PERSPECTIVE

Coral reef ecology in the Anthropocene

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Summary

1. We are in the Anthropocene – an epoch where humans are the dominant force of planetary change. Ecosystems increasingly reflect rapid human-induced, socioeconomic and cultural selection rather than being a product of their surrounding natural biophysical setting. This poses the intriguing question: to what extent do existing ecological paradigms capture and explain the current ecological patterns and processes we observe?

2. We argue that, although biophysical drivers still influence ecosystem structure and function at particular scales, their ability to offer predictive capacity over coupled social-ecological systems is increasingly compromised as we move further into the Anthropocene.

3. Traditionally, the dynamics of coral reefs have been studied in response to their proximate drivers of change rather than their underlying socioeconomic and cultural drivers. We hypothesise this is limiting our ability to accurately predict spatial and temporal changes in coral reef ecosystem structure and function.

4. We propose '*social-ecological macroecology*' as a novel approach to a) identify the interactive effects of biophysical and socioeconomic and cultural drivers of coral reef ecosystems across spatial and temporal scales, b) test the robustness of existing coral reef paradigms, c) explore whether existing paradigms can be adapted to capture the dynamics of contemporary coral reefs, and d) if they cannot, develop novel coral reef social-ecological paradigms, where human dynamics are part of the paradigms rather than the drivers of them.

5. Human socioeconomic and cultural processes must become embedded in coral reef ecological theory and practice as much as biophysical processes are today if we are to predict and manage these systems successfully in this era of rapid change. This necessary shift in our approach to coral reef science will be challenging and will require truly interdisciplinary collaborations between the natural and social sciences.

Key-words: Anthropocene, coral reef, ecology, macroecology, prediction, scale, social-ecological macroecology, social-ecological systems

Introduction

Natural biophysical gradients such as wave energy, primary production, and seawater temperature drive coral reef ecosystem structure and function across multiple scales and trophic levels, from microbes (Kelly *et al.* 2014) and plankton (Gove *et al.* 2016), to corals (Gove *et al.* 2015) and fish assemblages (Heenan *et al.* 2016). However, human impacts such as fishing (Edwards *et al.* 2014), nearshore nutrient enrichment (D'Angelo & Wiedenmann 2014), sedimentation (Wolanski, Martinez & Richmond 2009), and the warming and acidifying of our oceans (Albright *et al.* 2016; Hughes *et al.* 2018a) are pushing the environmental boundary conditions defined by natural biophysical drivers on many coral reefs globally. Furthermore, the distal socioeconomic and cultural drivers underlying these proximate impacts, such as trade, consumer demands, human migration, and carbon dioxide emissions, are all predicted to increase (Norström *et al.* 2016; Hughes *et al.* 2017). This presents a new reality where the majority of coral reefs will increasingly reflect human-induced, socioeconomic and cultural drivers rather than being a product of their long-term natural biophysical setting. How we study and describe reef ecology must include this paradigm shift in thinking if we are to predict and manage their dynamics effectively.

We propose an approach that will identify how key biophysical, socioeconomic and cultural drivers of reefs interact across scales to drive coral reef ecosystem patterns and processes. In doing so, this approach will arm us with the predictive capacity required to manage coral reef dynamics in this era of rapid change. We start by reviewing how natural biophysical drivers influence reefs, from dictating the dominance, behaviour, and trophic ecology of individual reef organisms, through to governing the spatial ecology of reef communities across the seascape. We then highlight how human socioeconomic and cultural drivers have become an important structuring force of contemporary coral reefs at particular scales. In doing so, we underline our lack of understanding regarding the degree biophysical, or human socioeconomic and cultural drivers dominate depending on the scale of observation, suggesting macroecological approaches as a potential solution. Finally, we question whether traditional coral reef paradigms capture this new interwoven reality and stress the need for a '*socio-ecological macroecology*' approach to develop paradigms for coral reefs in the Anthropocene.

