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Symbiotic dinoflagellate functional diversity mediates corals survival under ecological crisis

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Abstract:	<p>Coral reefs have entered an era of "ecological crisis" as climate change drives catastrophic reef loss worldwide. Coral growth and stress susceptibility are regulated by their endosymbiotic dinoflagellates (genus Symbiodinium). Phylogenetic diversity of Symbiodinium frequently corresponds with patterns of coral health and survival, but knowledge of functional diversity is ultimately required to reconcile broader ecological success over space and time. Here we explore functional traits underpinning the complex biology of Symbiodinium that spans free-living alga to coral endosymbiont. In doing so, we propose a mechanistic framework integrating the primary traits of resource acquisition and utilisation as a means to explain Symbiodinium functional diversity, and resolve the role of Symbiodinium in driving the stability of coral reefs under an uncertain future.</p>

1 Original Submission: Opinion

2 **Symbiotic dinoflagellate functional diversity mediates corals survival**
3 **under ecological crisis**

4

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11 See associated file “TREE perspective_outstanding Qs_Suggett.doc”

1 **Abstract**

2 **Coral reefs have entered an era of “ecological crisis” as climate change drives**
3 **catastrophic reef loss worldwide. Coral growth and stress susceptibility are**
4 **regulated by their endosymbiotic dinoflagellates (genus *Symbiodinium*).**
5 **Phylogenetic diversity of *Symbiodinium* frequently corresponds with patterns of**
6 **coral health and survival, but knowledge of functional diversity is ultimately**
7 **required to reconcile broader ecological success over space and time. Here we**
8 **explore functional traits underpinning the complex biology of *Symbiodinium* that**
9 **spans free-living alga to coral endosymbiont. In doing so, we propose a**
10 **mechanistic framework integrating the primary traits of resource acquisition**
11 **and utilisation as a means to explain *Symbiodinium* functional diversity, and**
12 **resolve the role of *Symbiodinium* in driving the stability of coral reefs under an**
13 **uncertain future.**

14

15 **Global deterioration of reefs through coral bleaching**

16 Coral reefs have become a global ecological casualty of the Anthropocene Epoch.
17 Ecosystem services provided by coral reefs sustain nearly 10% of all people on Earth
18 and support billion dollar industries in tourism and fisheries [1]. However, coral reefs
19 worldwide have moved into an era of “ecological crisis” from accelerating over-
20 exploitation and persistent anthropogenic threats. Elevated seawater temperature from
21 climate change poses the greatest threat, driving mass coral bleaching (see Glossary)
22 and associated mortality across entire regions with increasing frequency and intensity
23 [2].

24

1 The ecological foundation of coral reefs rests on the symbiosis between reef-building
2 corals and dinoflagellate microalgae (“zooxanthellae”) of the genus *Symbiodinium*
3 (Dinophyceae, Suessiales). When surface seawater temperature (SST) exceeds the
4 long-term maximum monthly mean for extended durations [3] this symbiosis
5 disassociates leading to rapid loss of *Symbiodinium* cells and/or their pigmentation.
6 Bleaching is defined by the conspicuous whitening of the coral tissue [4], and whilst
7 there is a clear hierarchy of bleaching susceptibility among coral species [5] (e.g., Fig.
8 1), the broad scale impacts of elevated SST on individual coral colonies are modified
9 by a variety of physical and biological processes, including inherent properties of the
10 coral host and *Symbiodinium* [6, 7]. Together these processes result in complex
11 bleaching mosaics across reefs with distinct inter- and intra-specific responses (Fig. 1)
12 that modify bleaching thresholds and hence the impact of heating. Consequently,
13 mass bleaching manifests when ecologically dominant coral-*Symbiodinium*
14 associations are exposed to temperatures above their thermal thresholds [2, 5] (Fig. 1).
15
16 Heat stress induced coral bleaching characterises continual progression of the
17 symbiosis disassociation that is governed by a variety of host and/or *Symbiodinium*
18 responses (Fig. 1), but distilling this process into a generalised response for
19 *Symbiodinium* is still particularly unresolved (Box 1). Unlike in higher plants where
20 thermal stress primarily affects RuBisCO activase [8], the cellular target broadly
21 underpinning *Symbiodinium* thermal stress susceptibility is still unknown. Various
22 putative sites, including, light harvesting complexes, the reaction centre complex of
23 photosystem II, thylakoid membranes, RuBisCO and carbon concentrating
24 mechanisms (CCMs), have all been described as targets of heat stress [9-12],
25 implying broad functional diversity with which cellular networks have evolved to

1 govern stress susceptibility across the genus [13]. However, potentially unifying traits
2 that govern stress tolerance have still not been identified (Box 1), thereby highlighting
3 that second-order traits governing stress tolerance may simply be poor metrics to
4 represent the complex physiologies ultimately regulating broad ecological success.
5 Instead we propose functional diversity underpinning stress susceptibility should be
6 based on the key first-order traits that govern *Symbiodinium* metabolic functioning,
7 and thus the growth and performance of their coral hosts, under both optimum and
8 sub-optimum environmental conditions.

