

1 Changing geo-ecological functions of coral reefs in the Anthropocene

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9

10 **Abstract**

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

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

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

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

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

36 **Keywords**

37 Anthropocene, carbonate budgets, coral reefs, ecological change, reef growth, rugosity, sediment
38 production
39

40

41 **Introduction**

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

52

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

72

73 Reef-building and vertical reef accretion, sand supply, and maintenance of structurally complex habitats
74 are key geo-ecological functions that underpin many of the ecosystem goods and services reefs
75 provide to society (Fig. 1). In the context of the rapidly changing condition of reefs in the Anthropocene
76 this review considers three major consequences of on-going reef disturbance for the geo-ecological

77 functionality of coral reefs: 1) impacts on contemporary carbonate production and bioerosion rates for
78 reef budget states and detrital sediment generation; 2) impacts associated with eco-morphological taxa
79 transitions, especially in terms of structural complexity and diversity; and 3) impacts on rates and
80 patterns of reef accretion (Fig. 1). These issues have major socio-economic relevance because they
81 are directly relevant to considerations of the physical resilience of reefs, and thus to understanding and
82 projecting changes in reef functionality in relation to issues such as coastal protection, fisheries, and
83 shoreline erosion.

84

85 **1. Impacts on contemporary carbonate production and bioerosion rates (the declining** 86 **carbonate budget problem)**

87 The carbonate budget of a reef is a measure of the net rate of calcium carbonate production, and this
88 has important implications as an influence on the potential for reef framework structural development
89 i.e., for reef-building, and for the maintenance of a reef's physical framework structure. Carbonate
90 budget processes reflect both local reef ecology and oceanographic setting (such as sea-surface
91 temperature, storm and prevailing wave intensity, ocean chemistry, and nutrient regime; Kleypas et al.,
92 1999), which in turn influence calcification rates and physical disturbance periodicity. The concept of
93 quantifying reef carbonate budgets as an approach to assessing geo-ecological functions and
94 processes on reefs stems from early studies that used either hydrochemical methodologies to define
95 net community calcification (e.g., Smith & Kinsey, 1976), or census-based approaches to quantify taxa-
96 level contributions to both carbonate production and bioerosion (e.g., Stearn et al., 1977, Scoffin et al.,
97 1980, Hubbard et al., 1990). Both methodologies have been employed across a range of recent studies
98 (e.g., Perry et al., 2012; Silbiger et al., 2014) and where used in tandem have shown good correlation
99 (Courtney et al., 2016). Whilst the global coverage and the diversity of sites for which detailed data
100 exists remains relatively small, these studies provide a basis for understanding the range of budget
101 states that define contemporary reefs and, in a very few cases, for monitoring disturbance driven

102 changes (Perry & Morgan, 2017; Manzello et al., 2018). Based on various field studies, shallow water
103 (<~15 m) carbonate production rates under optimal conditions in the lower latitude reef-building regions
104 are generally considered to average ~1-10 kg CaCO₃ m⁻² yr⁻¹ depending on reef zone, depth, and
105 ecoregion (Kinsey & Hopley 1991; Vecsei, 2004).

106

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

120

121 The budget processes and states that define deeper water reef zones (below about 20 m) remain
122 poorly documented, largely because they are below the limits of prolonged SCUBA diving. However, as
123 depth increases, light and wave turbulence reduce, driving transitions in the abundance of the taxa that
124 control the balance between carbonate production and loss. Coral assemblage shifts and changes in
125 the morphology of corals (increasing prevalence of plate-like growth forms) with depth are well
126 documented, and it is also known that coral calcification rates decline with depth, albeit in a species

127 specific and non-uniform way (Hubbard & Scaturo, 1985; Weinstein et al., 2016). Furthermore, as depth
128 increases the abundance of grazing parrotfish and urchins declines, and changes in the composition of
129 endolithic bioeroding communities occur (Perry & Harborne, 2016). In the Caribbean at least, endolithic
130 sponges become the dominant macroendolithic taxa and shifts from phototrophic to heterotrophic
131 microendoliths occur (Perry & Hepburn, 2008). The net effect is that the *in-situ* carbonate budgets of
132 deeper reef habitats (although poorly quantified) will progressively shift in favour of the erosional side of
133 the equation (Fig. 2A) (Weinstein et al., 2016), but with the overall reef budget augmented at some
134 sites by the import of rubble and sediment from shallower reef zones.