Biophysical drivers: setting natural bounds on coral reef ecosystems

By studying coral reefs in remote locations with limited direct human influence, we have learnt how coral reefs respond to, and are shaped by gradients in biophysical drivers such as wave energy, primary production, and seawater temperature (**Fig. 1**). High wave energy environments, for instance, can promote the dominance of low-lying benthic organisms such as turf algae, crustose coralline algae, and encrusting corals that are less vulnerable to physical dislodgement (Geister 1977; Gove *et al.* 2015). In contrast, lower wave energy environments tend to favour more structurally complex benthic communities, dominated by three-dimensional calcifying corals and upright macroalgae (Williams *et al.* 2013; Aston *et al.* 2018). Such increases in substrate complexity are often positively related to reef fish density and biomass (Graham & Nash 2012) due to increased refuge from predation (Rogers, Blanchard & Mumby 2014), and as such waves can indirectly mediate predator-prey dynamics on reefs. Across the Pacific Ocean, for example, the biomass of grazing herbivorous fishes peaks at islands with moderate wave exposure where the largest edible algal mass for these fishes tends to occur (Heenan *et al.* 2016). Wave energy can also influence reef fish community structure through interactions with fin morphology and swimming performance (Fulton, Bellwood & Wainwright 2005), with high wave energy environments capable of impacting the feeding success of some fishes and thus key ecosystem functions like herbivory (Bejarano *et al.* 2017).

Natural gradients in nutrient concentrations and primary production have predictable effects on coral reef ecosystems (Gove *et al.* 2016). For example, tropical islands located in more productive regions of the Pacific Ocean support a greater number of microbes with nutrient-related metabolisms (e.g., nitrate and nitrite ammonification) (Kelly *et al.* 2014), an increased cover of calcifying benthic organisms (Williams *et al.* 2015a), and a greater biomass of grazing herbivorous, planktivorous, and top-predatory fishes (Nadon *et al.* 2012; Williams *et al.* 2015b; Heenan *et al.* 2016). Gradients in nutrients and primary production also exist at smaller scales around individual islands. For example, when deep subsurface waves interact with bathymetry around islands they break and can pump water up through the thermocline. These so-called 'internal waves' can raise nutrient concentrations in the shallows (Leichter, Stewart & Miller 2003; Wang, Dai & Chen 2007; Aston *et al.* 2018), which in turn can promote heterotrophic feeding and growth rates in corals (Leichter & Salvatore 2006; Fox *et al.* 2018; Williams *et al.* 2018), and ultimately drive broad spatial transitions in benthic functional group dominance around islands (Aston *et al.* 2018). Coral reefs are also hydrodynamically connected by additional physical processes such as lagoonal outflow and surface downwelling that can move allochthonous nutrient sources between reef habitats (Williams *et al.* 2018) and, in the absence of confounding local human impacts, enhance reef productivity and function (Graham *et al.* 2018).

Seawater temperature is another key determinant of coral reef persistence and function. Most coral reef ecosystems occur in waters with a seasonal minimum sea-surface temperature of 18°C (Kleypas, McManus & Menez 1999). Marginal reef communities can form in waters below 22°C, and this can be explained by the interacting effect of temperature with light, nutrients, and aragonite saturation (Couce, Ridgwell & Hendy 2012). Bounded within these temperature limits, gradients in seawater temperature influence the dominance and life history of individual reef organisms. For example, hard coral cover decreases at lower temperatures, while macroalgae become more prevalent with latitudinal and cyclical seasonal drops in temperature (Glenn, Smith & Doty 1990; Fulton *et al.* 2014; Williams *et al.* 2015a). Browsing herbivorous fishes become more dominant in cooler waters, while warmer waters support an increased biomass of detritivorous fishes (Floeter *et al.* 2005; Hoey, Pratchett & Cvitanovic 2011; Heenan *et al.* 2016). Fish body size also varies predictably with temperature. Body size is inversely related to temperature due to the increased growth rate, earlier maturation, and shorter life span of individuals at higher temperatures (Atkinson 1994; Trip *et al.* 2008; Taylor, Trip & Choat 2018).

These natural constraints on a reef's biophysical and functional form do not act in isolation and appear predictable in the absence of confounding local human impacts (Williams *et al.* 2015a). However, anthropogenic activities have become a dominant driver of coral reef ecosystems across a broad range of socioeconomic and cultural contexts, increasing the complexity of drivers and their interactions that govern ecosystem state (**Fig. 2**).