9

10 **Ecosystem stability from *Symbiodinium* diversity**

11 Molecular level markers have established exceptional phylogenetic diversity inherent
12 within the genus *Symbiodinium* (Box 2), which plays a major role in whether and how
13 coral reef ecosystems respond to environmental perturbations [26]. Molecular
14 ecological-based studies have now repeatedly demonstrated that viability of the entire
15 coral symbiosis over space and time [14, 27-29] often corresponds with the species
16 (or genetic variant) of *Symbiodinium* present. Similarly, corals populating relatively
17 unfavourable environments, such as hot-acidic lagoons [36] or hot-saline catchments
18 [31], typically associate with specific *Symbiodinium* taxa (Box 2). Continued
19 improvements to molecular tools have therefore unquestionably established a central
20 role for *Symbiodinium* diversity in shaping environmental thresholds for coral
21 productivity and ultimately reef growth.

22

23 Basic evolutionary theory requires that the maintenance of phylogenetic diversity
24 must be driven by functional differences in *Symbiodinium*. However, we now lag far
25 behind molecular ecology with any comprehensive understanding of *Symbiodinium*

1 primary physiological attributes that determine coral ecological success given the
2 alga's immense phylogenetic diversity. This is clearly problematic where a change (or
3 maintenance) in function does not reflect a parallel change to phylogenetic diversity.
4 Notably, convergent evolution across bioregions such as the Caribbean (dominated by
5 clades A, B) versus Indo-Pacific (dominated by clades C, D), to common
6 environmental histories selecting for the same functional responses, e.g. high versus
7 low light "ecotypes" [37] that are genetically distinct. Conversely, divergent evolution
8 due to local scale environmental differences select amongst closely related genotypes
9 and/or populations. [33-34]. The net outcome is that clades, species and even
10 genotypes differ in their functional responses to changes in key resources, such as
11 light [37] and CO₂ [38], but also temperature stress [39]. Phylogeny thus cannot
12 provide an exclusive currency with which to resolve *Symbiodinium* diversity with
13 ecological function.

14

15 Disciplines ranging from oceanography [40-41] to plant ecology [42] have overcome
16 such difficulties linking diversity to ecological functioning, by turning to the inherent
17 traits ("emergent properties" of individual organisms) that ultimately govern the
18 processes defining ecosystem health. Functional traits provide a standardised measure
19 of the biogeochemical role organisms play, e.g. photosynthetic rate or nutrient
20 turnover, but also capture fundamental trade-offs with fitness such as investing energy
21 into cellular maintenance versus growth or nutritional mode [40-43]. Functional traits
22 thus define the ecological success of species, and hence overcome the uncertainties
23 associated with phylogenetic resolution and how it is applied to reconcile ecological
24 success. The central concept of functional diversity is not new to coral ecology, and
25 has in fact been recently considered a likely key operational unit driving ecological

1 success of corals [44] and coral-*Symbiodinium* associations [45]. Coral reef
2 management is increasingly turning to knowledge of key traits that regulate (or are
3 indicative of) coral health for innovative management practices [46], whilst state-of-
4 the-art ecological models that can evaluate winners and losers under complex
5 environmental conditions rely on knowledge of quantifiable traits governing
6 competitive ability [43, 47]. However, fundamentally, the ‘choice’ of trait(s) that best
7 defines *Symbiodinium* functional diversity still remains largely unexplored.

8

9 ***Symbiodinium* spp. fitness traits and trade-offs**

10 Understanding the functional roles that underpin the ecological success of
11 *Symbiodinium* spp. within the holobiont landscape (“what makes a good
12 endosymbiont”?) demands knowledge of resource acquisition and utilisation. Algal
13 [41] and plant [42] trait-based models commonly rest on end-to-end tracking of
14 resources that govern growth and cellular maintenance, and thus provide a logical
15 conceptual framework. *Symbiodinium* spp. genetic variants have clearly adapted to
16 thrive across a broad range of habitats and host associations, where resource
17 availability will differ (Fig. 2). Such diversity of ecological niche exploitation and
18 optimisation would suggest major selection pressure for trade-offs amongst key traits
19 [43, 47]; for example, broad ecological success of phytoplankton can generally be
20 explained via an evolved continuum of “r vs k” strategies [48, 49], whereby cell size
21 operates as a “master trait” governing allometric scaling rules for light harvesting [47]
22 and inorganic nutrient assimilation [43, 50]. *Symbiodinium* spp. genetic variants in
23 fact exist across a cell size continuum, albeit in a relatively narrow range (ca. 7-
24 14µm), that appears to explain variation in light harvesting but not utilisation

1 capability [32, 37]; however, whether this central principle similarly applies to
2 inorganic nutrient acquisition is as yet unexplored.

3

4 Dinoflagellates have particularly acquired a broad spectrum of physiological and life
5 history traits that have enabled ecological diversification beyond boundaries set by
6 allometric scaling rules (“dirty tricks”, *sensu* [51]). An array of strategies associated
7 with light harvesting and photoprotection [52-53] have been relatively well described
8 for *Symbiodinium* spp.. However, partitioning *Symbiodinium* spp. genetic variants
9 according to differences in light harvesting and utilisation actually results in few
10 functional groups [13, 37] suggesting trade-offs associated with nutrient acquisition
11 and allocation strategies may in fact be pivotal in explaining their diverse niche
12 exploitation [54] (Fig. 2). Such strategies in other microalgae include plasticity of: (i)
13 the number of inorganic nutrient uptake (“porter”) sites [50, 55], which in the case of
14 inorganic carbon is further complicated by the nature of CCMs and RuBisCO affinity
15 (including *Symbiodinium* spp., [38]); (ii) minimum cellular requirements for different
16 inorganic macro and micro nutrients [56], reflecting both pool size (active and stored)
17 and turnover of key constituents that support cellular growth vs maintenance; and (iii)
18 supplementing cellular energy (ATP) production through heterotrophy. *Symbiodinium*
19 spp. are notably active mixotrophs that can supplement their phototrophic metabolism
20 by feeding on bacteria [57] and simple sugars [58].