135

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

151

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

166

167 The potential for temporal budget transitions was conceptually explored in relation to different budget
168 state scenarios by Perry et al. (2008). In some cases, change, driven by a suite of interacting ecological
169 disturbances, is hypothesised to occur gradually or in a stepped fashion over a number of decades. In
170 other cases, change may occur rapidly, such as that associated with major bleaching events. However,
171 whilst the end point in both cases is broadly the same i.e., a diminished carbonate budget state, the
172 pathways to this point can differ markedly. On many shallow water Caribbean reefs, for example,
173 carbonate production rates have progressively declined over at least the last 30-40 years, as the
174 abundance of formerly dominant high rate carbonate producing branching coral taxa (specifically the
175 *Acropora* spp.) has declined (Perry et al., 2014a). At the same time chronic overfishing and the
176 widespread die-off of *Diadema antillarum* considerably reduced the abundance of many bioeroding

177 species (Carpenter, 1990). The net effect has been that many shallow water reefs have probably
178 shifted to states close to budgetary stasis and in some cases net erosion (Fig. 2B). These states can
179 lead to progressive breakdown and loss of surficial reef structural complexity (see Section 2 below) and
180 in some cases to loss of the wider reef structure itself (Lewis, 2002).

181

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

193

194 Whether and how rapidly reefs (and their budgets) can recover from major short-lived shock events is
195 thus of growing interest. Data from sites impacted by the 1998 bleaching event in the Indian Ocean
196 show that many reefs recovered to states of high coral cover and, where assessed, high net positive
197 budget states (Perry et al., 2015a). However, many Indian Ocean reefs were severely impacted again
198 by bleaching in 2016, resetting their ecology and budgets to net negative states (Perry & Morgan,
199 2017). The frequency of future severe bleaching events in such regions will thus strongly influence
200 whether the budgets of reefs again recover, and there are two key points that can be made here. The
201 first is that recent models suggest that in the absence of rapid climate mitigation actions, the frequency

202 of severe bleaching events will increase, and whilst predictions for the timing of annual severe
203 bleaching vary geographically, many sites are predicted to experience strong warming each year by at
204 least 2070 (van Hooidonk et al., 2016). The second point is that in some locations there is evidence
205 that not all reefs recovered from the 1998 event. For example in the Seychelles some reefs recovered,
206 but others “regime-shifted” to macroalgal-dominated states (Graham et al., 2015), the latter being
207 defined by persistent low or net negative budgets (Januchowski-Hartley et al., 2017). The broader
208 implications of this are that as regions are hit by future (more frequent) bleaching events so the ratio of
209 reefs that can recover may fall relative to those that become “regime-shifted”, either due to increasing
210 frequency of disturbance events or reduced ecological resilience.

211

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

225

226 A further, though generally poorly documented aspect of carbonate budget change relates to the
227 processes of reef sediment generation. Reef-derived sediment is a volumetrically important component
228 of the structure of most reefs (Hubbard, Miller & Scaturo 1990; Hubbard, Burke & Gill 1998), and thus a
229 key part of the reef-building process, as well as providing sedimentary material to sustain beaches and
230 shorelines. Most sediment generated on reefs and within reef-related habitats (lagoons) derives either
231 directly from organisms that secrete calcium carbonate skeletons (e.g., molluscs, foraminifera) and
232 which contribute post-mortem to the sediment reservoir, or are produced indirectly from skeletal
233 carbonate breakdown e.g., by specific species of fish and urchins (Scoffin, 1992). It follows therefore
234 that as the abundance of these direct and indirect sediment producing species/processes change,
235 driven by the same disturbance events discussed above, so the functional role of reefs as focal points
236 of sediment generation will change (Perry et al., 2011). Such change may be expressed either in terms
237 of the volumes or types of sediment produced, but the consequences of change are likely to be
238 especially marked where disturbances impact upon a narrow range of disproportionality important
239 sediment producing taxa (e.g., parrotfish – Perry et al., 2015b; benthic foraminifera – Collen & Garton,
240 2004). In such cases, loss of the relevant taxa may render sediment production rates insufficient to
241 sustain local beaches or islands.

