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Coral bleaching patterns are the outcome of complex biological and environmental networking

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1 **Abstract**

2 Continued declines in coral reef health over the past three decades have been punctuated by  
3 severe mass coral bleaching-induced mortality events that have grown in intensity and  
4 frequency under climate change. Intensive global research efforts have therefore persistently  
5 focused on bleaching phenomena to understand where corals bleach, when and why –  
6 resulting in a large – yet still somewhat patchy – knowledge base. Particularly catastrophic  
7 bleaching-induced coral mortality events in the past five years have catalysed calls for a more  
8 diverse set of reef management tools, extending far beyond climate mitigation and reef  
9 protection, to also include more aggressive interventions. However, the effectiveness of these  
10 various tools now rests on rapidly assimilating our knowledge base of coral bleaching into  
11 more integrated frameworks. Here, we consider how the past three decades of intensive coral  
12 bleaching research has established the basis for complex biological and environmental  
13 networks, which together regulate outcomes of bleaching severity. We discuss how we now  
14 have enough scaffold for conceptual biological and environmental frameworks underpinning  
15 bleaching susceptibility, but that new tools are urgently required to translate this to an  
16 operational system informing – and testing – bleaching outcomes. Specifically, network  
17 models that can fully describe and predict metabolic functioning of coral holobionts, and how  
18 this is regulated by complex doses and interactions amongst environmental factors.  
19 Identifying knowledge gaps limiting adoption of such models is the logical step to  
20 immediately guide and prioritise future experiments and observation. We are at a time-critical  
21 point where we can begin to resolve how coral bleaching patterns emerge from complex  
22 biological-environmental networks, and so more effectively inform rapidly evolving  
23 ecological management and social adaptation frameworks aimed at securing the future of  
24 coral reefs.

25

## 26 **Introduction**

27           Global degradation of coral reefs is fast becoming a legacy of the Anthropocene.  
28 Continued declines in reef health worldwide through accelerated industrialization,  
29 urbanization and agriculture (Osborne et al. 2017, Lapointe et al. 2019) have been punctuated  
30 by heat wave-driven catastrophic coral mortality events that have grown in intensity and  
31 frequency under climate change (Hughes et al. 2017, 2018, Eakin et al. 2019). Extreme heat  
32 wave events conspicuously manifest as mass coral bleaching – the process whereby large  
33 extents of coral rapidly pale through loss of their algal endosymbionts (e.g. Glynn 1996,  
34 Suggett & Smith 2011) via destabilization of the coral-algal symbiosis (e.g. Smith et al. 2005,  
35 Weis 2008, Davy et al. 2012, Matthews et al. 2018). Bleached corals rapidly die unless the  
36 host coral can secure alternate sources of energy (Grotolli et al. 2006, 2014), causing  
37 ecological cascades that impact reef-associated fish communities (Bellwood et al. 2006,  
38 Richardson et al. 2018, Benkwitt et al. 2019) and ultimately reef landscape erosion  
39 (Montefalcone et al. 2018, Leggat et al. 2019) that together transform ecological and  
40 biogeochemical service provision.

41           Instances of mass coral bleaching have been reported since the early 1980s, but it was  
42 not until 1998, just three years after the inception of *Global Change Biology*, when the first  
43 El Niño-driven global heat wave event resulted in catastrophic mass coral mortality  
44 worldwide (Eakin et al. 2019) – 1998 arguably placed coral bleaching on the world stage,  
45 kick-starting intensive efforts to understand the causes and effects (Cziesielski et al. 2019).  
46 Over 2,600 papers (*ISI Web of Science* search “coral” AND “bleaching”, 15<sup>th</sup> August 2019)  
47 have been published since 1998, whereby continually expanding knowledge gained has been  
48 periodically transformed by new tools and technologies that particularly advanced bleaching  
49 observations in nature or unlocked the biological mechanisms at play. Over the past 25 years,  
50 *Global Change Biology* has contributed as a major platform in disseminating many of the

51 breakthroughs from the global scientific community, including the process of bleaching at  
52 fundamental biological levels (e.g. Smith et al. 2005, Crawley et al. 2010, Chakravarti et al.  
53 2016, Pogoreutz et al. 2017, Ferrier-Pagès et al. 2018), bleaching susceptibility and tolerance  
54 patterns in nature (e.g. Vega-Thurber et al. 2013, Silverstein et al. 2014, Grottoli et al. 2014,  
55 Osborne et al. 2017, Osman et al. 2018) and ensuing ecological cascades (e.g. Bellwood et al.  
56 2006, Anthony et al. 2011, Osborne et al. 2017, Montefalcone et al. 2018, Richardson et al.  
57 2018, Wolff et al. 2018, Benkwitt et al. 2019), and in turn how these processes and patterns  
58 inform management (e.g. Selig et al. 2012, Logan et al. 2014, van Hooidonk et al. 2015,  
59 Anthony et al. 2015, Wolff et al. 2015).