21

22 Accounting for these various factors associated with resource acquisition and
23 utilisation introduces immense functional complexity, but it is possible to initially
24 distil this complexity to several first-order measurable traits, as commonly employed
25 for Dynamic Energy Budget (DEB) modelling [59]; specifically, nutrient uptake

1 kinetics, and cellular nutrient content relative to growth rate and cell size (see Fig. 2),
2 which together describe nutrient competitive ability [43]. Algae can preferentially
3 trade-off these resources into opportunistic growth versus persistent maintenance (a
4 classical view of *r* vs *k* selection; e.g. [42]); however, *Symbiodinium*, as with many
5 other dinoflagellates [20], can potentially short-circuit this trade-off through
6 additional secondary traits that likely disproportionately alter their competitive fitness.
7 Examples of such secondary traits include the extent to which fixed inorganic
8 nutrients are either excreted as dissolved organics [60], including by pathways such as
9 photorespiration that effectively aid photoprotection, or stored as particulate organics
10 for mobilisation during transient resource limitation [55-56]. Whilst differences in the
11 biochemical foundation for cellular fitness can be established from knowledge of
12 cellular nutrient (elemental) stoichiometry [56] and hence first-order traits, allocation
13 to specific constituents that enhance fitness are arguably secondary traits of interest.
14 For example, *Symbiodinium* spp. tolerance to stressors that promote bleaching is
15 enhanced by increasing protein pools that dissipate reactive oxygen species, ROS
16 (Box 1), but also through production of biogenic volatile signalling molecules [20].

17

18 **Metabolic coupling of coral-*Symbiodinium* associations**

19 Functional traits of interest need to span the complex life history dynamics of
20 *Symbiodinium*, where environmental constraints on fitness posed by life in symbiosis
21 are very different from those for free-living algal cells. A defining characteristic to
22 consider initially is the degree of specificity between certain *Symbiodinium* species
23 and their coral hosts, as well as mode of symbiont acquisition (vertical vs horizontal
24 transmission). Most coral species as adults associate with a single *Symbiodinium* type
25 (or share a few closely related types) [26], although some exceptional coral species

1 may host as many as 5–7 distinct types, as co-dominant [61] or rare [62] populations.
2 Consequently, genetically unique *Symbiodinium* populations may fluctuate in certain
3 coral species or persist across others [26]. Even so, types that contribute minimally to
4 the total population pool may ultimately yield a low net metabolic contribution to
5 their host [63]. Coral species that do harbour multiple *Symbiodinium* types in
6 abundance within a single colony appear to reflect complex algal-derived niche
7 partitioning (e.g., photoacclimation to different light levels) [62]. Similarly, for coral
8 species with shifts in dominant *Symbiodinium* type, ‘shuffling’ is best described in the
9 context of environmental history, e.g. the thermal trends driving bleaching and
10 subsequent recovery [54, 64-65], or complex multivariate interactions of several
11 physical-chemical (temperature, light, nutrient availability) and biological factors
12 acting in tandem [66] that are rarely fully characterised. Unique *Symbiodinium*
13 populations, especially within horizontally transmitted systems, may further represent
14 true localized adaptive radiations to specific *in hospite* environmental conditions [26,
15 31, 34]. Thus trait-based characterisation of *Symbiodinium* functional performance is
16 equally appropriate to best describe their realised niche space when *in hospite* as for
17 cells that are free-living.

18

19 Metabolic coupling within the coral-*Symbiodinium* relationship is exceptionally
20 complex and likely extends further to the milieu of constituents representing the true
21 holobiont (i.e., bacteria, archaea, fungi and viruses) [67]. Historically, efforts to
22 understand this coupling have focussed on photosynthetically derived carbon
23 translocation from *Symbiodinium* to coral, in the context of host 'control' over algal
24 populations via nitrogen and metabolite (“host release factor”) exchange (see [68] for
25 an extensive review; [69]) (Fig. 2). Much of this work has originated from other

1 symbioses (e.g., *Hydra* and the green alga *Chlorella* sp. or in anemone-*Symbiodinium*
2 systems) but provides important evidence for host-controlled nitrogen limitation as a
3 source of slower algal mitotic division [68]. First principles would suggest N-
4 limitation to cause an imbalance in the carbon-nitrogen ratio (and hence C:N:P [56])
5 and in turn reduced symbiont growth yet continued translocation of photosynthetically
6 fixed carbon [69]. However, exposure to inorganic nutrient supplements intriguingly
7 leads to a rebalance in symbiont C:N ratios toward nutrient sufficiency but sustained
8 algal growth arrest [70-71]. External eutrophication events can drive elevated
9 *Symbiodinium* N:P ratios as a result of direct inorganic N stimulation of the alga [71]
10 or fuelling the corals' nitrogen fixing bacterial community via indirect DOC
11 enrichment [72]. Such N enrichment drives P-starvation (higher N:P) to result in
12 significant *Symbiodinium* photoinhibition that exacerbates thermally-induced coral
13 bleaching [71]. Conversely, host feeding post "starvation" re-establishes
14 *Symbiodinium* nutrient quotas and algal growth [70] and substantially ameliorates
15 photoinhibition and coral bleaching during thermal stress [73].