242

243 **2. Impacts associated with eco-morphological taxa transitions (the changing reef complexity** 244 **problem)**

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

251 2018), and strongly influences wave energy dissipation over reefs (see next section and Fig. 4).
252 Because of the importance of hard coral cover in building and structuring reef frameworks (see Section
253 1 above), research on reef degradation has mostly focused on exploring the trends, drivers and
254 consequences of declining live coral cover and reef complexity. However, functioning depends, to a
255 large extent, on the life history strategies of corals, which are strongly linked to species morphological
256 and physiological attributes (Darling et al., 2012; McWilliam et al., 2018). At the same time species
257 growth rates, skeletal density, size and morphological complexity have been identified as primary traits
258 defining processes of carbonate production and habitat provisioning on reefs (Darling et al., 2012;
259 Alvarez-Filip et al., 2013; McWilliam et al., 2018). It is therefore unlikely that coral cover alone captures
260 the variability in reef structure and community calcification mediated by different coral taxa (Alvarez-
261 Filip *et al.* 2011a; Perry et al., 2015a). For instance reefs dominated by species with high structural
262 complexity and high growth rates are likely to not only maintain more diverse communities but also to
263 regulate the functional structure of reef communities (Alvarez-Filip et al., 2011b; Richardson et al.,
264 2017a;).

265

266 In this context, the distribution of coral species and their functionality create habitat heterogeneity (or
267 reef zones) within specific biogeographic regions. These are influenced by spatial variations in
268 environmental forces such as temperature, light penetration and sediment inputs. However, the rapid
269 environmental changes being caused by anthropogenic pressures are now non-randomly modifying the
270 distribution of coral species and, in many cases, promoting a shift in dominance towards taxa better
271 adapted to the new conditions. The net effect of this is to modify the functional performance of coral
272 communities (Carturan et al., 2018), because disturbance typically favors fewer generalist species that
273 are able to tolerate stress and therefore competitively dominate the landscape (Clavel et al., 2011;
274 Alvarez-Filip et al., 2015a). A major functional transition associated with ecological change therefore
275 relates to shifts in the abundance of corals with different morphological properties, or to different

276 disturbance-driven pathways of framework breakdown. Most simply these transitions can occur where,
277 for example, highly rugose branching coral taxa have been lost and replaced by low-relief coral forms,
278 leading to marked changes in habitat (and micro-habitat) diversity and complexity (Fig. 3), and to
279 changes in reef carbonate budgets (Figs. 3B, C).

280

281 In the Caribbean, for example, diseases, coral bleaching and local anthropogenic stressors have acted
282 synergistically to transform coral communities over the past 40-50 years (e.g., Jackson et al., 2014).
283 Throughout the region, the few species responsible for most of the structural complexity on reefs have
284 been replaced by opportunistic species (Green et al., 2008). Although it has been proposed that
285 species reconfiguration may prevent ecosystem collapse as populations of remaining coral species
286 could maintain ecosystem integrity under future climate change (Hughes et al., 2012), a growing body
287 of evidence shows that simplified reef communities alter ecosystem functioning and productivity, and
288 jeopardize the persistence of ecosystem goods and services (Alvarez-Filip et al., 2015b; Hughes et al.,
289 2018; Richardson et al., 2018). This is because shifted reefs are dominated by rapid colonizer species
290 that whilst relatively tolerant to thermal and/or physical stressors, have different morpho-functional
291 characteristics (Alvarez-Filip et al., 2011) and typically provide less structural habitat complexity (Green
292 et al., 2008; Van Woesik et al., 2011; Darling et al., 2012). Thus as coral assemblages change from
293 reefs dominated by large reef-building corals to smaller non-framework building species, declines in
294 both coral-community calcification and reef rugosity can occur that are independent of changes in total
295 coral abundance (Alvarez-Filip et al., 2013, Fig. 3C).

