Changing geo-ecological functions of coral reefs in the Anthropocene

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Abstract

1. The ecology of many coral reefs has changed markedly over recent decades in response to various combinations of local and global stressors. These ecological changes have important implications for the abundance of taxa that regulate the production and erosion of skeletal carbonates, and thus for many of the geo-ecological functions that coral reefs provide, including reef framework production and sediment generation, the maintenance of reef habitat complexity and reef growth potential. These functional attributes underpin many of the ecosystem goods and services that reefs provide to society.

2. Rapidly changing conditions of reefs in the Anthropocene are likely to significantly impact the capacity of reefs to sustain these geo-ecological functions. Although the Anthropocene footprint of disturbance will be expressed differently across eco-regions and habitats, the end point for many reefs may be broadly similar: i) progressively shifting towards net neutral or negative carbonate budget states; ii) becoming structurally flatter; and iii) having lower vertical growth rates. It is also likely that a progressive depth-homogenisation will occur in terms of these processes.

3. The Anthropocene is likely to be defined by an increasing disconnect between the ecological processes that drive carbonate production on the reef surface, and the net geological outcome of that production i.e., the accumulation of the underlying reef structure. Reef structures are thus likely to

become increasingly relict or senescent features, which will reduce reef habitat complexity and sediment generation rates, and limit reef potential to accrete vertically at rates that can track rising sea levels.

4. In the absence of pervasive stressors, recovery of degraded coral communities has been observed, resulting in high net positive budgets being regained. However, the frequency and intensity of climate-driven bleaching events is predicted to increase over the next decades. This would increase the spatial footprint of disturbances and exacerbate the magnitude of the changes described here, limiting the capacity of many reefs to maintain their geo-ecological functional roles. The enforcement of effective marine protection, or the benefits of geographic isolation or of favourable environmental conditions ("refugia" sites) may offer the hope of more optimistic futures in some locations.

Keywords

Anthropocene, carbonate budgets, coral reefs, ecological change, reef growth, rugosity, sediment production

Introduction

The ecology and structure of many tropical coral reefs has altered markedly over the past few decades. Drivers of this degradation range from direct damage from destructive human practices to the loss of ecological resilience because of harmful algal blooms resulting from the loss of herbivory and coastal eutrophication (e.g., Jackson et al., 2014). Global scale climate stressors, and especially those associated with elevated sea-surface temperature anomalies, have also extended the footprint of disturbance to even the most remote (from direct human influence) regions (Bruno & Valdivia 2016; Hughes et al., 2017). Reef deterioration may thus occur as a response to an individual stressor such as mass bleaching, but it also occurs in response to combinations of different stressors acting simultaneously, and occasionally synergistically, to increase coral mortality or reduce coral growth and reproduction (Darling et al., 2010).

A major consequence of these climatic and pervasive local stressors has often been a rapid decrease in the abundance of habitat-building corals (Gardner TA *et al.* 2003, Alvarez-Filip et al., 2013; Bruno & Selig 2007, Hughes et al., 2018), which has consequently reduced reef structural complexity and coral carbonate production rates (Perry et al., 2014a). Equally, many reefs have been impacted by changes (both increases and decreases) in the abundance of bioeroding taxa such as parrotfish, urchins, sponges and microendolithic organisms (Glynn & Manzello 2015). The collective effect has been to alter the rates and relative balance of carbonate producing and eroding processes (Perry et al., 2014b). Such changes are of increasing interest because these processes directly regulate net rates of carbonate production and sediment generation, and collectively can impact upon multiple geo-ecological functions on reefs (Perry et al., 2008). These functions include reef-building and the capacity of reefs to accrete vertically in response to sea-level rise (Kuffner & Toth, 2016; Perry et al., 2018), and the supply of sands necessary to sustain beaches and reef islands (Fig. 1). Changes in the abundance of the taxa that control reef budgets can also drastically modify the structural functions that corals provide, and may be caused by shifts in coral morpho-taxa dominance e.g., from complex, branching forms to low relief morphological assemblages, or as a result of rapid physical disturbance. Change may also occur as a result of an increase, relative to carbonate production, in rates of bioerosion such that reef structures are denuded. Whilst the structural configurations that arise can differ, the net effect is that the contemporary structural diversity of reefs is altered, with consequences for multiple reef-associated species and processes.

Reef-building and vertical reef accretion, sand supply, and maintenance of structurally complex habitats are key geo-ecological functions that underpin many of the ecosystem goods and services reefs provide to society (Fig. 1). In the context of the rapidly changing condition of reefs in the Anthropocene this review considers three major consequences of on-going reef disturbance for the geo-ecological functionality of coral reefs: 1) impacts on contemporary carbonate production and bioerosion rates for reef budget states and detrital sediment generation; 2) impacts associated with eco-morphological taxa transitions, especially in terms of structural complexity and diversity; and 3) impacts on rates and patterns of reef accretion (Fig. 1). These issues have major socio-economic relevance because they are directly relevant to considerations of the physical resilience of reefs, and thus to understanding and projecting changes in reef functionality in relation to issues such as coastal protection, fisheries, and shoreline erosion.