60         The most recent global back-to-back (2015-2017) bleaching events have re-affirmed  
61 the fragility of coral reef ecosystems to climate change and associated local social-  
62 environmental stressors (e.g. Hughes et al. 2017, 2018, Darling et al. 2019, Lapointe et al.  
63 2019) – for many, these events were a confronting first for how rapid and destructive  
64 bleaching-driven mortality occurs. Advances in bleaching forecasting (e.g. Heron et al. 2016,  
65 van Hooidonk et al. 2015, Kumagai et al. 2018) meant that the most recent events particularly  
66 provided new capacity for research communities to capture mass bleaching as it unfolded,  
67 transforming empirical knowledge of bleaching patterns in nature as well as improving  
68 understanding of the core biological and ecological responses at play (Hughes et al. 2017,  
69 2018, McClanahan et al. 2019; see also Eakin et al, 2019). We are, as a result, at an  
70 important, and exceptionally time-sensitive, turning point in our understanding of coral  
71 bleaching and how we move forward. Catastrophic loss of coral cover worldwide in less than  
72 5 years has catalysed global calls for a more diverse set of reef management tools, extending  
73 far beyond climate mitigation and reef protection to also include real-time active  
74 interventions (e.g. Anthony et al. 2017, National Academies of Sciences, Engineering, and  
75 Medicine 2019). However, the viability and success of any forward-looking management

76 undoubtedly now rests on rapidly consolidating our ever improving – yet still somewhat  
77 patchy – knowledge of how coral bleaching ultimately manifests as a result of complex  
78 biological and environmental networks. Here, we consider how the past three decades of  
79 coral bleaching research has established the basis for biological and environmental networks,  
80 and how urgently developing research within the framework of these networks will likely be  
81 central to more accurately predict, and therefore manage for, bleaching episodes.

82

### 83 **The mechanistic biological network underpinning bleaching severity**

84         Reconciling complex ecological outcomes of coral bleaching over space and time  
85 rests on isolating how the core biological constituents and pathways regulating coral  
86 holobiont fitness are governed by physico-chemical factors. Over three decades of  
87 experiments and observations have developed and refined the central bleaching paradigm  
88 (e.g. Cziesselski et al. 2019) whereby accumulation of reactive oxygen species (ROS), and/or  
89 reactive nitrogen species (RNS), leads to signaling cascades and in turn expulsion or  
90 xenophagy of the algal endosymbionts (Family: Symbiodiniaceae) from the coral host (Smith  
91 et al. 2005, Weis 2008, Tchernov et al. 2011, Davy et al. 2012). An overwhelming body of  
92 evidence has repeatedly demonstrated that perturbations to environmental factors  
93 underpinning optimum metabolic functioning can all result in bleaching; notably, temperature  
94 (Tchernov et al. 2004, Tolleter et al. 2013, Levin et al. 2016), light (Lesser & Farrell 2004,  
95 Downs et al. 2013), salinity (Aquilar et al. 2019, Gardner et al. 2016, Ochsenkühnet al. 2017)  
96 as well as inorganic nutrients including CO<sub>2</sub> (Anthony et al. 2008, Crawley et al. 2010), iron  
97 and other trace metals (Shick et al. 2011, Biscéré et al. 2018, Ferrier-Pagès et al. 2018), and  
98 the nitrogen-to-phosphate ratio (Wiedenmann et al. 2012, Fabricius et al. 2013, Pogoreutz et  
99 al. 2017). Stability of the symbiosis rests on fine-tuned resource exchange of primary  
100 metabolic currencies – C, N, P, electron carriers, etc. – amongst the algal symbionts, host

101 and/or broader associated microbiome (Suggett et al. 2017). Consequently, rapid changes in  
102 resource availability that is either externally provided (environmental flux) and/or internally  
103 sourced (enzymatic rates of currency uptake or internal recycling, ion channel functioning)  
104 drive metabolic imbalance that increases the potential to either accumulate or protect against  
105 ROS (e.g. Cziesielski et al. 2019, Wang et al. 2019). Many studies consistently demonstrate  
106 that declining metabolic competence is empirically accompanied by an increased emission of  
107 ROS. Thus ROS appears to be the “smoking gun”, but which metabolic pathways ‘pull the  
108 trigger’ remain very much unresolved.

109 Targeted reductionist experiments have commonly been used to explore numerous  
110 mechanistic hypotheses to potentially isolate how ROS – in its various forms (see Smith et al.  
111 2005, Lesser 2006) – can accumulate and overwhelm steady state metabolic functioning of  
112 the coral symbiosis. Whilst experiments have unearthed the many cellular constituents that  
113 potentially contribute to ROS induced stress in corals, they have also led to somewhat  
114 contradictory views of the primary constituent(s) at play; such contrary views are perhaps  
115 best evidenced from the wealth of heat stress assays on Symbiodiniaceae isolates to date (see  
116 Warner & Suggett 2016). Extreme high temperature sub-optimality (or “stress”)  
117 fundamentally slows enzymes, e.g. Rubisco (Lilley et al. 2010), that otherwise prevent a  
118 backlog of photochemically generated electrons within electron carrier systems. Enhanced  
119 excitation pressure increases the probability for ROS damage at the sites of light trapping  
120 (Lesser & Farrell 2004, Takahashi et al. 2008) unless electrons can be safely dissipated  
121 through alternative metabolic pathways, many of which also generate ROS (and/or RNS) as  
122 metabolic intermediaries (Suggett et al. 2008, Roberty et al. 2014). Where ROS accumulates,  
123 and hence targets, represents the net outcome of crosstalk between many dynamic metabolic  
124 pathways operating in concert. Thus, how ROS stress manifests will inevitably depend on the  
125 environmental conditions and taxon of interest. Such dependency may be further

126 compounded over time where Symbiodiniaceae taxon can acclimatize (Takahashi et al. 2013)  
127 or even evolve (Chakravarti et al. 2017) heat tolerance when maintained for prolonged  
128 periods under sub-lethal upper temperatures, which may in turn reflect the capacity for  
129 associated, possibly obligate, bacterial communities of Symbiodiniaceae (Lawson et al. 2018)  
130 to modify resource availability and/or ROS accumulation.