16

17 Existing evidence of changes to *Symbiodinium* physiological performance from
18 altered nutrient availability would suggest that cellular nutrient content relative to cell
19 size could provide a first-order measurable trait to consider *Symbiodinium* functional
20 diversity and competitive ability *in hospite*, and hence importantly a direct
21 comparison currency with cells that are free-living (Fig. 2). Bulk elemental
22 stoichiometries could not only encapsulate how growth environment regulates
23 resource availability relative to inherent requirements across different *Symbiodinium*,
24 but also overcome the challenge in balancing symbiont type versus population size
25 (cell size and number of a single genetic variant) to fulfil overall translocation

1 demands [74-75]. Corals that maintain flexibility in association with more than one
2 *Symbiodinium* type [Kemp], would require different population sizes to offset any
3 differences in nutrient uptake and/or release across types to ensure translocation
4 output is sustained.

5
6 Host corals regulate both light [4, 76] and CO₂ (dissolved inorganic carbon, DIC) [77]
7 availability for *Symbiodinium* photosynthesis. In fact, the host may regulate DIC
8 delivery more heavily than N or P. When *Symbiodinium* are present, numerous
9 symbiotic anthozoans show substantial transcriptional upregulation for carbonic
10 anhydrase (CA), the enzyme responsible for interconverting CO₂ and HCO₃⁻ and
11 providing DIC for photosynthesis as well as calcification. Recent work has confirmed
12 both external as well as internal CA activity in several corals [78-79], and corals
13 harness a sharp proton gradient to significantly lower the pH (down to ~ 4.0)
14 surrounding the symbiont sitting within the host-derived membrane, or
15 “symbiosome”, via a vacuolar H⁺-ATPase [77]. Hence substantial energetic
16 investment by the host supports the DIC demands of photosynthesis [79]. Whilst the
17 dynamics describing the light dependency of *Symbiodinium* photosynthesis *in hospite*
18 are generally well described [76], those describing DIC (indeed other dissolved
19 inorganic nutrients, e.g. N, P) dependency are not; clearly these therefore also
20 represent promising first order traits with which to define *Symbiodinium* functional
21 performance and how it alters over space and time (Fig. 2).

22
23 Fundamentally, we have sparse knowledge regarding cellular nutrient quotas and
24 uptake kinetics for *Symbiodinium*; however, as has been repeatedly demonstrated
25 across other microalgae [40, 43], these traits inherently modulate the physiological

1 and competitive response of cells. Clearly this represents an area ripe to explore the
2 ever-widening gap in knowledge between diversity and ecological success for
3 *Symbiodinium*, which *in hospite* likely drive metabolic trade-offs for the host coral.
4 Inherent nutrient supply, along with *in hospite* light and thermal conditions, may be
5 key attributes in determining the interspecific competitive outcome among different
6 yet compatible symbionts. Thus, “shuffling” of compatible symbionts may have less
7 to do with specific host ‘control’ but rather reflect an outcome of shifting host
8 metabolic processes [67], and hence a function of trade-offs amongst first-order algal
9 traits (e.g., cell size, macro and micro nutrient/elemental quotas, and strategies for
10 light-temperature acclimation) [54]. Variation in the first-order traits that determine
11 the cellular energy budget drives broad niche exploitation [59] and hence the scope
12 for functional diversity across *Symbiodinium* genetic variants. However, the exact
13 first-order trait profile will determine the ecological success of any given symbiont;
14 specifically: how, when, and to what extent *Symbiodinium*-coral associations are
15 sustained and the capacity for *Symbiodinium* to thrive ex-hospite. In focussing on
16 second-order traits of interest e.g. ROS production (Box 1), for some time as key
17 factors influencing *Symbiodinium*-coral fitness, we have in fact overlooked the first-
18 order traits that functionally connect *Symbiodinium* to their surrounding environments
19 (Fig. 2).

20

21 **Concluding Remarks**

22 Understanding how *Symbiodinium* spp. are optimised to function across different host
23 corals and reef environments is more critical than ever as reefs face global “ecological
24 crisis”. Functional diversity theoretically mediates the response of *Symbiodinium* to
25 changing environmental conditions, and provides a means to reconcile (and

1 complement) the growing wealth of knowledge aligning *Symbiodinium* phylogenetic
2 diversity with coral ecological success. In evaluating key traits that govern cellular
3 growth and physiology, we have proposed a mechanistic physiological framework
4 (Fig. 2) that directly complements the rapid uptake of molecular-based descriptors of
5 both *Symbiodinium* phylogeny and function. Trait-based models provide a means to
6 evaluate this physiological framework against ecological success but only through
7 measuring the key first-order traits. We therefore call for renewed focus into resource
8 acquisition and utilisation as a fundamental regulator of competitive ability (see
9 Outstanding Questions), as a first step to resolve *Symbiodinium* spp. niche boundaries
10 across habitats and specific host-symbiont associations, and hence the role of
11 *Symbiodinium* in driving productive and diverse coral reefs as they enter an uncertain
12 future.