Socioeconomic and cultural drivers: a new reality for coral reefs

The footprint of human activity is evident on coral reefs at all trophic levels. Fishing has dramatically reduced overall fish biomass on coral reefs (Williams *et al.* 2011; MacNeil *et al.* 2015; Graham *et al.* 2017), with an emphasised loss of herbivores (Edwards *et al.* 2014) and top predators (Sandin *et al.* 2008; Valdivia, Cox & Bruno 2017; Cinner *et al.* 2018) and thus the key ecosystem functions they perform. Fishing can also disrupt the basic physiology and behavior of target species, including the sex change dynamics (Taylor 2014) and flight responses of reef fishes (Januchowski-Hartley *et al.* 2012), both of which have the potential to affect overall reef ecosystem function (Madin *et al.* 2010).

Land-use change alters sedimentation regimes and nutrient input to reefs (Wolanski, Martinez & Richmond 2009). In conjunction with fishing (McClanahan *et al.* 2003), these effects can favour the competitive superiority of fleshy algae (Barott *et al.* 2012) to ultimately promote their overall dominance (Smith, Hunter & Smith 2010; Smith *et al.* 2016). Dredging and plastic pollution are increasing coral disease prevalence on reefs (Pollock *et al.* 2014; Lamb *et al.* 2018), which in turn contributes to a loss of live coral cover and reduced reef calcification rates. Humans are also re-structuring coral reef microbial communities (Kelly *et al.* 2014), and promoting the abundance of disease-causing bacteria and viruses (Dinsdale *et al.* 2008). Remarkably, human-introduced invasive rats can lower fish growth rates and levels of herbivory on reefs by predating on seabirds that would otherwise deliver offshore nutrient subsidies to shallow waters bordering the islands (Graham *et al.* 2018).

Globally, human-induced warming of the ocean is resulting in increasingly frequent mass coral bleaching events (Hughes *et al.* 2018a) that are transforming coral assemblages (Hughes *et al.* 2018b) and in some cases causing regime shifts to fleshy macroalgae (Graham *et al.* 2015). In combination with human-induced ocean acidification (Albright *et al.* 2016), these shifts in benthic composition have broader ecosystem effects, from compromising the growth of reef structures (Perry *et al.* 2013; Perry *et al.* 2018) to changing the diversity, abundance, and behaviour of other reef-associated organisms (Keith *et al.* 2018; Richardson *et al.* 2018; Stuart-Smith *et al.* 2018). Hence, myriad interconnected human drivers are rapidly changing the structure and function of reefs (Pendleton *et al.* 2016).

The proximate human impacts to reefs described above are, themselves, ultimately dictated by underlying distal socioeconomic and cultural drivers, such as global trade, markets and finance, as well as the movement and behavioral choices of people and their associated demands on coastal resources (Kittinger *et al.* 2012; Hicks *et al.* 2016a; Norström *et al.* 2016) (**Fig.2**). While the coral reef research community has made significant advances in measuring the response (decline) of coral reef ecosystems to these distal socioeconomic and cultural drivers, we have not done so intentionally in an *a priori* manner. Instead, we have indirectly measured their effect by studying their emergent proximate impacts, such as commercial and recreational fisheries (Fig. 2). We hypothesise this is limiting our ability to accurately predict spatiotemporal changes of contemporary reef ecosystems. We further suggest that these human socioeconomic and cultural drivers can combine to become such a dominating structuring force of reef ecosystem state that they overwhelm any influence of a reefs' surrounding natural biophysical setting. Williams et al. (2015a) tested this hypothesis by quantifying the relationship between coral reef benthic communities and gradients in biophysical drivers across Pacific islands that spanned a gradient of human density. At island-mean scales, they demonstrated that biophysical drivers were able to strongly predict coral reef ecosystem state when human density was low, but that these relationships were lost or fundamentally altered when human population density increased. We propose that this loss of predictive power over reef ecosystem state will be regained when human socioeconomic and cultural variables are instead fully integrated into analyses and used as predictors in the modeling framework. Further, we argue that implementing a multi-scaled macroecology approach will provide a more nuanced understanding of how biophysical, socioeconomic, and cultural drivers interact across spatial and temporal scales to influence coral reef patterns and processes.

