as the rabbitfish *Siganus sutor*, are fast-growing and sustain fisheries production where tropical macroalgae have replaced reef-building corals as the dominant habitat-former (Robinson *et al.* 2019). Such provision of ecosystem services through novel means (Woodhead *et al. this issue*) challenges some existing coral reef paradigms and requires we re-appraise how we might manage tropical macroalgal reefs (Fulton *et al. this issue*).

Novel ecosystem configurations are also challenging our 'traditional' approaches to reef conservation and management as a whole, particularly where they are forming at the expense of past native assemblages (Graham *et al.* 2014). '*Tropicalisation*' of temperate reefs is occurring as tropical species extend their ranges poleward, creating novel predator-prey dynamics and shifts in the dominant habitat-forming taxa (Vergés *et al. this issue*). These novel reef configurations and ecosystem service opportunities are driving debate as to how such situations should be managed from an ethical perspective, particularly as management strategies become increasingly interventionist (Vergés *et al. this issue*). This demands that we re-assess how we define coral reef ecosystem function, and what in fact makes for a *functioning* coral reef ecosystem in the Anthropocene.

Re-thinking coral reef functional futures: the path ahead

To steer coral reefs towards a desirable functional future, we must first acknowledge that ecosystem services are co-produced by the ecosystem and society (Woodhead *et al. this issue*). As coral reefs change, so too does our use of them. As society changes, technological innovations may create novel opportunities for ecosystem services to be drawn from coral reefs. These changes to the ecosystem and society will not benefit all user groups equally, and winners and losers will emerge (Vergés *et al. this issue;* Woodhead *et al. this issue*). Moving forwards, therefore, how we decide and manage for a particular functional outcome requires careful thought and a strong inclusion of social science in ecosystem management (Hicks *et al.* 2016b). This is true for both ensuring continued and equitable use of coral reefs, and to effectively develop and maintain conservation initiatives.

One aspect currently hindering our progress, is a "functionality crisis" (Bellwood *et al.* this issue). To date, we have lacked a clear and universal definition of the term '*function*' and many assumed links between function and coral reef processes lack empirical evidence. The works contained within this special feature call for a universal definition and propose that 'function' be defined as "*the movement or storage of energy or material*", such that all functions are part of a continuum (Bellwood *et al.* this issue). An 'ecosystem function' therefore, refers to the movement or storage of energy or material within an ecosystem. By using this definitional framework, we should be able to increase research comparability and guide more effective management towards particular functional outcomes. To be successful, we must establish causal links between functional traits, the species that possess them and specific ecosystem processes. The focus should move towards quantifying *ecosystem function* rather than the providers of those functions (Bellwood *et al.* this issue).

The range of coral reef conditions and geographic locations in the Anthropocene has widened, moving us in to a new realm of uncharted functional space (Fig. 1). Novel functions have and may continue to arise, or currently unrecognised ‘sleeping’ functions may become key functions in the future. This era in coral reef ecology requires a new approach to coral reef science, one that acknowledges the complex socio-ecological nature of coral reefs. The works call for us to question historical coral reef paradigms and test their capacity to capture the dynamics of Anthropocene reefs across scales (Fulton *et al. this issue;* Williams *et al. this issue*). If these paradigms fail, we must revise them or develop new ecological theory that embeds human socioeconomic and cultural processes at their heart. This will require us to bridge scientific disciplines, such as social-ecological systems research and macroecology, to develop and utilise innovative approaches to how we study, describe and manage Anthropocene reefs (Williams *et al. this issue*).

Conclusions

Interactions between human society and coral reefs are changing in unprecedented ways and rates. The dynamics of Anthropocene reefs are increasingly governed by a network of cross-scale human socioeconomic and cultural processes set upon the backdrop of a reef’s natural biophysical setting. Human-induced global climate change has emerged as the dominant structuring force of coral reefs, overwhelming their local contexts and causing them in many cases to adopt novel configurations. These shifts mean that in some locations past ecosystem functions are being lost, while in others novel ecosystem functions and services are emerging as human society adapts. Future reef configurations and the continued adaptation of society will likely result in functions not yet seen or recognised as important. These changes require we re-think what we mean by a *functional future* for coral reefs, what is *functionally desirable* in the Anthropocene, and how we manage these complex socio-ecological systems to ensure particular functional endpoints.

Authors' contributions

Both authors laid down the foundations for this special feature and coordinated its development and integration. GJW wrote the first version of the editorial with input from NAJG. We thank James Bell for initiating the special feature invite, and Charles Fox for his editorial oversight, including on this piece. We also thank Jennifer Meyer for her editorial guidance and Amanda Dillon and David Bellwood for their creative input and critique of Figure 1, respectively.

Conflict of interest

The authors were guest editors of this special feature.

Data Accessibility

No data were used in this editorial.