13

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4

1 **Text Box 1: *Symbiodinium* as cellular sources of coral stress**

2 Coral host-specific responses that operate to effectively increase thermal tolerance [7]
3 have become increasingly well described; notably reduced oxidative stress via
4 mitochondrial excitation pressure that produces reactive oxygen species (ROS) (e.g.
5 fluorescent proteins, tentacular retraction [15]), increased production of ROS
6 detoxifying proteins and organelle stability (e.g. mitochondria [16]) or silencing of
7 ROS-triggered caspases that in turn induce apoptosis [17]. ROS is produced by the
8 coral's microbial community, in particular by *Symbiodinium* photosynthetic
9 dysfunction and associated bacterial metabolism, as well as host mitochondria [18].
10 However, how physiological dysfunction initiates and progresses to drive ROS
11 emissions remains unresolved (but see [19]); in the case of *Symbiodinium* this has
12 reflected challenges in utilising genomics to unlock the inherent cellular networks and
13 how they are regulated.

14

15 Dinoflagellates as a group have a variety of unique characteristics [20], including
16 permanently condensed chromosomes, extremely large genomes and a significantly
17 higher reliance on post-translational regulation, in contrast to transcriptional
18 regulation, compared to other organisms. Therefore, while the magnitude of gene
19 expression changes is generally less than 2-fold, up to 30% of the transcriptome can
20 alter [21, 22], making it difficult to identify specific responses at this scale. Even so,
21 such tools have begun to highlight parallels with how the host responds to heat stress;
22 notably, a major re-organisation of the ROS antioxidant network in heat tolerant
23 *Symbiodinium* [21-23], which clearly reflects simultaneous physiological observations
24 of reduced ROS emissions for more heat tolerant *Symbiodinium* [12, 13, 21].
25 Enhancing ROS detoxification capability in fact appears a key mechanism with which

1 heat tolerance can be acquired trans-generationally in *Symbiodinium* populations [24].
2 Such responses may thus be core and hence impose cellular trade-offs to processes
3 that are secondary in affording thermal tolerance; for example, under stress clear
4 upregulation in heat shock proteins (HSPs) is noted for the coral host (>32 fold)
5 whereas *Symbiodinium* may [25] or may not [23] downregulate HSPs. Therefore,
6 whilst the “source” of stress is becoming well documented, understanding how this is
7 driven by (or feeds back to) a unifying target regulating *Symbiodinium* cellular
8 dysfunction remains unknown [9-13].

1 **Text Box 2: Species diversity amongst the genus *Symbiodinium***

2 Molecular tools continue to unlock the immense phylogenetic diversity inherent to the
3 genus *Symbiodinium* [26-29]. At the broadest scale *Symbiodinium* spp. is divided into
4 9 distinct evolutionary lineages (i.e. clades, A-I) via divergence of the small
5 ribosomal subunit RNA (SSU). More variable DNA regions, including the internal
6 transcribed spacer regions (ITS), chloroplast large subunit (cp23S) and cytochrome
7 oxidase b (cob) have subsequently resolved immense subcladal diversity [27]
8 typically classified alpha-numerically (e.g. C1, C3z). Of these, ITS2 has been most
9 widely adopted, but requires consideration alongside additional rapidly evolving
10 regions (e.g. psbA^{ncr}) to resolve evolutionarily distinct species (multilocus barcoding,
11 [30-31]). Integration of barcoding-based phylogeny with fundamental biological (e.g.
12 morphology, physiology) and ecological (e.g. host specificity) patterns has provided
13 the core framework for novel *Symbiodinium* species descriptions [31-33]. Molecular
14 platforms have recently transitioned to high throughput pyrosequencing for barcode
15 retrieval, and added further depth to phylogenetic differentiation through more
16 accurate detection of low-abundance background *Symbiodinium* [28-29, 34]. Here,
17 phylogeny is considered within an operational taxonomic unit (OTU) framework to
18 identify ecologically discrete entities [29, 34], including the role of intra-genomic
19 variability, to resolve taxonomic sub-groups [35].

20

21 Analysis of genetic recombination has become an important complimentary tool to
22 examine *Symbiodinium* species level diversity [36]. Using the biological species
23 concept, populations that exchange alleles through sexual recombination are the same
24 species, and hence population genetics based on allele frequency similarity across
25 multiple loci delimit species over space and time. Such delimitation of species based

1 on this ‘incompatible breeding’ may be complicated where populations frequently
2 reproduce asexually but only very rarely sexually and/or conspecific populations that
3 previously diverged in isolation of one another become mixed [34]. Even so, the
4 approach has proved powerful for establishing novel *Symbiodinium* species
5 boundaries that persist over broad geographic regions [26].

6

7 Molecular based technical advances thus continue to highlight immense phylogenetic
8 variation and speciation. ITS2 variation alone suggests existence of 10s-100s of
9 *Symbiodinium* species, but this is likely an underestimate. Multi-locus and high
10 throughput techniques would suggest 100s-1000s of putative species, which are
11 particularly changing our ecological view of *Symbiodinium* ITS2 types previously
12 considered to be widespread generalist species, e.g. ITS2 type C3 harboured by many
13 highly stress sensitive coral species of *Acropora* [31, 35].