1. Impacts on contemporary carbonate production and bioerosion rates (the declining carbonate budget problem)

The carbonate budget of a reef is a measure of the net rate of calcium carbonate production, and this has important implications as an influence on the potential for reef framework structural development i.e., for reef-building, and for the maintenance of a reef's physical framework structure. Carbonate budget processes reflect both local reef ecology and oceanographic setting (such as sea-surface temperature, storm and prevailing wave intensity, ocean chemistry, and nutrient regime; Kleypas et al., 1999), which in turn influence calcification rates and physical disturbance periodicity. The concept of quantifying reef carbonate budgets as an approach to assessing geo-ecological functions and processes on reefs stems from early studies that used either hydrochemical methodologies to define net community calcification (e.g., Smith & Kinsey, 1976), or census-based approaches to quantify taxa-level contributions to both carbonate production and bioerosion (e.g., Stearn et al., 1977, Scoffin et al., 1980, Hubbard et al., 1990). Both methodologies have been employed across a range of recent studies (e.g., Perry et al., 2012; Silbiger et al., 2014) and where used in tandem have shown good correlation (Courtney et al., 2016). Whilst the global coverage and the diversity of sites for which detailed data exists remains relatively small, these studies provide a basis for understanding the range of budget states that define contemporary reefs and, in a very few cases, for monitoring disturbance driven changes (Perry & Morgan, 2017; Manzello et al., 2018). Based on various field studies, shallow water (<~15 m) carbonate production rates under optimal conditions in the lower latitude reef-building regions are generally considered to average ~1-10 kg $CaCO_3$ m^{-2} yr^{-1} depending on reef zone, depth, and ecoregion (Kinsey & Hopley 1991; Vecsei, 2004).

Reef budget states are an expression of the strong linkage that exists between reef ecology and budget processes, and thus significant inter- and intra-reef variability in budget states should intuitively be expected. At the individual reef scale this will be expressed most clearly on an across-reef basis, with the taxa driving production and bioerosion naturally varying between habitats and depth zones (Perry & Hepburn, 2008; Fig. 2). Shallow (<~15 m) fore-reef sites have historically tended to be dominated by high rates of coral and coralline algal carbonate production and bioerosion (especially associated with parrotfish and urchin grazing), but with the production side of the budget generally dominant. The net effect has been that budget states in shallow fore-reef habitats tend to be strongly net positive (Fig. 2A), thus sustaining *in-situ* reef framework accumulation. At the same time these high rates of carbonate production represent a source, under physical disturbance conditions, for rubble export that can contribute to reef crest and reef flat formation (Scoffin, 1993; Blanchon et al. 2017), as well as undergoing (along with sediment) off-reef export into deeper waters to form expansive talus slopes (Hubbard et al. 1990).

The budget processes and states that define deeper water reef zones (below about 20 m) remain poorly documented, largely because they are below the limits of prolonged SCUBA diving. However, as depth increases, light and wave turbulence reduce, driving transitions in the abundance of the taxa that control the balance between carbonate production and loss. Coral assemblage shifts and changes in the morphology of corals (increasing prevalence of plate-like growth forms) with depth are well documented, and it is also known that coral calcification rates decline with depth, albeit in a species specific and non-uniform way (Hubbard & Scaturo, 1985; Weinstein et al., 2016). Furthermore, as depth increases the abundance of grazing parrotfish and urchins declines, and changes in the composition of endolithic bioeroding communities occur (Perry & Harborne, 2016). In the Caribbean at least, endolithic sponges become the dominant macroendolithic taxa and shifts from phototrophic to heterotrophic microendoliths occur (Perry & Hepburn, 2008). The net effect is that the *in-situ* carbonate budgets of deeper reef habitats (although poorly quantified) will progressively shift in favour of the erosional side of the equation (Fig. 2A) (Weinstein et al., 2016), but with the overall reef budget augmented at some sites by the import of rubble and sediment from shallower reef zones.