131 Heat stress susceptibility in fact appears fundamentally dependent on how a whole  
132 network of ‘tolerance promoters’ – cellular constituents that act to neutralize exposure to  
133 stressors – including ROS scavenger and heat shock proteins (Lesser & Farrell 2004, Suggett  
134 et al. 2008, Takahashi et al. 2008, Davy et al. 2012, Levin et al. 2016, Gierz et al. 2017,  
135 Goyen et al. 2017; reviewed in Cziesielski et al. 2019), occur for any given Symbiodiniaceae  
136 taxon (Fig. 1). Recent transcriptomic studies have indeed confirmed that different heat stress  
137 sensitivity – via ROS generation and photosynthetic reaction centre degradation – between  
138 closely related genotypes of the same Symbiodiniaceae species is governed by a whole  
139 repertoire of cellular constituents operating to differing extents (Levin et al. 2016, Gierz et al.  
140 2017). Consequently, heat stress sensitivity (or tolerance) is likely better described as a series  
141 of ‘phenotypes’ that capture alternate modes of tolerance promotion (Goyen et al. 2017) and  
142 thus encapsulate the broad functional diversity in metabolic functioning that has evolved  
143 amongst the Symbiodiniaceae (Suggett et al. 2017). This notion is even more relevant where  
144 heat stress accompanied by other stressors further expands the range of bleaching stress-  
145 response phenotypes observed for Symbiodiniaceae (e.g. high light, Downs et al. 2013; high  
146 CO<sub>2</sub>, Crawley et al. 2010; phosphate limitation, Wiedenmann et al. 2013).

147 Considering stress-induced bleaching as a metabolically networked process – as  
148 opposed to pinned on a single (primary) cellular constituent – is even more central when  
149 placing Symbiodiniaceae within the context of the coral symbiosis (see Palmer 2018). ROS  
150 (and RNS) emission from Symbiodiniaceae cells are thought to act as a signaling cue to the



151 surrounding coral host tissues triggering dysbiosis (and hence bleaching) (Smith et al. 2005,  
152 Weis et al. 2008, Davy et al. 2012). Consequently, “shuffling” one Symbiodiniaceae taxon to  
153 another, with different repertoires of tolerance promotion (Levin et al. 2016) likely serves as  
154 a primary means to mitigate stress induced ROS (RNS) susceptibility (e.g. Silverstein et al.  
155 2014, Howells et al. 2016). Such “shuffling” therefore serves as a form of biological  
156 recombination to maintain host-symbiont metabolic homeostasis as the resource landscape  
157 changes (Suggett et al. 2017, Matthews et al. 2018). Coral hosts further exhibit a complex  
158 repertoire of tolerance prompters that regulate sensitivity to bleaching; for example, ROS  
159 scavenging and heat shock proteins (Dixon et al. 2015, Gardner et al. 2016, 2017, Traylor-  
160 Knowles et al. 2017, Aguilar et al. 2019; reviewed in Cziesielski et al. 2019), as well as  
161 constituents for regulating excitation energy (Lutz et al. 2015) and silencing apoptosis  
162 (Tchernov et al. 2011) (Fig. 1). Coral hosts also have the added advantage of up-regulating  
163 feeding to support the energetic demands in repair of ROS damaged constituents (Grottoli et  
164 al. 2006, 2014). Consequently, any one Symbiodiniaceae taxon can exhibit very different  
165 heat tolerance properties when hosted by different coral hosts but in the same environment  
166 (Hoadley et al. 2019), presumably since the host-symbiont metabolic network, and notably  
167 the resource landscape available to both partners to limit ROS accumulation and/or aid repair  
168 of damaged constituents, are altered. Such capacity to network tolerance promotion amongst  
169 coral host and Symbiodiniaceae partners, as well as surface associated bacteria that may aid  
170 to consume ROS (Diaz et al. 2016, Ziegler et al. 2019), may well determine the finer scale  
171 patterns of stress susceptibility within and between coral populations.

172

### 173 **Environmental interactions regulate networked bleaching at the ecosystem scale**

174 Evidence has overwhelmingly established the role of heat waves as the primary driver  
175 of coral bleaching, and in particular mass bleaching events (Hughes et al. 2018, Eakin et al.

176 2019, McClanahan et al. 2019). Heat wave severity is commonly estimated as Degree  
177 Heating Weeks (DHWs), the cumulative time with which sea surface temperature (SST)  
178 exceeds the maximum monthly mean SST, thereby exceeding the seasonal ‘norms’ that are  
179 already near corals’ upper thermal thresholds. Both empirical (e.g. Hughes et al. 2017, 2018,  
180 McClanahan et al. 2019) and experimental mechanistic (e.g. Ainsworth et al. 2016, Leggat et  
181 al. 2019) studies have repeatedly demonstrated how increasing DHWs exacerbate bleaching,  
182 unless corals have inherent capacity to thrive well below the maximum monthly mean SST  
183 (see Osman et al. 2018). Increased ocean warming over the past three decades has resulted in  
184 both ‘warmer summers’ and ‘reduced winter reprieves’ (Heron et al. 2016), amplifying the  
185 severity of both DHWs mass beaching events (Hughes et al. 2017, 2018, Eakin et al. 2019).