296

297 While reef community transitions in the Caribbean have thus commonly resulted from a gradual
298 process of ecosystem degradation and loss of ecological resilience, there are many examples in the
299 Indo-Pacific of reefs that have experienced different trajectories of change. In this eco-region, rapid
300 declines in coral cover and shifts in coral abundance have commonly occurred in response to strong

301 acute events such as ocean warming-induced mass bleaching (Hughes et al., 2017). Mass bleaching
302 events and subsequent coral mortality result in a radical shift in the composition and functional traits of
303 coral assemblages, drastically transforming reef landscapes across large spatial scales (Gilmour et al.,
304 2013; Hughes et al., 2018). Tabular and branching corals, which are fast-growing, three-dimensional
305 species that commonly dominate many Indo-Pacific reefs, tend to be disproportionately affected by post-
306 bleaching mortality (Gilmour et al., 2013; Perry & Morgan, 2017; Hughes et al., 2018). Thus, in many
307 cases, reefs shift away from the dominance of morphologically complex coral species, to assemblages
308 dominated by taxa with simpler morphological characteristics and slower growth rates, resulting in rapid
309 loss of coral community-scale complexity (e.g. Perry & Morgan, 2017; Hughes et al., 2018; Fig. 3B).
310 Although recovery of degraded reefs is largely dependent on the growth of remnant corals (Halford et
311 al., 2004; Gilmour et al., 2013), there is evidence showing that in the absence of further stressors reefs
312 can recover both in terms of overall coral cover and habitat complexity (Gilmour et al., 2013; Graham et
313 al., 2015). However, predicted increases in the frequency of bleaching-level thermal stress are likely to
314 impede recovery potential on many reefs (van Hooidonk et al., 2016).

315

316 An emerging challenge in coral reef ecology is therefore to understand the functional consequences of
317 shifts in coral abundance and composition. Ecological assemblage phase shifts have direct relevance
318 to the issues of changing carbonate budgets discussed above because different morphological groups
319 of corals are generally defined by different calcification and linear extension rates (González-Barrios &
320 Álvarez-Filip, 2018). Coral reef habitats dominated by stress-tolerant taxa may thus become defined by
321 persistent low (relative to regional optimal) budget states (Manzello et al., 2018). Abrupt, regional-scale
322 shifts in coral assemblages may also radically reduce the abundance and diversity of species traits that
323 facilitate key ecological functions (Hughes et al., 2018; McWilliam et al., 2018). Dominance patterns of
324 coral assemblages therefore seem to be the most important driver of the functioning of coral reefs, and
325 thus the future of these ecosystems might depend not only on general reductions of local and global

326 stressors, but also on the maintenance of keystone coral species. As anthropogenic pressures
327 continue, understanding how initial habitat configurations prior to disturbance will influence changes in
328 coral communities, and reef-associated species such as fish (Alvarez-Filip et al., 2011b; Richardson et
329 al., 2017b, 2018), will be critical for developing forewarnings of resilience loss and the threat of
330 functional collapse, such that management efforts may be appropriately assigned.