The processes that control reef budget states also naturally vary with environmental conditions over larger spatial scales, and most obviously, with latitude. Thus, and although again poorly quantified, there is a trend towards lower and then progressively neutral budget states towards the latitudinal limits of coral growth (Grigg 1982; Yamano et al., 2012), as the balance between the amount of carbonate produced and what is removed progressively shifts in favour of the latter. There has been some speculation that one consequence of ocean warming may be to drive northerly or southerly expansions in coral species ranges (and thus reef-building), and there is some evidence of this occurring in the past (Greenstein & Pandolfi, 2008). If so, one might hypothesise that subtle shifts will occur towards slightly more positive budgets in areas where reef building may not presently occur (Precht & Aronson, 2004). However, in reality little net change in overall budget states may actually arise. Firstly, because light constraints with increasing latitude may reduce coral growth (Kleypas et al. 1999; Muir et al., 2015). Secondly, because ocean acidification may stimulate enhanced destructive processes, for instance favouring the proliferation of bioeroding endolithic organisms (Enochs et al., 2016), while negatively affecting coral calcification and reef-building (Manzello et al., 2008). Thus the interaction of these factors may limit any possible warming benefits in higher latitude areas.

The strong links that exist between marine environmental conditions, reef ecology and carbonate budget states thus raise the question of how budget states may respond or transition following prolonged or high frequency ecological or environmental perturbations. Indeed, one of the defining questions in terms of the physical functionality of reefs in the Anthropocene is whether detrimental budget regimes are becoming more persistent or widespread as the footprint of multiple environmental disturbances increases. In this context changes in coral assemblages, resulting either from short-term climate driven (e.g., coral bleaching) or more prolonged anthropogenically-driven community transitions, are likely to result in marked transitions in rates of reef carbonate production. At the same time reef ecological changes may drive major shifts in the abundance of reef bioeroding taxa. These changes may reflect either: i) the loss of coral communities and associated habitat structural complexity that support specific bioeroding species (Perry & Harborne, 2016); or ii) more direct impacts such as those associated with the selective targeting of large parrotfish by fishers (Bellwood et al., 2011) or disease (Lessios et al., 1984). Collectively, these impacts may directly modify either the carbonate production side of the budget equation or rates of bioerosion, or both.

The potential for temporal budget transitions was conceptually explored in relation to different budget state scenarios by Perry et al. (2008). In some cases, change, driven by a suite of interacting ecological disturbances, is hypothesised to occur gradually or in a stepped fashion over a number of decades. In other cases, change may occur rapidly, such as that associated with major bleaching events. However, whilst the end point in both cases is broadly the same i.e., a diminished carbonate budget state, the pathways to this point can differ markedly. On many shallow water Caribbean reefs, for example, carbonate production rates have progressively declined over at least the last 30-40 years, as the abundance of formerly dominant high rate carbonate producing branching coral taxa (specifically the *Acropora* spp.) has declined (Perry et al., 2014a). At the same time chronic overfishing and the widespread die-off of *Diadema antillarum* considerably reduced the abundance of many bioeroding species (Carpenter, 1990). The net effect has been that many shallow water reefs have probably shifted to states close to budgetary stasis and in some cases net erosion (Fig. 2B). These states can lead to progressive breakdown and loss of surficial reef structural complexity (see Section 2 below) and in some cases to loss of the wider reef structure itself (Lewis, 2002).

In contrast, where previously “healthy” shallow water reefs are impacted by short-lived but high magnitude stress events, such as those associated with sea-surface temperature anomaly events, carbonate production rates can collapse almost instantaneously. At the same time bioerosion rates often remain high, at least initially (Perry & Morgan, 2017), meaning that the budgets of reefs rapidly transition to strongly net negative states (Eakin, 2001) and surficial structural complexity declines through progressive reef framework collapse (Lasagna et al., 2010). The extent and magnitude of change in deeper fore-reef habitats is poorly quantified but can be reasonably assumed to be less marked, because these deeper sites are more buffered from the extreme effects of direct and indirect human disturbance (Muir et al., 2017), and are less impacted by bleaching (Baird et al., 2018). However, given that coral calcification rates are lower at depth, where such sites are impacted by disturbance, the magnitudes of budget decline would be predicted to be severe.

Whether and how rapidly reefs (and their budgets) can recover from major short-lived shock events is thus of growing interest. Data from sites impacted by the 1998 bleaching event in the Indian Ocean show that many reefs recovered to states of high coral cover and, where assessed, high net positive budget states (Perry et al., 2015a). However, many Indian Ocean reefs were severely impacted again by bleaching in 2016, resetting their ecology and budgets to net negative states (Perry & Morgan, 2017). The frequency of future severe bleaching events in such regions will thus strongly influence whether the budgets of reefs again recover, and there are two key points that can be made here. The first is that recent models suggest that in the absence of rapid climate mitigation actions, the frequency of severe bleaching events will increase, and whilst predictions for the timing of annual severe bleaching vary geographically, many sites are predicted to experience strong warming each year by at least 2070 (van Hooidonk et al., 2016). The second point is that in some locations there is evidence that not all reefs recovered from the 1998 event. For example in the Seychelles some reefs recovered, but others “regime-shifted” to macroalgal-dominated states (Graham et al., 2015), the latter being defined by persistent low or net negative budgets (Januchowski-Hartley et al., 2017). The broader implications of this are that as regions are hit by future (more frequent) bleaching events so the ratio of reefs that can recover may fall relative to those that become “regime-shifted”, either due to increasing frequency of disturbance events or reduced ecological resilience.