186 Bleaching can in fact be induced through subjecting corals to sub-optimal conditions  
187 of any factor, not just temperature, central to growth and survivorship. High light enhances  
188 photosynthetic excitation and hence potential to emit ROS (RNS) (Lesser & Farrell 2004),  
189 thereby exacerbating the effect of warming events (Jokiel & Brown 2004); as such, exposure  
190 to herbicides (Negri et al. 2011) that mimic high light-induced ‘bottlenecking’ of electron  
191 carriers that otherwise dissipate excitation energy similarly increases the potential for ROS  
192 accumulation via heat stress. Capacity to consume ROS but also repair constituents damaged  
193 (targeted) by ROS further rests on sufficient cellular ‘building materials’ and hence inorganic  
194 nutrient availability. For example, low phosphate availability, and hence high N:P, reduces  
195 integrity of lipid membranes that are targeted by ROS and thus exacerbates stress-induced  
196 bleaching (Wiedenmann et al. 2013); so much so, that decadal scale declines in Florida’s  
197 reefs have recently been attributed to persistently high N:P through eutrophication (LaPointe  
198 et al. 2019; also, Vega-Thurber et al. 2013). A particularly intriguing factor, but perhaps still  
199 the most unexplored, is oxygen availability. Hypoxia (insufficient supply of O<sub>2</sub> for ‘normal’  
200 functioning) trigger ROS (RNS) cascades that appear similarly initiated by heat induced ROS

201 (Hughes et al. in review), potentially explaining why bleaching can be triggered under heat  
202 stress in darkness (Tolleter et al. 2013). As such, hypoxia events driven by dead zone  
203 advection, but also local eutrophication that accelerate ‘reef microbialisation’ to enhance  
204 biological oxygen demand (Haas et al. 2016), can drive mass bleaching in the absence of heat  
205 (Altieri et al. 2017).

206 Bleaching ultimately occurs where severe (“lethal”) doses of any one environmental  
207 factor occurs, but importantly also if moderate (“sublethal”) doses of factors operate in  
208 concert (e.g. Anthony et al. 2011, Vega-Thurber et al. 2013, Ban et al. 2014); the intensive  
209 experimental and observation efforts to date documenting coral bleaching has resulted in a  
210 dizzying array of outcomes depending on environmental context (Fig. 2). Importantly, all  
211 environmental factors noted above have been documented to influence the severity with  
212 which heat stress-induced bleaching occurs, when and where – such that we now have an  
213 exceptionally complex environmental network where in effect, “all roads can lead to [some  
214 form of] coral bleaching” (Fig. 2). Interactions amongst environmental factors regulating  
215 coral metabolism operate in several key ways to determine how the ‘winners and losers’ are  
216 observed at the ecosystem scale (e.g. Carilli et al. 2010, Ban et al. 2014, Ellis et al. in press),  
217 yet we are still far from a complete understanding of this network:

218 Classic single factor experiments have been central to isolate mechanistic biological  
219 pathways or the response of ecological outcomes to any one factor. However, single factor  
220 perturbations are not representative of the complex biogeochemistry of reef habitats or indeed  
221 future climate scenarios (see Camp et al. 2018a), so much so that they may mis-inform as to  
222 how successfully taxa tolerate multi-factor interactions. For example, corals adapted to  
223 tolerate enhanced CO<sub>2</sub> have been shown to downregulate molecular chaperones that would  
224 ultimately enhance heat stress sensitivity (Kenkel et al. 2018). More sophisticated multifactor  
225 experiments have demonstrated how cumulative or synergistic interactions exacerbate the

226 severity of stress – whilst there are now many examples – the enhancement of heat stress  
227 sensitivity under high light is particularly common (Lesser & Farrell 2004, Jokiel & Brown  
228 2004, Robison & Warner 2006). Such interactions inevitably mean that factors can also  
229 operate antagonistically, e.g. reduced severity of heat stress under low light (e.g. Mumby et  
230 al. 2001) or cyclone-driven cooling (Carrigan & Puotinen 2014) (Fig. 2). The two cases of  
231 light as a regulatory factor to heat stress susceptibility here fundamentally highlights that  
232 non-linearity in the dose-response effect will result in different outcomes. Such non-linear  
233 response effects can also be seen for other regulatory factors, e.g. nutrients (Fabricius et al.  
234 2013), where relatively small additions in fact may aid heat tolerance, but larger additions  
235 rapidly accumulate stress and amplify heat stress sensitivity. Whilst the increasing transition  
236 towards multifactor experiments over time has been central in identifying these interactions  
237 (e.g. Boyd et al. 2018), they still remain limited in scale to be meaningful. Notably, we are far  
238 from understanding at what point interactions amongst multiple factors transition from  
239 positive to negative outcomes, or indeed when they operate cumulatively or antagonistically,  
240 and hence the sophisticated *dynamics* needed to accurately predict – or indeed interpret –  
241 networked outcomes to complex environmental scenarios.