331

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

333 A major functional consequence of the ecologically-driven transitions on reef carbonate budgets is the
334 capacity to change reef accretion (vertical growth) potential. Reef growth is in part a function of the
335 carbonate budget of a reef, but represents a measure of the net rate of vertical reef framework
336 accumulation over time i.e., how much of the framework carbonate that is produced adds to the surface
337 of the reef. The term potential is important because whilst a net positive budget state can be considered
338 the minimum for reef accretion to occur, other factors such as rates of physical framework removal are
339 also important. Indeed, previous authors have defined different conceptual budget states that reflect
340 variations in the relative balance between framework “input” (carbonate production, external sediment
341 and rubble inputs) and “export” (biological, physical and chemical erosion) processes (Kleypas et al.,
342 2001). From a reef growth perspective these conceptual states provide a useful framework within which
343 to envisage the interacting input and output factors that determine short term budget states. The
344 relative balance between production and export processes then aggregate to influence long-term reef-
345 building potential, essentially by dictating the net amount of carbonate being produced that
346 accumulates in a given environment.

347

348 Under what might be considered optimal reef-building conditions, the “norm” is most commonly a
349 situation where the production-dominated state persists more or less continuously to drive net in-situ
350 reef framework accumulation and reef accretion (Kleypas et al., 2001). Indeed, the Holocene record of

351 reef-building, as discerned from core records, provides numerous examples of semi-continuous vertical
352 reef-building (Montaggioni, 2005; Gischler 2015), with vertical reef accretion persisting until otherwise
353 sea-level constrained (Perry & Smithers, 2011), or where other external environmental factors (e.g.,
354 water quality, ocean temperatures) limit accretion (Toth et al, 2018). Conversely, there are examples of
355 reefs that have developed under very different long-term environmental conditions, and which represent
356 alternative examples of reef-building states. One well-documented example occurs in nearshore
357 settings where persistent terrestrial sediment inputs influence the reef budget under “import-dominated”
358 conditions (Browne et al., 2013). In such settings framework production (coral growth) clearly remains
359 important, but core records show that a high proportion of the accumulating reef structure comprises
360 fine-grained terrigenoclastic sediments that represent a long-term external input to the reef-building
361 budget (Perry et al., 2012). In contrast, there are examples of persistent “export-dominated” reefs
362 where all or most framework carbonate produced annually is removed by seasonal storms or cyclones
363 (e.g., along the S. African coast; Riegl, 2001). The net effect is an absence of long-term framework
364 accumulation and no net reef accretion.

365

366 The examples cited above clearly point to marked natural spatial heterogeneity in reef-building
367 potential. However, a question that arises in the context of Anthropocene-era change is how rapidly and
368 to what extent is the potential for reef accretion now being diminished? Declines in contemporary
369 accretion rates may occur where within-site production rates are reduced relative to rates of biological,
370 physical or chemical erosion, thus driving shifts from production to erosion dominated budgetary states.
371 As outlined in previous sections, these transitions may arise either from progressive ecological
372 deterioration (over decadal timescales), or acute and high magnitude disturbance events (e.g., severe
373 bleaching). In the latter case, recent historical evidence suggests that, depending on species and
374 recovery rates, periods of perhaps 10-15 years largely free from disturbance may be sufficient to
375 enable reefs to regain their former states of high carbonate production and accretion potential (Perry et

376 al., 2015a; Figure 3A). However, the potential for such “boom-bust-boom” cyclicality is increasing
377 uncertain given projections of more frequent high magnitude bleaching events driven by warming
378 events.