The long-term outcome of further and sustained ecological disturbance in the Anthropocene era may therefore be a progressive transition on many shallow-water reefs away from historical (high) carbonate budget states to persistent low net positive or negative overall budget states, threatening the integrity of reef structures. Indeed, across many degraded reefs bioerosion may become a defining control on reef budgets (Kuffner & Toth, 2016), although it is presently unclear how the progressive loss of structural complexity may act as a feedback that limits bioerosion rates over time (Perry & Harborne, 2016). Exceptions to this may, however, occur either i) in areas where very effective marine protection or inherent geographic isolation limits the magnitude of human disturbance (Cinner *et al.* 2018; Guest *et al.* 2018), thus facilitating more rapid recovery from climate-driven disturbances; or ii) where marine environmental conditions e.g. elevated turbidity regimes (Cacciapaglia & van Woesik 2016), or depth (Baird et al. 2018) may limit the magnitude of climate-driven disturbance. Such locations offer the hope of more optimistic futures for some reefs and/or the potential to act as refugia sites and sources for species replenishment.

A further, though generally poorly documented aspect of carbonate budget change relates to the processes of reef sediment generation. Reef-derived sediment is a volumetrically important component of the structure of most reefs (Hubbard, Miller & Scaturo 1990; Hubbard, Burke & Gill 1998), and thus a key part of the reef-building process, as well as providing sedimentary material to sustain beaches and shorelines. Most sediment generated on reefs and within reef-related habitats (lagoons) derives either directly from organisms that secrete calcium carbonate skeletons (e.g., molluscs, foraminifera) and which contribute post-mortem to the sediment reservoir, or are produced indirectly from skeletal carbonate breakdown e.g., by specific species of fish and urchins (Scoffin, 1992). It follows therefore that as the abundance of these direct and indirect sediment producing species/processes change, driven by the same disturbance events discussed above, so the functional role of reefs as focal points of sediment generation will change (Perry et al., 2011). Such change may be expressed either in terms of the volumes or types of sediment produced, but the consequences of change are likely to be especially marked where disturbances impact upon a narrow range of disproportionality important sediment producing taxa (e.g., parrotfish – Perry et al., 2015b; benthic foraminifera – Collen & Garton, 2004). In such cases, loss of the relevant taxa may render sediment production rates insufficient to sustain local beaches or islands.

2. Impacts associated with eco-morphological taxa transitions (the changing reef complexity problem)

The structure and function of ecosystems are deeply linked to the identity of the species that create habitats, and in tropical reef ecosystems, scleractinian corals have a disproportionate influence on ecosystem structure, function and stability. This is because corals create, modify and maintain the complex three-dimensional framework structure. These complex structures have substantial ecological, economic and social relevance. For instance, reef complexity is strongly linked to fish and invertebrate diversity and the ecological interactions among them (Graham & Nash 2013; Morillo-Velarde *et al.*

2018), and strongly influences wave energy dissipation over reefs (see next section and Fig. 4). Because of the importance of hard coral cover in building and structuring reef frameworks (see Section 1 above), research on reef degradation has mostly focused on exploring the trends, drivers and consequences of declining live coral cover and reef complexity. However, functioning depends, to a large extent, on the life history strategies of corals, which are strongly linked to species morphological and physiological attributes (Darling et al., 2012; McWilliam et al., 2018). At the same time species growth rates, skeletal density, size and morphological complexity have been identified as primary traits defining processes of carbonate production and habitat provisioning on reefs (Darling et al., 2012; Alvarez-Filip et al., 2013; McWilliam et al., 2018). It is therefore unlikely that coral cover alone captures the variability in reef structure and community calcification mediated by different coral taxa (Alvarez-Filip *et al.* 2011a; Perry et al., 2015a). For instance reefs dominated by species with high structural complexity and high growth rates are likely to not only maintain more diverse communities but also to regulate the functional structure of reef communities (Alvarez-Filip et al., 2011b; Richardson et al., 2017a;).

