


Review

Nutrient Availability and Metabolism Affect the Stability of Coral–Symbiodiniaceae Symbioses

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Coral reefs rely upon the highly optimized coral–Symbiodiniaceae symbiosis, making them sensitive to environmental change and susceptible to anthropogenic stress. Coral bleaching is predominantly attributed to photo-oxidative stress, yet nutrient availability and metabolism underpin the stability of symbioses. Recent studies link symbiont proliferation under nutrient enrichment to bleaching; however, the interactions between nutrients and symbiotic stability are nuanced. Here, we demonstrate how bleaching is regulated by the forms and ratios of available nutrients and their impacts on autotrophic carbon metabolism, rather than algal symbiont growth. By extension, historical nutrient conditions mediate host–symbiont compatibility and bleaching tolerance over proximate and evolutionary timescales. Renewed investigations into the coral nutrient metabolism will be required to truly elucidate the cellular mechanisms leading to coral bleaching.

Coral Reefs under Anthropogenic Stress

Coral reef ecosystems are hotspots of biodiversity and productivity which provide vital and extensive ecosystem services [1–3]. However, these values of coral reefs are under threat due to global mass bleaching events triggered by ocean warming [4]. **Coral bleaching** (see [Glossary](#)) is a stress response to elevated heat and light levels, where corals lose their algal symbionts (**Symbiodiniaceae**) [5,6]. Corals acquire most of their energy through photosynthates translocated by the algal symbionts [7], and the loss of this energy source for long periods can result in starvation and mortality [5]. Bleaching mortality can lead to reductions in coral cover, species and genetic diversity, which shifts reefs away from a coral-dominated state and impedes ecosystem resilience [8,9]. Although some reefs remain resilient, and there exists potential to adapt to warming oceans through natural means [10] and human interventions [11], strong reductions in anthropogenic carbon emissions are ultimately required to ensure the persistence of coral reefs.

Coral reefs are also impacted by local stressors, which reduce **water quality** and have the potential to interact with warming to increase coral bleaching susceptibility [12]. Changes in land use adjacent to reefs can result in primary **nutrient enrichment** that may be further altered through biological and physical processes [12]; organisms across a range of trophic levels can secondarily modify the nutrient environment [12,13], and localized fishing results in the removal of significant nutrient subsidies from reefs [14]. Climate change also influences marine biogeochemistry at a global scale, where increased storm activity intensifies enrichment events through riverine flux and water column mixing [12,15,16]. In contrast, ocean warming increases water column stratification which reduces nutrient availability [12,17]. Synergistically, global and local drivers and subsequent biological processes not only impact nutrient levels on coral reefs but also change the forms and ratios of nutrients, making **nutrient limitation** possible [12]. Recent experiments suggest

Highlights

Mass coral bleaching is occurring at an unprecedented rate due to anthropogenic ocean warming, and it represents the greatest threat to coral reef ecosystems globally.

Coral bleaching is predominantly attributed to photo-oxidative stress under elevated temperature and light, but recent experiments have unveiled nutritional mechanisms that can regulate bleaching.

Bleaching may result when the coral–Symbiodiniaceae symbiosis shifts from a mutualistic to a parasitic relationship under thermal stress.

Nutrient availability, specifically the forms and ratios of nutrients such as nitrogen and phosphorus, mediates algal symbiont parasitism.

Stable metabolic compatibility between the coral host and algal symbiont can ameliorate bleaching and increase resilience to environmental stress.

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that nutrient limitation, rather than nutrient enrichment *per se*, lowers the temperature at which coral bleaching occurs [18–20].

This review therefore discusses and synthesizes the direct impacts of external nutrient availability on the health of tropical **scleractinian corals** and demonstrates how this, together with internal nutrient metabolism, underpins the thermal tolerance of the **coral holobiont**.