Work has begun to address the crucial data and knowledge gaps linking the structure and function of natural ecosystems to the distal socioeconomic and cultural drivers that underpin their proximate drivers of change. Examples include the socioeconomic drivers of biodiversity loss and societal response capacities of hyperdiverse tropical ecosystems (Barlow *et al.* 2018), quantitative data on land grabbing and the international trade of coral reef resources (Norström *et al.* 2016), and the increasing amount of social science quantitative indicators people can use in social-ecological systems research and sustainability science (Hicks *et al.* 2016b). These types of data can improve our ability to predict the dynamics of natural ecosystems (Hicks *et al.* 2016a), including coral reefs. For example, distance to markets is a better predictor of the condition of reef fisheries than local human population densities in the vicinity of the reefs (Cinner *et al.* 2013). Further, combining travel times to reefs, as a measure of their accessibility (Maire *et al.* 2016), with human population sizes within a given distance, produces a metric known as 'gravity', which is a stronger predictor of fisheries exploitation on any given reef than human population density alone (Cinner *et al.* 2016; Cinner *et al.* 2018). When reef fisheries are quantified as either doing better (bright spots) or worse (dark spots) than expected given their natural biophysical bounds, it is human socioeconomic and cultural data such as customary taboos, marine tenure, and levels of local engagement in management, that are able to better predict the two outcomes (Cinner *et al.* 2016). We highly advocate these recent approaches and anticipate that unless we start to more routinely monitor, decipher, and account for socioecological links across scales we will become unable to predict spatiotemporal changes to coral reef ecosystem dynamics. We need to move to a point where we are integrating this thinking in to new ecological theories and paradigms that explicitly insert humans in to the equation across scales. As such, we require a new multi-scaled macroecological approach to coral reef ecology that is aligned with our current time, i.e., the Anthropocene.

Looking to the future: coral reef ecology in the Anthropocene

The past century has seen an evolution in ecological thinking, with theories and frameworks continuously updated and refined based on our ever-increasing understanding of natural systems. Coral reef science is no exception. Early theories and descriptions of the origins, structure, and distribution of coral reefs (Darwin 1842) were extended to encompass a more mechanistic, ecological, and process-based understanding of these diverse ecosystems (Odum & Odum 1955). Concurrently, the broad field of ecology was evolving across multiple terrestrial and aquatic systems. The longstanding Clementsian view of unidirectional ecological succession (Clements 1936) gave way to an appreciation of more complex interacting processes governing ecosystem dynamics and non-equilibrium theory (Odum 1969; Whittaker 1970). Concepts of ecological resilience then developed (Holling 1973) and were later directly applied to non-equilibrium systems like coral reefs (Connell 1978; Nyström, Folke & Moberg 2000). More recently, resilience theory has expanded to embrace a social-ecological systems framework that explicitly treats humans as internal rather than external to the system (Berkes & Folke 1998; Biggs *et al.* 2012). These works have given rise to a range of ecological paradigms that have formed our views on what defines coral reef ecosystems, what shapes them, and how they function.

What is now unequivocal is that human imprints can be observed at all biophysical scales, across all levels of biological organisation, and in the processes upon which ecological theories rest, such as species dispersal, colonisation, invasion, extinction, isolation, tolerance, and competition (Ellis 2015). Acknowledging that humans have emerged as a significant force in nature, "natural" biophysical processes that previously determined the assembly, dynamics, structure and functional ecology of ecological communities, may now be overwhelmed by anthropogenic activities (**Fig. 2**). This new situation poses an intriguing question: *to what extent do traditional ecological paradigms capture and explain the ecological patterns and processes we observe in the Anthropocene?*

The unprecedented breakdown of isolation by human migration and trade has caused dramatic changes to the dispersion and diversity of species globally (Meyerson & Mooney 2007; Westphal *et al.* 2008; Banks *et al.* 2014), with both positive and negative impacts to ecosystem services (Charles & Dukes 2007; Pejchar & Mooney 2009; Schlaepfer, Sax & Olden 2011). This loss of isolation is potentially compromising the explanatory and predictive power of traditional ecological models. For example, when Helmus *et al.* (2014)

investigated the species–isolation relationship for anole lizards among Caribbean islands they found that anole biogeography reflects anthropogenic processes, such as economic isolation of human populations, rather than geographic processes postulated in traditional island biogeography theory. Similar perturbations to the effectiveness and relevance of traditional ecological models and paradigms are likely occurring in the ocean.