In this context, the distribution of coral species and their functionality create habitat heterogeneity (or reef zones) within specific biogeographic regions. These are influenced by spatial variations in environmental forces such as temperature, light penetration and sediment inputs. However, the rapid environmental changes being caused by anthropogenic pressures are now non-randomly modifying the distribution of coral species and, in many cases, promoting a shift in dominance towards taxa better adapted to the new conditions. The net effect of this is to modify the functional performance of coral communities (Carturan et al., 2018), because disturbance typically favors fewer generalist species that are able to tolerate stress and therefore competitively dominate the landscape (Clavel et al., 2011; Alvarez-Filip et al., 2015a). A major functional transition associated with ecological change therefore relates to shifts in the abundance of corals with different morphological properties, or to different disturbance-driven pathways of framework breakdown. Most simply these transitions can occur where, for example, highly rugose branching coral taxa have been lost and replaced by low-relief coral forms, leading to marked changes in habitat (and micro-habitat) diversity and complexity (Fig. 3), and to changes in reef carbonate budgets (Figs. 3B, C).

In the Caribbean, for example, diseases, coral bleaching and local anthropogenic stressors have acted synergistically to transform coral communities over the past 40-50 years (e.g., Jackson et al., 2014). Throughout the region, the few species responsible for most of the structural complexity on reefs have been replaced by opportunistic species (Green et al., 2008). Although it has been proposed that species reconfiguration may prevent ecosystem collapse as populations of remaining coral species could maintain ecosystem integrity under future climate change (Hughes et al., 2012), a growing body of evidence shows that simplified reef communities alter ecosystem functioning and productivity, and jeopardize the persistence of ecosystem goods and services (Alvarez-Filip et al., 2015b; Hughes et al., 2018; Richardson et al., 2018). This is because shifted reefs are dominated by rapid colonizer species that whilst relatively tolerant to thermal and/or physical stressors, have different morpho-functional characteristics (Alvarez-Filip et al., 2011) and typically provide less structural habitat complexity (Green et al., 2008; Van Woesik et al., 2011; Darling et al., 2012). Thus as coral assemblages change from reefs dominated by large reef-building corals to smaller non-framework building species, declines in both coral-community calcification and reef rugosity can occur that are independent of changes in total coral abundance (Alvarez-Filip et al., 2013, Fig. 3C).

While reef community transitions in the Caribbean have thus commonly resulted from a gradual process of ecosystem degradation and loss of ecological resilience, there are many examples in the Indo-Pacific of reefs that have experienced different trajectories of change. In this eco-region, rapid declines in coral cover and shifts in coral abundance have commonly occurred in response to strong acute events such as ocean warming-induced mass bleaching (Hughes et al., 2017). Mass bleaching events and subsequent coral mortality result in a radical shift in the composition and functional traits of coral assemblages, drastically transforming reef landscapes across large spatial scales (Gilmour et al., 2013; Hughes et al., 2018). Tabular and branching corals, which are fast-growing, three-dimensional species that commonly dominate many Indo-Pacific reefs, tend to be disproportionally affected by post-bleaching mortality (Gilmour et al., 2013; Perry & Morgan, 2017; Hughes et al., 2018). Thus, in many cases, reefs shift away from the dominance of morphologically complex coral species, to assemblages dominated by taxa with simpler morphological characteristics and slower growth rates, resulting in rapid loss of coral community-scale complexity (e.g. Perry & Morgan, 2017; Hughes et al., 2018; Fig. 3B). Although recovery of degraded reefs is largely dependent on the growth of remnant corals (Halford et al., 2004; Gilmour et al., 2013), there is evidence showing that in the absence of further stressors reefs can recover both in terms of overall coral cover and habitat complexity (Gilmour et al., 2013; Graham et al., 2015). However, predicted increases in the frequency of bleaching-level thermal stress are likely to impede recovery potential on many reefs (van Hooidonk et al., 2016).

An emerging challenge in coral reef ecology is therefore to understand the functional consequences of shifts in coral abundance and composition. Ecological assemblage phase shifts have direct relevance to the issues of changing carbonate budgets discussed above because different morphological groups of corals are generally defined by different calcification and linear extension rates (González-Barrios & Álvarez-Filip, 2018). Coral reef habitats dominated by stress-tolerant taxa may thus become defined by persistent low (relative to regional optimal) budget states (Manzello et al., 2018). Abrupt, regional-scale shifts in coral assemblages may also radically reduce the abundance and diversity of species traits that facilitate key ecological functions (Hughes et al., 2018; McWilliam et al., 2018). Dominance patterns of coral assemblages therefore seem to be the most important driver of the functioning of coral reefs, and thus the future of these ecosystems might depend not only on general reductions of local and global stressors, but also on the maintenance of keystone coral species. As anthropogenic pressures continue, understanding how initial habitat configurations prior to disturbance will influence changes in coral communities, and reef-associated species such as fish (Alvarez-Filip et al., 2011b; Richardson et al., 2017b, 2018), will be critical for developing forewarnings of resilience loss and the threat of functional collapse, such that management efforts may be appropriately assigned.