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Figure legends

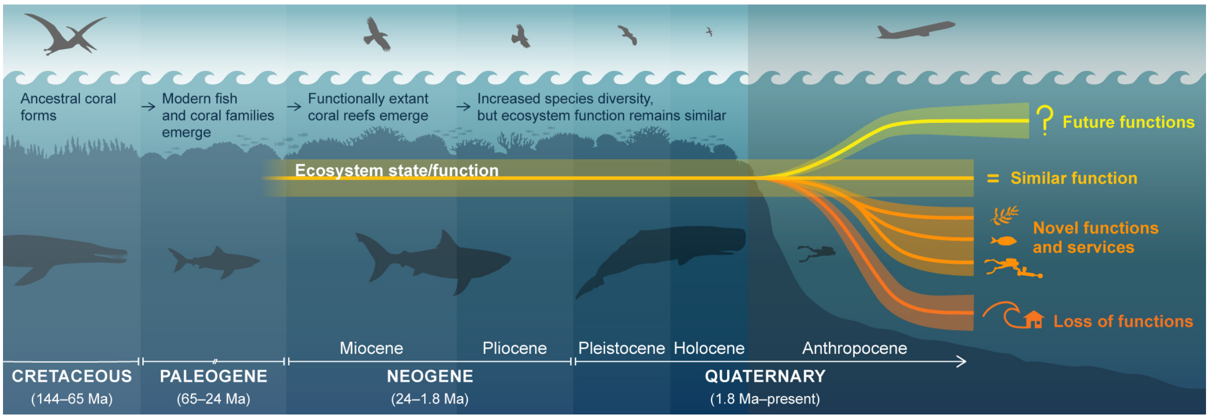

FIGURE 1 The changing scope of coral reef functional space into the Anthropocene. Functionally extant coral reefs emerged ~24 million years ago (Ma) in the early Neogene and existed in a relatively stable form prior to entering the Anthropocene. In recent decades, the scope and bounds of coral reef ecosystems has expanded and their functional future is now much more uncertain than in the geological past. For some reefs past functions remain, for others key functions are being lost. As novel reef configurations form and society responds, novel functions and ecosystem services are emerging. Future reef configurations and the continued adaptation of society will likely result in functions we have not yet seen or recognised as important.

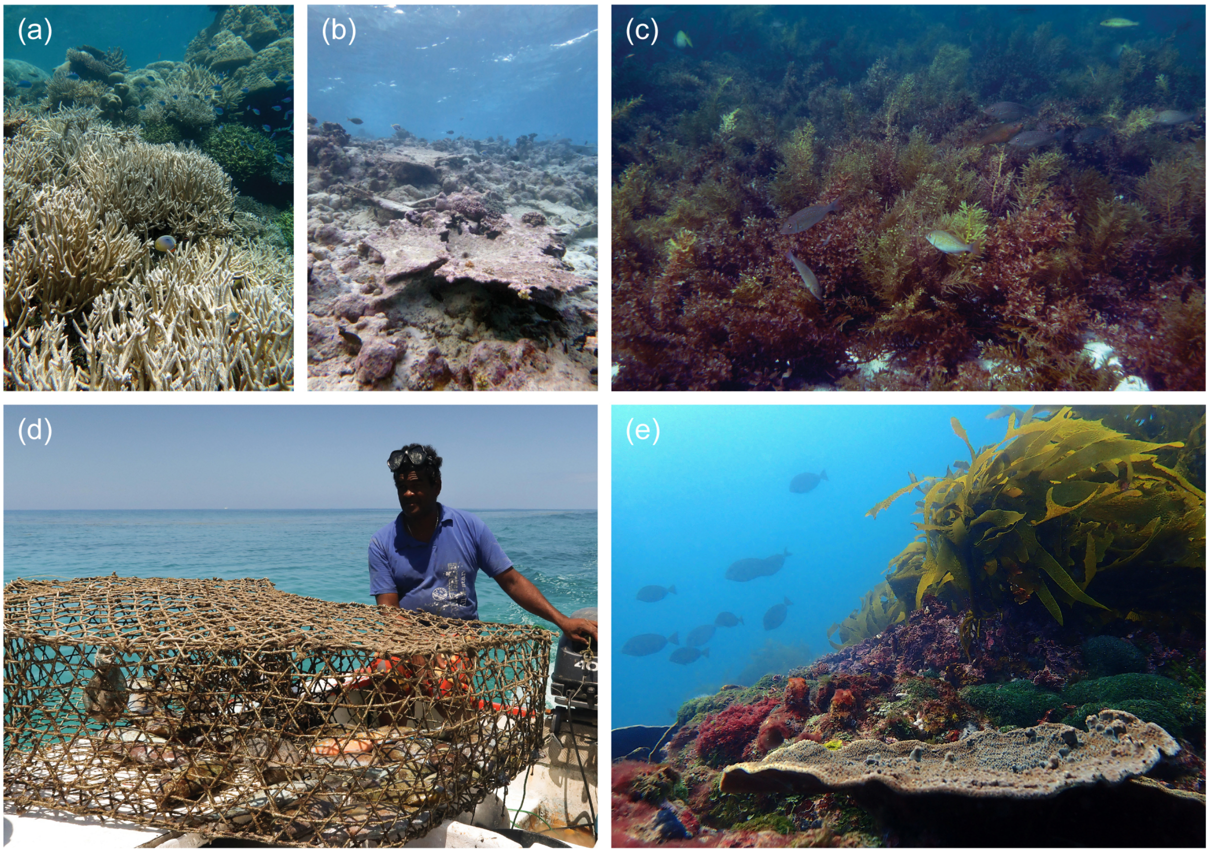

FIGURE 2 Functional shifts and novel dynamics that characterise coral reefs in the Anthropocene. Structurally-complex reefs with high accretion rates and carbonate production (a) are transitioning to net-erosional states following mass coral mortality, causing a flattening of reef seascapes (b). Tropical macroalgal beds are often viewed as the negative endpoint to a coral-algal regime shift, but some species occur naturally in high abundance close to coral reefs and contribute to overall reef function. For example, tropical *Sargassum* beds act as important nursery habitats for juvenile reef fish (c) and can sustain productive adult fish populations and fisheries where they have replaced corals as the dominant habitat-former (d). As coral reefs are being lost from some locations, in others novel reef configurations are emerging, in some cases via range extensions and the '*tropicalisation*' of temperate reefs that results in novel dynamics and new opportunities for human exploitation (e). Photo credits: Chris Perry (a-b) Christopher Fulton (c), James Robinson (d), and Adriana Vergés (e).