14

1 **Glossary Box**

2

3 **Coral bleaching:** Process with which corals pale (whiten) from loss of *Symbiodinium*
4 cells and/or pigmentation from host coral tissues.

5

6 **Fitness:** Capacity of an organism to pass its genes to successive generations, as
7 determined by the ability to survive and reproduce by inherent competitive traits.

8

9 **Photosystem II (PSII):** Protein complex that generates electrons for photosynthesis
10 by oxidizing water in algae. Dysfunction of PSII activity is a common assay of heat
11 stress sensitivity in *Symbiodinium*.

12

13 **Reactive Oxygen Species (ROS):** Chemically active molecules containing oxygen
14 (“free radicals”) produced via mitochondria and/or chloroplast metabolic pathways;
15 notably, singlet oxygen, superoxide, and hydrogen peroxide.

16

17 **RuBisCo:** Ribulose-1,5-bisphosphate carboxylase/oxygenase is the enzyme involved
18 in the first step of CO₂ fixation, and considered the most abundant enzyme on Earth.
19 It is modulated by the catalytic chaperone RuBisCo activase.

20

21 **Secondary metabolites:** Organic compounds that are not directly required for growth
22 and reproduction; for example, toxins and volatiles that negatively affect fitness of
23 competitors.

24

1 **Traits:** Measureable characteristics of an organism that are inherited or
2 environmentally controlled. Can encompass cellular, physiological, morphological
3 and life history characteristics.

4

5 **First- vs second-order traits:** Traits that form the foundations for functioning are
6 considered “central” (first-order) whereas other traits that arise from operation of
7 first-order traits (or only under certain environmental conditions) are considered
8 second-order.

9

10 **Vertical vs horizontal transmission:** In corals the process where larvae retain
11 *Symbiodinium* cells from parent colonies (vertical transmission or “closed symbiosis”)
12 versus uptake from the surrounding environment (horizontal transmission or “open
13 symbiosis”).