3. Impacts on rates and patterns of reef growth (the reducing reef accretion problem)

A major functional consequence of the ecologically-driven transitions on reef carbonate budgets is the capacity to change reef accretion (vertical growth) potential. Reef growth is in part a function of the carbonate budget of a reef, but represents a measure of the net rate of vertical reef framework accumulation over time i.e., how much of the framework carbonate that is produced adds to the surface of the reef. The term potential is important because whilst a net positive budget state can be considered the minimum for reef accretion to occur, other factors such as rates of physical framework removal are also important. Indeed, previous authors have defined different conceptual budget states that reflect variations in the relative balance between framework "input" (carbonate production, external sediment and rubble inputs) and "export" (biological, physical and chemical erosion) processes (Kleypas et al., 2001). From a reef growth perspective these conceptual states provide a useful framework within which to envisage the interacting input and output factors that determine short term budget states. The relative balance between production and export processes then aggregate to influence long-term reef-building potential, essentially by dictating the net amount of carbonate being produced that accumulates in a given environment.

Under what might be considered optimal reef-building conditions, the "norm" is most commonly a situation where the production-dominated state persists more or less continuously to drive net in-situ reef framework accumulation and reef accretion (Kleypas et al., 2001). Indeed, the Holocene record of reef-building, as discerned from core records, provides numerous examples of semi-continuous vertical reef-building (Montaggioni, 2005; Gischler 2015), with vertical reef accretion persisting until otherwise sea-level constrained (Perry & Smithers, 2011), or where other external environmental factors (e.g., water quality, ocean temperatures) limit accretion (Toth et al, 2018). Conversely, there are examples of reefs that have developed under very different long-term environmental conditions, and which represent alternative examples of reef-building states. One well-documented example occurs in nearshore settings where persistent terrestrial sediment inputs influence the reef budget under "import-dominated" conditions (Browne et al., 2013). In such settings framework production (coral growth) clearly remains important, but core records show that a high proportion of the accumulating reef structure comprises fine-grained terrigenoclastic sediments that represent a long-term external input to the reef-building budget (Perry et al., 2012). In contrast, there are examples of persistent "export-dominated" reefs where all or most framework carbonate produced annually is removed by seasonal storms or cyclones (e.g., along the S. African coast; Riegl, 2001). The net effect is an absence of long-term framework accumulation and no net reef accretion.

The examples cited above clearly point to marked natural spatial heterogeneity in reef-building potential. However, a question that arises in the context of Anthropocene-era change is how rapidly and to what extent is the potential for reef accretion now being diminished? Declines in contemporary accretion rates may occur where within-site production rates are reduced relative to rates of biological, physical or chemical erosion, thus driving shifts from production to erosion dominated budgetary states. As outlined in previous sections, these transitions may arise either from progressive ecological deterioration (over decadal timescales), or acute and high magnitude disturbance events (e.g., severe bleaching). In the latter case, recent historical evidence suggests that, depending on species and recovery rates, periods of perhaps 10-15 years largely free from disturbance may be sufficient to enable reefs to regain their former states of high carbonate production and accretion potential (Perry et al., 2015a; Figure 3A). However, the potential for such “boom-bust-boom” cyclicity is increasing uncertain given projections of more frequent high magnitude bleaching events driven by warming events.

Where accretion rates do decline, and there is emerging evidence that this is an increasingly widespread Anthropocene scenario (Perry et al., 2018), there are a number of major implications in terms of reef geo-ecological functionality. One of the most significant is the question of whether reefs will retain capacity to keep up with rates of accelerating sea-level rise (SLR). Evidence from Holocene core records of reef growth, when ecological conditions and thus by inference carbonate budget states are considered to have been more optimal, suggest that many reefs exhibited an impressive capacity to either “keep-up” or to “catch-up” during periods of rapid SLR (Neumann & Macintyre, 1985). Indeed, measured vertical accretion rates from the early Holocene, when sea-levels were rising rapidly, may have been up to ~15 mm yr^{-1} in both the tropical western Atlantic and Indo-Pacific regions (Dullo, 2005). Longer-term average accretion rates in both regions were lower, in the tropical western Atlantic ~3-4 mm yr^{-1} (Hubbard, 2008) and a little below this in the Indo-Pacific region (Dullo, 2005). Whilst some high coral cover sites may sustain vertical accretion rates sufficient to match near-future sea-level rise (van Woesik & Cacciapaglia 2018), the critical point is that many contemporary coral reefs are now defined by vertical accretion rates that will be insufficient to keep pace with sea-level rise. Indeed, recent assessments of reef accretion potential at sites around the tropical western Atlantic and Indian Ocean regions suggest that accretion rates presently average only 1.8 mm yr^{-1} and 2.0 mm yr^{-1} respectively (Perry et al., 2018).