242         Dose delivery in terms of magnitude is further regulated by time-dependency;  
243 specifically, how the dose response of any one factor accumulates (or dampens) over time.  
244 Lethal outcomes can be achieved through acute or chronic doses, but this outcome may hinge  
245 on very different mechanistic responses. The past 30 years of heat stress experiments to  
246 evaluate the bleaching process have employed heating protocols that transition a huge range  
247 of acute to chronic dosage – not all mimic development of DHW severity that occurs  
248 chronically over weeks to months in nature to drive mass bleaching (e.g. Ainsworth et al.  
249 2016, Hughes et al. 2017, McClanahan et al. 2019). Whilst acute heat stress assays have been  
250 central in generating a wealth of knowledge by which different coral species bleach (e.g.

251 Gardner et al. 2017, Biscéré et al. 2018) or different Symbiodiniaceae photoinactivate (e.g.  
252 Suggett et al. 2008, Roberty et al. 2014, Goyen et al. 2017), they preclude capacity for  
253 thermal acclimatization (Takahashi et al. 2013, Ainsworth et al. 2016), which in turn may be  
254 driven by availability of other resources. Therefore, it is still uncertain how well outcomes  
255 from acute heat stress assays accurately inform our capacity to interpret responses to chronic  
256 exposure – resolving such uncertainty is critical given that developing more synoptic views  
257 of bleaching susceptibility over space and time will inevitably need to rest on standard high-  
258 throughput, and hence rapid and acute, field-based experimental assays (e.g. Morikawa &  
259 Palumbi 2019). Again, more sophisticated recent experiments that have altered the temporal  
260 history of thermal exposure, e.g. patterns by which DHWs build (Ainsworth et al. 2016) or  
261 introducing natural day-night temperature variance (Klein et al. 2019), have demonstrated  
262 important – often non-linear – time-based dependencies in the severity with which heat stress  
263 results in bleaching. Similarly, highly detailed assessment of thermal histories is now  
264 demonstrating how localized differences in bleaching severity may be fundamentally  
265 determined by pre-DHW warming (Ainsworth et al. 2016) or cooling (McClanahan et al.  
266 2019).

267 Time-based regulation focusing on the specific ‘pulse’ stress (*sensu* Anthony et al.  
268 2015) of transient heat waves that drive bleaching, are of course relative to the background  
269 ‘press’ stress of ocean warming that pushes corals closer to lethal thresholds. Models  
270 demonstrate that heat wave frequency and severity will grow with further ocean warming  
271 (Frölicher et al. 2018). This is likely also true for the regulatory factors, notably oxygen  
272 availability, where eutrophication events that drive hypoxia are occurring against the  
273 backdrop of ocean warming-driven deoxygenation (e.g. Altieri et al. 2017). Consequently,  
274 whilst environmental models describing reef trajectories are becoming increasingly  
275 sophisticated (e.g. Baird et al. 2018, Kumagai et al. 2018, Wolff et al. 2018, Ellis et al. in

276 press), we now need to urgently develop these to account for how net bleaching outcomes  
277 reflect dose-dependencies within the entire environmental network (Fig. 2), and in turn the  
278 affect the inherent underlying metabolic network(s) (Fig. 1). This is no small task but central  
279 to guiding more informed management decisions and interventions based on what will  
280 bleach, where and when.

281

## 282 **Operationalizing management in the framework of bleaching-dependent networks**

283         Recent catastrophic loss of corals globally (Hughes et al. 2018, Eakin et al. 2019) has  
284 catalyzed the need to consider, and rapidly operationalize, novel management interventions  
285 (Anthony et al. 2015, 2017). Established practices largely employ marine protected areas  
286 (MPAs) and water quality management, but alone appear currently insufficient to offset  
287 climate change (e.g. Hughes et al. 2017). Reducing climate gas emissions is the core solution  
288 to stem catastrophic large-scale coral loss – thus, whilst climate change mitigation rests as the  
289 fundamental priority for current (not just reef) management directives, it does carry risks as a  
290 sole solution. Current IPCC Representative Concentration Pathway (RCP) scenarios are  
291 governed by the capacity for national-scale governance to implement emission reduction and  
292 mitigation strategies. Whilst the most optimistic strategies (RCP2.6) will limit further  
293 warming, heat wave frequency and global mean SSTs will persist elevated for decades  
294 (Frölicher et al. 2018). More pessimistic strategies (RCP4.5 and above) will drive further  
295 warming and heat wave frequency. Consequently, reefs will at best remain close to their  
296 thermal limits, and thus at risk from catastrophic heat wave events as well as other climatic  
297 and environmental factors that regulate heat stress sensitivity and bleaching outcomes (Fig.  
298 2), for at least decadal time frames (Frieler et al. 2013, Kwiatkowski et al. 2015, Beyer et al.  
299 2018). Without significant rates of thermal adaptation (see Donner et al. 2005, Logan et al.  
300 2014), even the most optimistic forecast therefore poses very real concerns for the short to

301 mid-term future of global reef health – hence more aggressive interventions have been  
302 proposed to at least “buy time” (Anthony et al. 2015), and indeed are in various states of  
303 trials worldwide (e.g. National Academies of Sciences, Engineering, and Medicine 2019).  
304 Whilst investing in such interventions has been argued to distract from tackling emissions  
305 reductions, nations are in fact left with little alternative than to adopt novel, immediate and  
306 aggressive reef management interventions, where they already have low emissions and  
307 significant reliance on marine protection (Wolff et al. 2015).