379

380 Where accretion rates do decline, and there is emerging evidence that this is an increasingly
381 widespread Anthropocene scenario (Perry et al., 2018), there are a number of major implications in
382 terms of reef geo-ecological functionality. One of the most significant is the question of whether reefs
383 will retain capacity to keep up with rates of accelerating sea-level rise (SLR). Evidence from Holocene
384 core records of reef growth, when ecological conditions and thus by inference carbonate budget states
385 are considered to have been more optimal, suggest that many reefs exhibited an impressive capacity to
386 either “keep-up” or to “catch-up” during periods of rapid SLR (Neumann & Macintyre, 1985). Indeed,
387 measured vertical accretion rates from the early Holocene, when sea-levels were rising rapidly, may
388 have been up to ~15 mm yr⁻¹ in both the tropical western Atlantic and Indo-Pacific regions (Dullo,
389 2005). Longer-term average accretion rates in both regions were lower, in the tropical western Atlantic
390 ~3-4 mm yr⁻¹ (Hubbard, 2008) and a little below this in the Indo-Pacific region (Dullo, 2005). Whilst
391 some high coral cover sites may sustain vertical accretion rates sufficient to match near-future sea-level
392 rise (van Woesik & Cacciapaglia 2018), the critical point is that many contemporary coral reefs are now
393 defined by vertical accretion rates that will be insufficient to keep pace with sea-level rise. Indeed,
394 recent assessments of reef accretion potential at sites around the tropical western Atlantic and Indian
395 Ocean regions suggest that accretion rates presently average only 1.8 mm yr⁻¹ and 2.0 mm yr⁻¹
396 respectively (Perry et al., 2018).

397

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

401 Tropical Cyclone intensity are realised (Bhatia *et al.* 2018). Several recent studies have modelled SLR
402 impacts on wave energy regimes across reefs (e.g., Storlazzi *et al.*, 2011; Beetham *et al.*, 2017) and
403 three key controls related to reef structure and accretion rates emerge: i) reef width and profile; ii)
404 surface structural complexity; and iii) reef growth relative to the rate of water depth increase. The first of
405 these, reef width and profile, are unlikely to change markedly over relevant future timescales since
406 these parameters are a function of antecedent topography and long-term reef growth. More likely to
407 change are parameters ii) and iii). Coral cover and assemblage composition strongly influence reef
408 surface structural complexity, and this is important because complexity exerts a frictional effect on
409 waves (Harris *et al.*, 2018). Thus, reef surface complexity changes discussed above (section 2) have
410 the potential to directly impact wave attenuation. Maintenance of reef surface elevation relative to sea
411 level is also important because water depth modulates across-reef and nearshore wave energy
412 regimes. Mean water depth increases will occur where vertical growth rates lag behind actual or relative
413 increases in sea-level. Emerging evidence suggests that for many reefs the Anthropocene era is likely
414 to be defined by declines in both accretion rates and surficial complexity (rugosity) (Fig. 4). Thus, whilst
415 a few reefs may currently maintain capacity to track SLR and limit wave attenuation (Fig. 4 – Group A),
416 a great many will not (Fig. 4 – Group C) and some have already lost this capacity (Fig. 4 – Group D).
417 Indeed, recent assessments of reef growth – SLR interactions under different SLR scenarios through to
418 2100 suggest that tropical western Atlantic reefs will experience increases in water depths above reefs
419 of ~40 cm by 2100 under the RCP 4.5 (Representative Concentration Pathway) scenario, and ~60 cm
420 under RCP 8.5, whilst in the Indian Ocean region average water depth increases of ~47 cm and ~71
421 cm are predicted under these scenarios (Perry *et al.*, 2018). Many reefs are therefore expected to offer
422 less resistance to water flow, thus increasing the risks of coastal erosion and flooding of low-lying
423 areas, with associated heightened economic and social costs for coastal communities.
424

425 A further implication of changing reef ecology and declining budget states that will exacerbate the
426 impacts on reef-building may arise from changes to the supply-side of the reef-building process. The
427 Holocene record of reef-building clearly shows that reef construction at a given site is typically
428 dominated by a relatively restricted suite of coral taxa, and that this material is often converted to coral
429 rubble during high energy physical disturbances (Hubbard et al., 1998). This coral rubble is often
430 largely derived from fast-growing branched coral taxa, which subsequently: i) represents a
431 volumetrically important component of accumulating reef frameworks, and ii) has historically sustained
432 shallow fore-reef and reef crest building as a result of breakage and rubble transport (Blanchon et al.,
433 2017). However, changes in coral species composition and in the abundance of relevant morpho-taxa
434 (especially branched corals) means that the supply side of this reef growth dynamic is changing. For
435 example, in the Caribbean previously dominant shallow water branched corals (*Acropora* spp.) have
436 been largely replaced by low-relief taxa, such as *Agaricia* spp., *Porites* spp. and *Siderastraea* spp.
437 (Green et al. 2008; Perry *et al.* 2014a), and these do not represent appropriate substitutes in terms of
438 the supply side of the rubble-driven reef building process. Thus, changes in shallow water reef ecology
439 can lead to marked reef-growth shifts that will impact both the impacted habitat, but also adjacent
440 shallower and deeper reef zones which normally derive coral rubble from the impacted zone.