In the marine environment, humans have influenced species biogeography by the unintentional and intentional introduction of species through transport and trade. Examples include ballast water release from cargo ships, aquaculture, and the aquarium industry (Padilla & Williams 2004). Moreover, we have created artificial 'islands' that are no longer static stepping-stones, but instead, float and move. Human-derived flotsam is providing a dispersal mechanism for tropical Atlantic fishes to cross the deep-water Mid-Atlantic Barrier (Luiz *et al.* 2012) and is facilitating alien species invasions (Gregory 2009). Floating plastic waste harbours distinct microbial assemblages, the so-called 'Plastisphere' (Zettler, Mincer & Amaral-Zettler 2013), with this unique biotope providing a mechanism by which disease-causing pathogens of reef corals spread in the Anthropocene (Lamb *et al.* 2018). Recent biophysical dispersal models have even offered the provocative suggestion that human infrastructure, such as oil and gas installations across the North Sea, can form a highly inter-connected regional network of coral ecosystems capable of supplying larvae to natural populations downstream (Henry *et al.* 2018). In these instances, to fully understand and be able to predict the observed ecological dynamics at play requires a new strategy. The human socioeconomic and cultural processes governing such modifications to species dispersal and diversity must become an integral part of ecological theory and practice as much as biological and geophysical processes are today (Ellis 2015; Österblom *et al.* 2017).

The pervasive global influence of humans in governing the spatial dynamics of ecological systems requires new theoretical advances to study, define, and sustainably manage them (Herrick & Sarukhán 2007; Hulme-Beaman *et al.* 2016; Rose *et al.* 2016; Cadotte *et al.* 2017). Coral reefs are no exception; they face a new reality with their dynamics governed by cross-scale interacting biophysical and human socioeconomic and cultural drivers (Norström *et al.* 2016; Hughes *et al.* 2017) (**Fig. 2**) and we question whether traditional coral reef paradigms accurately capture this complexity.

Moving forward, humans (and their activities) must become an integral part of coral reefs and their dynamics. For this purpose, we propose '*social-ecological macroecology*' as a novel concept for studying coral reefs in the 21st century. This approach embeds macroecology – the study of organism-environment relationships at large spatial and temporal scales (Brown & Maurer 1989; Keith *et al.* 2012; Heffernan *et al.* 2014), within a social-ecological systems framework. In doing so, social-ecological macroecology explicitly inserts the presence, behaviour, dynamics, and ecology of the human species into the equation, and does so across spatial and temporal scales. We stress the critical role of a macroecology approach – the scale of observation directly influences the ecological finding(s), their interpretation, and their subsequent use in guiding coral reef management.

Taking a social-ecological macroecology approach to studying coral reefs will require some innovative thinking and we suggest four core pathways to this approach:

1. **Identify the interactive effects of biophysical and human socioeconomic and cultural drivers of coral reef ecosystems across spatial and temporal scales**. This will improve our predictive capacity, such that we understand how changing one parameter, either biophysical, socioeconomic or cultural, at any specific scale interacts with other drivers at other scales to alter coral reef ecosystem structure and function.

2. **Test the robustness of classic coral reef paradigms.** We need to revisit and test whether classic ecological paradigms developed, in many instances, outside of the social-ecological systems framework, are still able to capture the dynamics of Anthropocene reefs accurately.

3. **Adapt current coral reef paradigms.** If classic paradigms fail to capture the spatiotemporal dynamics of reefs today accurately, we should explore whether adapting these paradigms, by including human dynamics as drivers, substantially improve their predictive capacity.