308         MPAs are undoubtedly essential for aiding the health of reef systems (see Darling et  
309 al. 2019), in particular from reducing fisheries pressure that perturb ecosystem states towards  
310 algal dominance that in turn places corals at greater risk from mortality or capacity to recruit  
311 (e.g. Steneck et al. 2018), to provide some “buffering” from extreme events (Roberts et al.  
312 2017). Coupled to this is effective regulation of land-derived nutrient balances entering reef  
313 systems that similarly promote algal growth and/or exacerbate sensitivity to heat induced  
314 bleaching (Fig. 2). For example, coastal nutrient discharge from the Everglades has  
315 contributed to the periods of bleaching on the Florida reef tract (Lapointe et al. 2019), and  
316 reduced nutrient subsidies from loss of seabirds around oceanic reefs has altered reef  
317 recovery trajectories post-bleaching (Benkwitt et al. 2019). Operationalizing management in  
318 the context of environmental networks that enhance (or potentially mitigate) bleaching is  
319 therefore essential for novel “land to reef” integrated approaches underpinning resilience-  
320 based management (Deleveaux et al. 2018, McLeod et al. 2019). Whilst protection afforded  
321 to reefs by MPAs does not generally appear to reduce the impact of thermal anomalies (Selig  
322 et al. 2012), it can aid reef recovery (Mellin et al. 2016). With this in mind, management  
323 efforts and investment could prioritise reefs with greater resilience, focusing on corals with  
324 inherently greater stress tolerance (or recovery potential) or operate as climate change refugia  
325 (e.g. Beyer et al. 2018, Osman et al. 2018). However, in doing so, management (re-)

326 prioritisation must be careful that efforts to minimise exposure to one stressor does not  
327 increase exposure to another (see Bruno et al. 2018), returning us a central issue: how can  
328 MPA (re-) planning be effectively achieved without understanding the complex  
329 environmental network that governs bleaching susceptibility? Realising such a goal clearly  
330 rests on rapidly improving capacity to monitor reef environment condition, but also applying  
331 this data to more advanced network models that can track how changing reef environments  
332 (Fig. 2; see also, Ellis et al. in press) trigger alternate metabolic cascades and hence bleaching  
333 outcomes (Fig. 1) (Baird et al. 2018 Kumagai et al. 2018).

334         A huge canvas of more aggressive management interventions have been proposed for  
335 coral reefs (Anthony et al. 2017, van Oppen et al. 2017, National Academies of Sciences,  
336 Engineering, and Medicine 2019, and references therein) – approaches range from mitigation  
337 of incident environmental stressors (e.g. reef cooling or shading, Couce et al. 2013,  
338 Kwaitkowski et al. 2015) to enhancing stress resistance (e.g. Chakravarti et al. 2017, Chan et  
339 al. 2018) and/or recovery (e.g. larval enhancement, dela Cruz & Harrison 2017; reef re-  
340 colonisation via substrate stabilization, coral propagation and out-planting, Baums et al.  
341 2019, Boström-Einarsson et al. 2018). Many of these approaches are already in different  
342 stages of feasibility evaluation as to what could be successful, where and when (and at what  
343 scale), should they be needed. Importantly, whilst the most aggressive synthetic biology tools  
344 are seen as a ‘last option’ should all other climate gas emission reductions and reef  
345 management options fail, their lead-in time can take decades and hence equally time sensitive  
346 as those already in more advanced stages of development and application (Anthony et al.  
347 2017, van Oppen et al. 2017). Efforts to implement locally tailored (small scale) but cheap  
348 coral propagation and re-planting practices to supplement existing MPA-based management  
349 are accelerating globally (Boström-Einarsson et al. 2018). However, success of these various  
350 efforts – and hence accurate evaluation of feasibility – again rests on resolving what



351 environmental factors have contributed to the fitness of corals being used to re-build reefs:  
352 are the survivors more stress tolerant or simply “lucky” via refugia? (e.g. Camp et al. 2018b).  
353 Developing tools that can identify coral populations with enhanced stress tolerance (Baums et  
354 al. 2019, Morikawa & Palumbi 2019) or indeed the complex environmental networks that  
355 precondition enhanced survival (Camp et al. 2018a) are undoubtedly a priority. Using  
356 knowledge of site-specific differences in thermal histories has indeed proven central in the  
357 success of propagating coral populations more resistant to thermally induced bleaching  
358 (Morikawa & Palumbi 2019), but how this can further scale to include other factors  
359 moderating bleaching severity will require more advanced environmental assessment  
360 capability.

361 Identification of ‘stress tolerance promoters’ as a central principle in guiding more  
362 aggressive intervention approaches – either for providing ‘diagnostics’ for targeted  
363 management decisions or for biological manipulation – is underpinned by resolving the  
364 metabolic network that drives bleaching susceptibility. In the case of thermal tolerance, how  
365 heat tolerance promoters (as per Fig. 1) are expressed is inevitably regulated by resource  
366 availability, and hence the specific cocktail of environmental factors and metabolic network  
367 (re-) organisation for any given time (e.g. Gardner et al. 2017, Wright et al. in press). A major  
368 limitation at present is therefore whether selection for enhanced tolerance promoters to any  
369 one stressor (e.g. heat) also gains a competitive advantage for any other environmental  
370 (metabolic network) combinations. For example, hosting heat tolerant Symbiodiniaceae  
371 strains can enhance bleaching tolerance (e.g. Howells et al. 2016, Hoadley et al. 2019), but  
372 may not necessarily support fitness under environmental ‘norms’ (Ortiz et al. 2013). The  
373 fundamental unknowns of – and predictive outcomes from – ‘fitness trade-offs’ has been  
374 tackled in other fields by moving to metabolic pathway analysis (“fluxomics”) (e.g. Beckers  
375 et al. 2016, Salon et al. 2017), based on knowledge of the entire biological system of the