A major consequence of these changes in accretion rates is that many reefs may increasingly lose the ability to maintain their functional roles in terms of buffering coasts from wave energy exposure, and the ability to track rising sea levels. This will be an especially critical issue if projections of increasing

Tropical Cyclone intensity are realised (Bhatia *et al.* 2018). Several recent studies have modelled SLR impacts on wave energy regimes across reefs (e.g., Storlazzi et al., 2011; Beetham et al., 2017) and three key controls related to reef structure and accretion rates emerge: i) reef width and profile; ii) surface structural complexity; and iii) reef growth relative to the rate of water depth increase. The first of these, reef width and profile, are unlikely to change markedly over relevant future timescales since these parameters are a function of antecedent topography and long-term reef growth. More likely to change are parameters ii) and iii). Coral cover and assemblage composition strongly influence reef surface structural complexity, and this is important because complexity exerts a frictional effect on waves (Harris et al., 2018). Thus, reef surface complexity changes discussed above (section 2) have the potential to directly impact wave attenuation. Maintenance of reef surface elevation relative to sea level is also important because water depth modulates across-reef and nearshore wave energy regimes. Mean water depth increases will occur where vertical growth rates lag behind actual or relative increases in sea-level. Emerging evidence suggests that for many reefs the Anthropocene era is likely to be defined by declines in both accretion rates and surficial complexity (rugosity) (Fig. 4). Thus, whilst a few reefs may currently maintain capacity to track SLR and limit wave attenuation (Fig. 4 – Group A), a great many will not (Fig. 4 – Group C) and some have already lost this capacity (Fig. 4 – Group D). Indeed, recent assessments of reef growth – SLR interactions under different SLR scenarios through to 2100 suggest that tropical western Atlantic reefs will experience increases in water depths above reefs of ~40 cm by 2100 under the RCP 4.5 (Representative Concentration Pathway) scenario, and ~60 cm under RCP 8.5, whilst in the Indian Ocean region average water depth increases of ~47 cm and ~71 cm are predicted under these scenarios (Perry et al., 2018). Many reefs are therefore expected to offer less resistance to water flow, thus increasing the risks of coastal erosion and flooding of low-lying areas, with associated heightened economic and social costs for coastal communities.

A further implication of changing reef ecology and declining budget states that will exacerbate the impacts on reef-building may arise from changes to the supply-side of the reef-building process. The Holocene record of reef-building clearly shows that reef construction at a given site is typically dominated by a relatively restricted suite of coral taxa, and that this material is often converted to coral rubble during high energy physical disturbances (Hubbard et al., 1998). This coral rubble is often largely derived from fast-growing branched coral taxa, which subsequently: i) represents a volumetrically important component of accumulating reef frameworks, and ii) has historically sustained shallow fore-reef and reef crest building as a result of breakage and rubble transport (Blanchon et al., 2017). However, changes in coral species composition and in the abundance of relevant morpho-taxa (especially branched corals) means that the supply side of this reef growth dynamic is changing. For example, in the Caribbean previously dominant shallow water branched corals (*Acropora* spp.) have been largely replaced by low-relief taxa, such as *Agaricia* spp., *Porites* spp. and *Siderastraea* spp. (Green et al. 2008; Perry *et al.* 2014a), and these do not represent appropriate substitutes in terms of the supply side of the rubble-driven reef building process. Thus, changes in shallow water reef ecology can lead to marked reef-growth shifts that will impact both the impacted habitat, but also adjacent shallower and deeper reef zones which normally derive coral rubble from the impacted zone.

Collectively, these ideas point to an increasing disconnect between the underlying framework structure of contemporary reefs, which can represent the products of carbonate accumulation over several millennia, and reef carbonate budgets and thus accretion potential. In other words, in some regions, the underlying reef structure is essentially becoming a relict feature with little/no new carbonate being added. The idea of a progressive decoupling between contemporary reef ecology and the maintenance of the underlying reef structure is not necessarily a solely Anthropocene phenomenon (Kuffner & Toth, 2016; Toth et al. 2018). Indeed, it has previously been discussed as a response to changing environmental conditions around the latitudinal or environmental limits of reef-building (van Woesik &

Done, 1997). However, as live coral cover diminishes and net carbonate budgets decline, the number of reefs where the underlying reef structure essentially becomes a relict or senescent feature (i.e. where reef "turn-off" has occurred; Buddemeier & Hopley, 1988) will increase, with profound implications for the capacity of reefs to maintain their critical geo-ecological functional roles (Kuffner & Toth, 2016). Indeed, many of the geo-ecological ecosystem services that reefs provide may increasingly depend on the underlying relict or senescent structures of reefs as carbonate budgets, surficial structural complexity and reef accretion processes decline.