14

15

1 **Figure Legends**

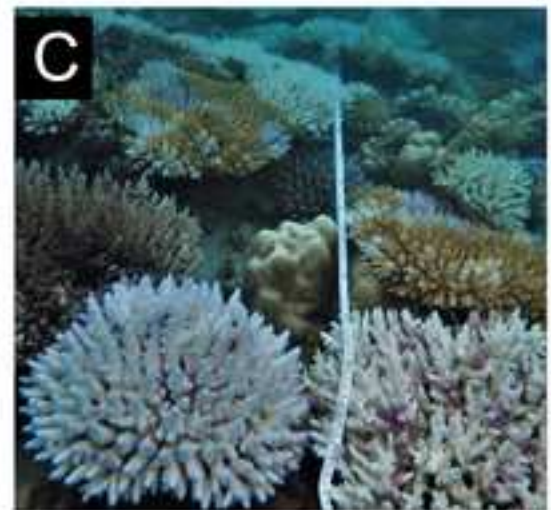
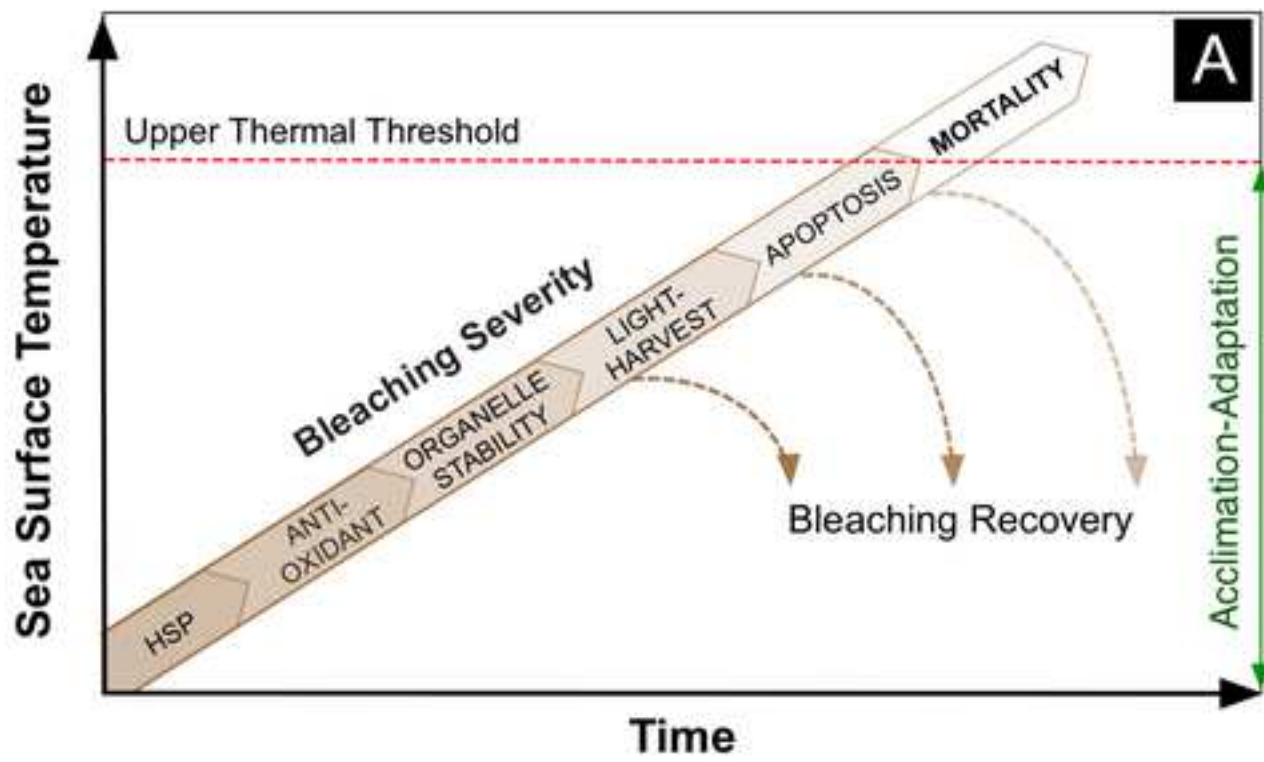
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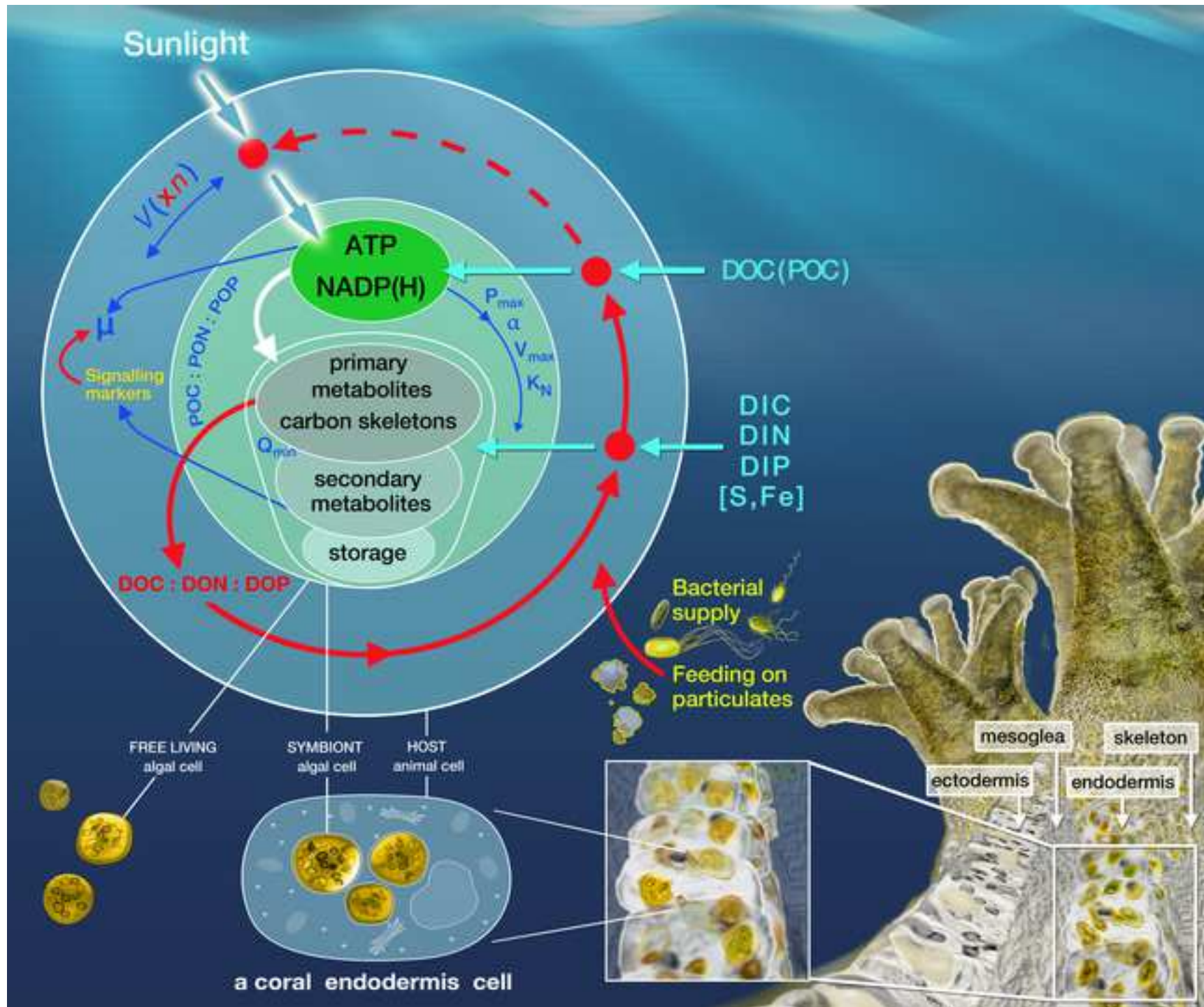
3 **Figure 1. Generalised scheme of coral-*Symbiodinium* functional trait responses to**
4 **thermal stress-induced bleaching.** (A) Increased temperatures over-time induce a
5 cascade of responses (Box 1) as the coral-*Symbiodinium* association is pushed
6 towards the upper thermal thresholds for symbiosis viability (“point of no return”).
7 These responses are either common to both coral and symbiont (upregulation of ROS
8 detoxification networks, reduction to light harvesting through increased host
9 fluorescence protein expression or decreased symbiont light harvesting complex
10 (LHC) pigments, and induction of apoptosis), or specific to coral or symbiont
11 (preferential alteration of heat shock proteins, HSPs; mitochondrial versus thylakoid
12 stabilisation for host and symbiont, respectively). Sustained heating at or beyond the
13 threshold causes mortality or requires acclimation or adaptation by selecting for
14 upregulation of the various traits driving heat stress tolerance (in which case the upper
15 threshold temperature alters by changing how traits providing thermal tolerance are
16 expressed). Cooling can initiate recovery. How these processes operate across host-
17 *Symbiodinium* associations in reef systems is highly dynamic and can manifest as
18 different severities of bleaching at intra-species (e.g. (B) *Porites lutea* colonies) [34]
19 and inter-species (e.g. (C) Alternate species within the same genus of *Acropora*; (D)
20 Alternate genera, bleaching sensitive plating *Montipora* sp. vs species of *Acropora*)
21 [2, 5] levels within any given reef area. Mono-specific host-*Symbiodinium* sp.
22 associations manifest as mass bleaching (e.g. (E) *Acropora muricata* beds hosting
23 *Symbiodinium* ITS2 type C3 in the Seychelles). Photographs (B-E) are courtesy of
24 Emma Camp, University of Technology Sydney.