376 organism of interest, to predict an integrated functional response to changing environments –  
377 or in the case of synthetic biology, to a manipulated gene or set of genes of interest.  
378 Transitioning to a systems-level scale of bleaching outcomes as a dynamic networked  
379 response has been catalyzed by recent transformations in genomic (Levin et al. 2016,  
380 Traylor-Knowles et al. 2017, Ziegler et al. 2017, Chan et al. 2018, Aguilar et al. 2019), and  
381 even more recently metabolomic (Matthews et al. 2018), capability in corals and coral-  
382 associated microbes (reviewed in Czielski et al. 2019). Even so, we are far from  
383 developing the system-wide understanding needed to develop metabolic pathway analysis.  
384 Rapidly addressing this lack of capacity seems obvious, if not essential, to better inform  
385 efforts attempting to enhance coral tolerance to complex environmental scenarios. Similarly,  
386 to aid development of more sophisticated diagnostics that may ultimately require a repertoire  
387 of variables be quantified simultaneously. Whilst we currently have the scaffold for  
388 *conceptual* maps underpinning bleaching susceptibility (Figs. 1, 2), we urgently need to  
389 translate these to *operational* maps governing bleaching outcomes.

390

## 391 **Conclusion**

392 Mass coral bleaching has driven catastrophic loss of coral cover and ecosystem service  
393 provision from coral reefs worldwide. Three decades of intensive global research into coral  
394 bleaching processes and patterns has been essential in gaining critical mass to identify the  
395 many constituents governing bleaching susceptibility over space and time. Immense  
396 knowledge gains have identified how bleaching manifests from the operation of few  
397 environmental stressors at any one time, highlighting how bleaching outcomes will inevitably  
398 stem as the net outcome of complex multifactor networks operating at organism (cellular) and  
399 ecosystem (environmental) scales. However, despite the time-sensitive nature of managing  
400 against further bleaching-induced coral loss, we are far from operationalizing our current

401 knowledge base into rapidly evolving ecological management and social adaptation  
402 frameworks aimed at securing the future of coral reefs. To achieve this goal, it is critical that  
403 we rapidly invest in developing tools that can fully describe – and predict – metabolic  
404 dysfunction of coral holobionts, and how this is regulated by complex dosage amongst  
405 multiple environmental factors. In doing so, that we use the knowledge gaps currently  
406 limiting adoption of these tools to govern and prioritise our next phase of experiments and  
407 observations. Whilst the research community has recently coalesced to develop more unified  
408 efforts for what/how to report and measure (Coral Bleaching Research Collaborative  
409 Network) and so overcome knowledge patchiness, aligning this capability alongside models  
410 and applications that can integrate biological and environmental networking will be critical to  
411 more effectively diagnose, and hence treat, the global acceleration of coral bleaching.

412

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422

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## Figure Legends

**Figure 1.** Conceptual coral biological network regulation of the “ROS (RN) reservoir”. Key components comprising the coral holobiont – the coral host, Symbiodiniaceae and wider microbiome (notably bacteria) – all contribute to ROS (RN) production. Whilst net production is locally restricted to each component, the potential for crosstalk by highly reactive ROS (RN) results in an effective pool. Each component regulates this pool via their own metabolism sustaining signaling activities for cellular homeostasis and pathogen protection (immunity). However, under perturbations that drive suboptimum environmental exposure, or restricted resource availability, this pool accumulates beyond the capacity for homeostasis requiring up-regulation of tolerance promoters to reduce this pool size (dashed open arrows) or otherwise sites are targeted (solid arrows) that result in metabolic dysfunction and/or cellular consistent degradation. Triggers begin with environmentally driven metabolic cues (\*enzyme slow-down, e.g. Rubisco, and changing ion channel functioning in elemental homeostasis, e.g.  $\text{Ca}^{2+}$ ). The inter-play between tolerance promoters versus dysfunction determine whether ROS (RN) accumulation proceeds via internal positive or negative feedbacks. The past thirty years of coral-bleaching based research has identified a large number of tolerance promoters and/or sites targeted; notably in the Symbiodiniaceae (reviewed in Warner & Suggett 2016), antennae “superquenching”, alternative electron flows (AEF), photosystem II reaction centre (D1) repair, heat shock proteins (HSP) and carbon anhydrases (CA), Calvin Cycle (CC) functioning, various antioxidants (including DMSP, superoxide dismutases (SODs) and alternative oxidases (AOXs) and peroxidases) and ultimately programmed cell death (PCD). Host systems express several of the same, as well as additional, constituents (see main text) including electron consumers (CoQ) and chromophores, and factors such as HIF (Hypoxia Inducible Factor). Evidence is largely

derived from highly targeted reductionist studies to provide the scaffold for this conceptual network. However, systems-based metabolic maps will be required to fully establish network wiring and functioning and how it determines bleaching outcomes.