Concluding remarks

A major consequence of coral reef ecological transitions is that the Anthropocene is likely to be defined by an increased decoupling between current reef ecological states and the physical functions that reefs provide. This conclusion is based on the fact that on many reefs a progressive or rapid transition away from high historical carbonate budget states to states of low net positive or negative production is now occurring. This change threatens many of the key geo-ecological functions that reefs provide: their structural composition and microhabitat diversity, their capacity to generate sufficient sediments to sustain adjacent beaches and shorelines, their capacity to continue accreting vertically at rates that can match sea-level rise, and thus their functionality as wave attenuating structures. It is reasonable to hypothesise that these changes will be most marked in shallower water settings which are most exposed to warming events, often harbour the most susceptible coral taxa, and which are most "exposed" to direct human stressors. Although not entirely immune from ecological change, deeper reef habitats (below ~20 m) may be more protected. Thus, the Anthropocene footprint on reefs may be expressed rather differently across habitats and depth zones. It is also reasonable to hypothesise that budget states across individual reefs may become increasingly depth-homogenised, threatening the strong links that exist between structurally and ecologically complex shallow water reef habitats and the well-being of coastal human populations. These issues point to the need for further research to better understand: 1) how the processes of carbonate production and bioerosion interact as reef habitats change; 2) how these same processes vary with depth and latitude across reefs; 3) the extent to which remaining healthy reefs may be able to sustain the key geo-ecological functions outlined above; and 4) the extent to which ecological restoration efforts are feasible (at least over small spatial scales) to restore reef geo-ecological functionality. These functional attributes (reef-building and reef accretion, sand generation and assemblage-driven habitat complexity and diversity) underpin many of the ecosystem goods and services that reefs provide to society and thus strategies to protect or restore them represents a major Anthropocene challenge.

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Author contributions

CTP and L-A F co-conceived the idea and co-wrote the manuscript.

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Figure captions

Fig. 1 Schematic showing the main processes that control reef carbonate budgets and the key geo-ecological functions that reefs provide that relate to budget processes and states.

Fig 2. Schematic showing depth distribution of key processes influencing biological carbonate budgets on reefs and their relative importance (note no actual rates implied) in different depth zones under A) pre-Anthropocene historical conditions, and B) Anthropocene era conditions. Resultant net budget states in each depth zone are shown on the right (based on the ternary budget states plot of Perry et al. 2008).

Figure 3. The resilience of different scales of structural complexity to ecological change
(A) Hierarchical scales of reef structural complexity. Geomorphology-scale complexity results from long-term accretion (100-1000s years); community-scale complexity is provided by the skeleton of

mainly large massive and branching coral forms; cryptic-scale complexity is associated with rubble and holes and crevices created by and among coral structures. (B, C) Conceptual plots showing changes in the relative abundance of framework versus opportunistic coral taxa, in the three levels of reef structural complexity, and in net carbonate budget states over time in response to (B) acute stressors such as mass bleaching events after which community recovery occurs, and (C) the non-random decline of corals under a chronic stress(ors). In (B) community-scale complexity declines rapidly after the collapse of dead branching and tabular species, although this collapsed structure still provides some degree of cryptic complexity. In the absence of other sources of stress, coral communities recover gradually thus increasing the abundance of complex coral forms. Geomorphologic complexity remains essentially unaffected during these processes. The carbonate budget collapses immediately after the stress event but progressively recovers to former states as the reef community recovers. Although not depicted in the figure, recovery will be impeded if the frequency of acute stressors increases over time. In (C) geomorphologic-scale complexity is largely unaffected by ecological changes on coral communities but declines slightly as bioeroding forces start to affect the reef matrix. Community-scale complexity declines when the skeletons of the most structurally complex corals collapse, and then the trend of decline is observed although an increase in the abundance of small-opportunistic coral species. Cryptic-scale complexity is relatively unaffected by the immediate collapse of coral skeletons as coral rubble and boulders provide a variety of crevices and holes. However, with time this structure gradually erodes, infills with sediment and consolidates such that the structure is increasing homogenized. The carbonate budgets of these reefs progressively decline.

Figure 4. Potential impacts of changing vertical reef accretion and reduced structural complexity on the coastal protection functions that reefs provide. (A) Plot showing reef accretion rates relative to reef rugosity for sites across the tropical western Atlantic (TWA) and Indian Ocean (IO) regions (data from Perry et al. 2018) in the context of the Reef Health Index of Harris et al. (2018). (B) Schematics

showing the effects of different scenarios of reef keep-up potential (as a function of accretion rate) and substrate friction (as a function of rugosity) in terms of limiting coastal wave exposure risk – scenarios a-d relate to the different states identified in (A).

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