25

1 **Figure 2. Generalised scheme of resource acquisition and utilisation**
2 **underpinning *Symbiodinium* competitive fitness.** External light and dissolved
3 inorganic (DIC, DIN, DIP, S, Fe, etc.) and/or organic (POC, DOC) nutrient uptake
4 drive cellular functioning, as well as determine the competitive outcome of
5 phytoplankton in general [48]. Generation of energy (ATP) and reductant (NADP(H))
6 in *Symbiodinium* cell chloroplasts and mitochondria sustains active uptake and
7 assimilation of nutrients into organic compounds. In turn these compounds are stored,
8 drive formation of primary metabolites (e.g. formation of key carbon “skeletons”;
9 lipids, carbohydrates and proteins) and secondary metabolites that may also act in
10 signalling. According to theory developed for phytoplankton [40, 43] trade-offs in
11 how these resources are acquired and utilised can explain ecological competitiveness,
12 and generally accounted for using several key terms, highlighted in blue: Extent of
13 light absorption (α), maximum photosynthesis rate (P^{\max}); the maximum uptake rate
14 (V_{\max}), half saturation constant (K_N), and minimum quota (Q_{\min}) for any one nutrient;
15 quantity and hence stoichiometry of cellular particulate (POC:PON:POP:etc...), and
16 excreted dissolved (DOC:DON:DOP:etc...) nutrients; as well as cell volume (V).
17 Together these terms govern maintenance versus division, and hence the net
18 achievable growth rate (μ), to reflect first order traits of competitive fitness. Such
19 terms are governed by the growth environment and thus will be regulated when cells
20 are *in hospite* (indicated by red lines and arrows) as well as free-living: Host corals
21 also acquire external nutrients from both feeding and their broader microbial
22 associations. Hosts modify the inherent light field [15] for *Symbiodinium* and have
23 been suggested to excrete specific dissolved compounds [60] (signalling markers) that
24 control delivery of inorganic nutrients back to the symbiont, i.e. distinct metabolites
25 (“host release factors”, [68]). Again, the net outcome is regulation of the net

- 1 achievable growth (μ), but *in hospite* will be relative to the overall population size
- 2 required to meet host metabolic demands (*Symbiodinium* cell number, n). All
- 3 aforementioned processes play a central role in the trade-off between cellular
- 4 maintenance in the alga vs. the direct release of translocated material to the host coral.





Coral reef survival to ecological crisis through dinoflagellate functional diversity–

Suggett *et al.*

Highlights

Coral ecosystem health is strongly influenced by *Symbiodinium* diversity.

Ecological success of *Symbiodinium* cannot be resolved from phylogenetic diversity alone.

Traits describing resource acquisition and incorporation capture *Symbiodinium* functional diversity.

Symbiodinium species shifts reflect changing metabolic requirements of the host.

Functional diversity will determine the resilience of coral reefs to environmental change.

Coral reef survival to ecological crisis through dinoflagellate functional diversity–

Suggett *et al.*

Outstanding Questions

Can first-order traits (e.g. cellular uptake and allocation) alone explain niche breadth, *including* anomalous stress tolerance, or must they be considered alongside second order-traits (e.g. capacity to upregulate ROS detoxification pathways)?

How diverse are micro- (trace) relative to macro- (C, N, P, S) nutrient uptake and utilization properties in describing *Symbiodinium* ‘functional types’?

Does ecological resilience through “symbiont shuffling” reflect match/mis-match between changing host metabolic requirements and *Symbiodinium* consortia with alternate metabolic (nutrient uptake and allocation) profiles?

What is the extent of metabolic and resource trade-offs required to persist across alternate life history stages? Does *Symbiodinium* require “host resource surrogates” as a free-living alga (e.g. obligate associations with other microbes)?

How important are heterotrophic strategies for supporting *Symbiodinium* nutritional and/or metabolic requirements? Can *Symbiodinium* feed on host as well as microbial metabolites?

To what extent does functional diversity of nutrient strategy reflect evolutionary radiation (and/or potentially support phylogenetic re-constructions) of the genus *Symbiodinium*?



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