441

442 Collectively, these ideas point to an increasing disconnect between the underlying framework structure
443 of contemporary reefs, which can represent the products of carbonate accumulation over several
444 millennia, and reef carbonate budgets and thus accretion potential. In other words, in some regions, the
445 underlying reef structure is essentially becoming a relict feature with little/no new carbonate being
446 added. The idea of a progressive decoupling between contemporary reef ecology and the maintenance
447 of the underlying reef structure is not necessarily a solely Anthropocene phenomenon (Kuffner & Toth,
448 2016; Toth et al. 2018). Indeed, it has previously been discussed as a response to changing
449 environmental conditions around the latitudinal or environmental limits of reef-building (van Woerik &

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

457

458 **Concluding remarks**

459 A major consequence of coral reef ecological transitions is that the Anthropocene is likely to be defined
460 by an increased decoupling between current reef ecological states and the physical functions that reefs
461 provide. This conclusion is based on the fact that on many reefs a progressive or rapid transition away
462 from high historical carbonate budget states to states of low net positive or negative production is now
463 occurring. This change threatens many of the key geo-ecological functions that reefs provide: their
464 structural composition and microhabitat diversity, their capacity to generate sufficient sediments to
465 sustain adjacent beaches and shorelines, their capacity to continue accreting vertically at rates that can
466 match sea-level rise, and thus their functionality as wave attenuating structures. It is reasonable to
467 hypothesise that these changes will be most marked in shallower water settings which are most
468 exposed to warming events, often harbour the most susceptible coral taxa, and which are most
469 “exposed” to direct human stressors. Although not entirely immune from ecological change, deeper reef
470 habitats (below ~20 m) may be more protected. Thus, the Anthropocene footprint on reefs may be
471 expressed rather differently across habitats and depth zones. It is also reasonable to hypothesise that
472 budget states across individual reefs may become increasingly depth-homogenised, threatening the
473 strong links that exist between structurally and ecologically complex shallow water reef habitats and the
474 well-being of coastal human populations. These issues point to the need for further research to better

475 understand: 1) how the processes of carbonate production and bioerosion interact as reef habitats
476 change; 2) how these same processes vary with depth and latitude across reefs; 3) the extent to which
477 remaining healthy reefs may be able to sustain the key geo-ecological functions outlined above; and 4)
478 the extent to which ecological restoration efforts are feasible (at least over small spatial scales) to
479 restore reef geo-ecological functionality. These functional attributes (reef-building and reef accretion,
480 sand generation and assemblage-driven habitat complexity and diversity) underpin many of the
481 ecosystem goods and services that reefs provide to society and thus strategies to protect or restore
482 them represents a major Anthropocene challenge.

483

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487

488 **Author contributions**

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

490

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735

736 Figure captions

737

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

740

741 *Fig 2. Schematic showing depth distribution of key processes influencing biological carbonate budgets
742 on reefs and their relative importance (note no actual rates implied) in different depth zones under A)
743 pre-Anthropocene historical conditions, and B) Anthropocene era conditions. Resultant net budget
744 states in each depth zone are shown on the right (based on the ternary budget states plot of Perry et al.
745 2008).*

746

747 *Figure 3. The resilience of different scales of structural complexity to ecological change*

748 *(A) Hierarchical scales of reef structural complexity. Geomorphology-scale complexity results from
749 long-term accretion (100-1000s years); community-scale complexity is provided by the skeleton of*

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

770

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

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

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