4. **Develop novel coral reef social-ecological paradigms**. In some cases, adapting existing coral reef paradigms may not be enough; we will need to develop novel rules and theories to create '*social-ecological paradigms*,' where human dynamics are part of the paradigms rather than the external drivers of them.

We will need to continually re-visit and test the performance of any of the adapted or novel paradigms developed under this approach due to the unprecedented rate of social and ecological change in the Anthropocene. In following these guidelines, coral reef ecologists should be able to identify, at any given spatial or temporal scale of observation, which interacting predictors (biophysical, socioeconomic or cultural) offer the best predictive capacity over coral reef ecosystem structure and function.

Conclusions

We remain convinced that human social, cultural and economic processes must become an integral part of ecological theory and practice as much as biological, geological and physical processes are today. This warrants a revisiting of traditional coral reef ecological paradigms and theories and either adapting them so that they capture contemporary dynamics of intertwined social-ecological systems, or developing novel social-ecological theories. This will be challenging and will require truly interdisciplinary collaborations between researchers in the natural and social sciences.

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Author contributions

G.J.W, N.A.J.G, J-B.J, A.V.N, and M.N conceived the research idea and led its development with all the other authors providing input. G.J.W led the writing with all authors contributing to the discussion and editing of the paper.

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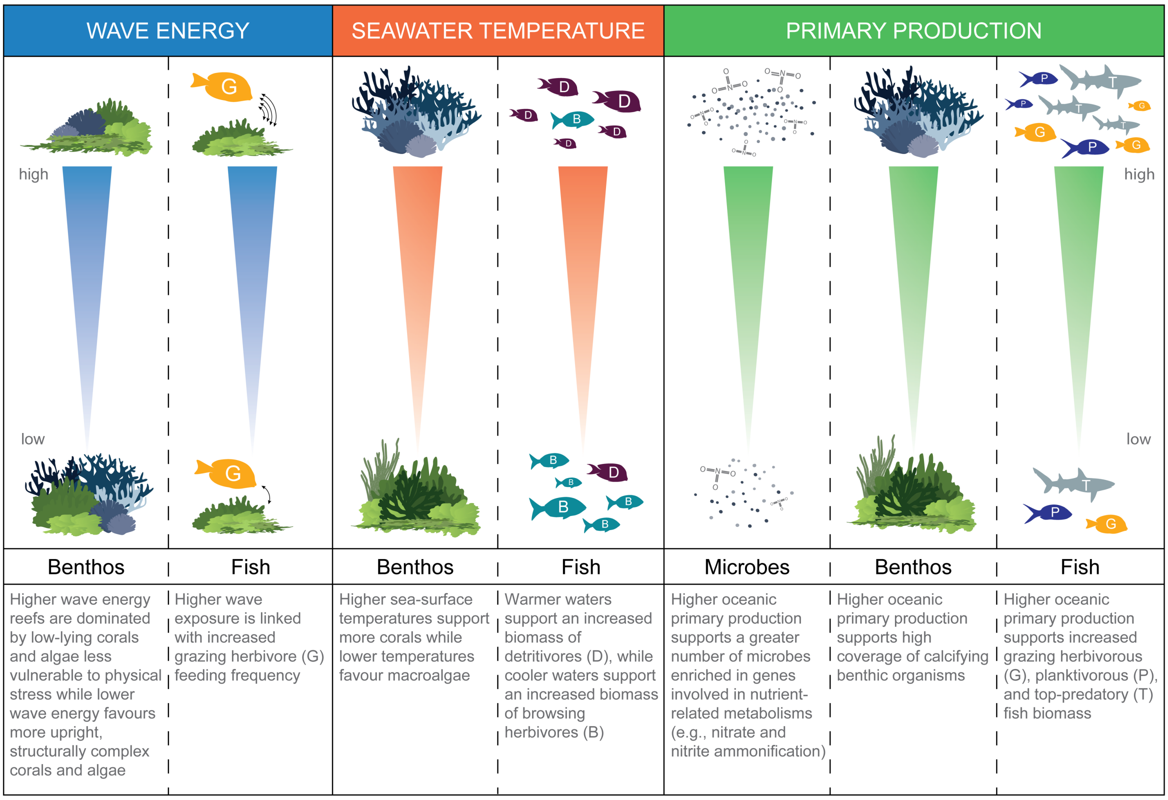
Figures and figure legends