**Figure 2.** Conceptual environmental network regulating coral optimum metabolic performance – and hence coral bleaching phenotypes. Whilst high temperatures are the primary cause of mass bleaching, other environmental factors that are central to coral metabolic optimization – notably availability of light, O<sub>2</sub> (and so Biological Oxygen Demand, BOD), CO<sub>2</sub>, salinity and (organic and inorganic) nutrient availability – can either induce bleaching in their own right, but also interact with other factors to regulate the net bleaching outcome (extent or severity) – see main text. Importantly, research from the last thirsty years has shown that all of these factors regulate the severity with which heat stress drives mass bleaching outcomes. For example, some of these factors can cause dampening (e.g. cyclone cooling, reduced light) or exacerbate (low salinity, high light) heat stress. Most factors – and hence the effect size – likely operate non-linearly such that they may in fact provide enhanced tolerance under low dose, but susceptibility under higher dose (e.g. nutrients, see main text). Currently evaluating how bleaching outcomes reflect the operation of this entire network is limited by lack of environmental data to dial in-or-out factors but also their relative dose-dependencies over time. Some factors are exclusively driven by broad-scale climate change (warming, acidification), some by local-scale industry agriculture and urbanization (e.g. eutrophication, “pollutants” such as \*mining waste, herbicides etc.), and some by both climate change and local impacts (e.g. deoxygenation). Reducing emissions that drive climate change is the primary solution to tackling heat stress-induced bleaching, but clearly social adaptation and mitigation programs that tackle factors inherent

to both climate change and local impacts are also likely to have a strong effect in reducing bleaching severity over time.



Figure 1

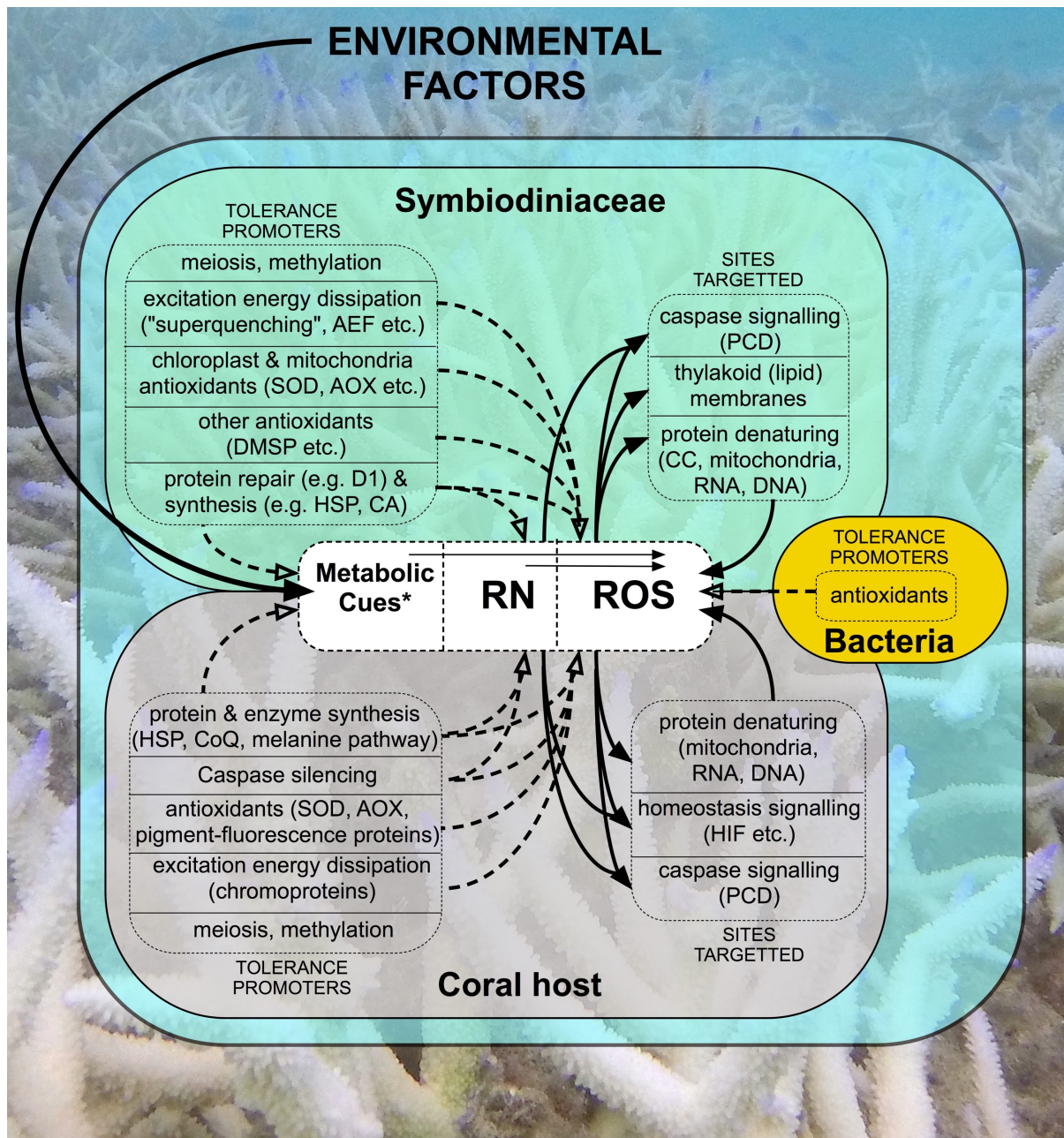


Figure 2