WAVE ENERGY		SEAWATER TEMPERATURE		PRIMARY PRODUCTION		
Benthos	Fish	Benthos	Fish	Microbes	Benthos	Fish
Higher wave energy reefs are dominated by low-lying corals and algae less vulnerable to physical stress while lower wave energy favours more upright, structurally complex corals and algae	Higher wave exposure is linked with increased grazing herbivore (G) feeding frequency	Higher sea-surface temperatures support more corals while lower temperatures favour macroalgae	Warmer waters support an increased biomass of detritivores (D), while cooler waters support an increased biomass of browsing herbivores (B)	Higher oceanic primary production supports a greater number of microbes enriched in genes involved in nutrient-related metabolisms (e.g., nitrate and nitrite ammonification)	Higher oceanic primary production supports high coverage of calcifying benthic organisms	Higher oceanic primary production supports increased grazing herbivorous (G), planktivorous (P), and top-predatory (T) fish biomass

Figure 1. Examples of the natural bounds set by gradients in biophysical drivers on coral reef ecosystem structure and function across trophic levels, from microbes to sharks.

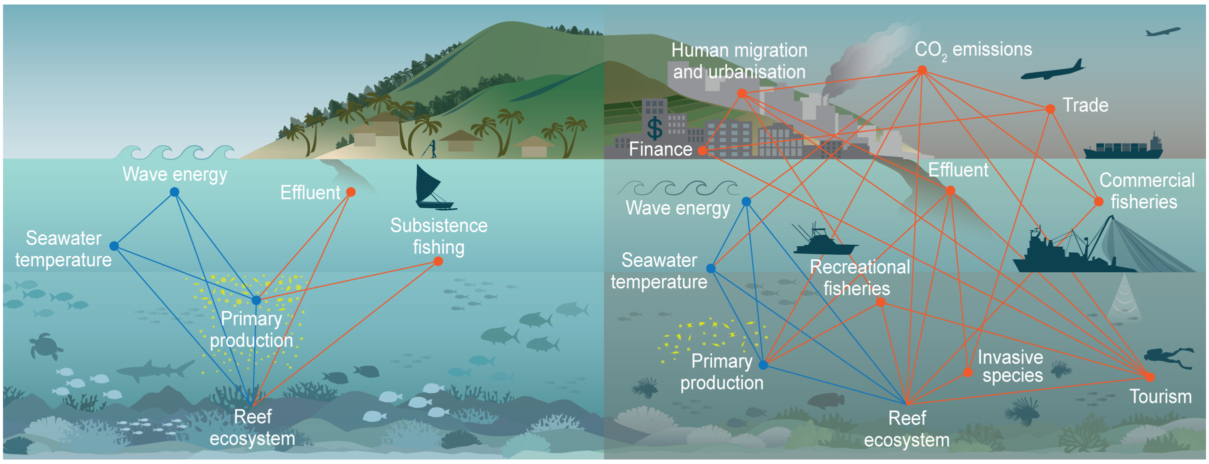


Figure 2. Drivers of coral reef ecosystems pre- and post- Anthropocene. Before coral reefs entered the Anthropocene, their ecosystem state was heavily governed by natural biophysical drivers, even in the presence of small subsistence-based human populations (left). This is still the case for some remote, uninhabited coral reef islands and atolls that are far removed from direct human impacts. However, many coral reefs today are impacted by local human drivers, such as commercial and recreational fishing and effluent discharge from land (right). Importantly, these proximate drivers of reef ecosystem state are themselves ultimately dictated by a complex network of underlying socioeconomic and cultural drivers (right). The biophysical drivers are still present on Anthropocene reefs, but their relative influence in governing reef ecosystem state is likely greatly reduced. Because of this, we propose the need for '*social-ecological macroecology*' which embeds macroecology – the study of organism-environment relationships at large spatial and temporal scales, within a social-ecological systems framework.