Maintenance and Breakdown of the Coral–Symbiodiniaceae Symbiosis

The nutritional interactions between corals and their algal symbionts permits the existence of coral reefs in oligotrophic waters [7]. Tight nutrient recycling within the symbiosis provides the algal symbionts with respiratory CO₂ and nitrogenous waste products, and in exchange the coral host receives photosynthetically fixed carbon [21]. Additionally, the algal symbionts efficiently assimilate dissolved inorganic nitrogen and phosphorus into the holobiont [13,22]. Corals also acquire nutrients through heterotrophic feeding [23] and their **microbiome** through translocation and digestion [24]. The relative modes of nutrient acquisition depend on the individual capabilities of each holobiont member, for example **nitrogen fixation** by **diazotrophs** may compensate for limited inorganic or heterotrophic nitrogen uptake [25,26], and heterotrophy may compensate for reduced autotrophic capabilities [23]. Metabolic compatibility between individual coral hosts and their algal symbiont communities likely underpins holobiont performance and their tolerance to environmental stress [27,28]. But when corals bleach, they are depleted of their major nutrient source and their chances of recovery are partly determined by their ability to restore algal symbiont autotrophy or compensate through heterotrophic nutrient acquisition [29–31]. Additionally, nutrient acquisition and loss through the microbiome changes when corals bleach [26,32–35]. While corals use heterotrophically acquired nutrients to help maintain and recover their algal symbiont populations [30,36], the relative contribution of inorganic nutrient sources to coral autotrophic recovery is not well understood.

At the cellular level, the contemporary and widely accepted understanding of coral bleaching is one triggered by temperature and light-induced photodamage to the algal symbionts, leading to **oxidative stress** in both partners [37]. However, recent studies have shown coral bleaching in the absence of heat, light, and/or oxidative stress [18,35,38–41], highlighting the existence of alternative pathways to coral bleaching (Box 1). Importantly, there is now mounting evidence for the role of nutritional mechanisms in the response of corals to thermal stress and the initiation of bleaching [18,25,38,42–47]. Therefore, the internal nutrient metabolism and external nutrient environment should be considered, in addition to **photo-oxidative stress**, when predicting the response of corals to thermal stress.

The role of nutrients in the early stages of coral bleaching has long been hypothesized [48], but it was Wooldridge [49] who first posited that temperature increases could shift the algal symbiont populations from mutualism to parasitism. At elevated temperatures, the relative contribution of the symbionts to the carbon metabolism of the symbiosis is hypothesized to decrease [49], due to reduced photosynthate translocation and/or increased host metabolism. Additionally, the symbiont's heat/light protection mechanisms, including **super-quenching**, could halt carbon fixation without oxidative stress [50]. Under these scenarios, the coral host is forced to catabolize its own carbon reserves to maintain CO₂ and **adenosine triphosphate (ATP)** delivery for symbiont photosynthesis. Once these stores diminish, photosynthetic dysfunction ensues and triggers coral bleaching through the photo-oxidative pathway [37,49–51]. **Carbon limitation** has often been reported in cnidarian–Symbiodiniaceae symbioses [52–59], and this carbon limitation model of bleaching is supported by recent empirical studies [30,36,42,43,45,47,50,60] and extends the photo-oxidative theory. Furthermore, external nutrient availability may also mediate coral bleaching susceptibility through these mechanisms [18,30,36,38,42,61]. Therefore, the

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Box 1. Coral Bleaching in the Absence of Photo-oxidative Stress

Coral bleaching is contemporarily understood to result from photo-oxidative damage to both corals hosts and their algal symbionts [37]. More specifically, increased temperatures render the algal symbionts susceptible to incoming light, resulting in photodamage and the production of **reactive oxygen species (ROS)** that can cause cellular damage to both host and symbiont tissues [37]. However, recent studies have shown that coral bleaching can also occur without the characteristic photo-oxidative stress response [35,38–40].

Tolletier *et al.* [39] observed that thermal bleaching of corals and the coral model *Aiptasia* can occur in the dark, independent of ROS. Bleaching was similar in nature to control organisms (kept under light), demonstrating that high temperatures can directly damage the photosystems of the algal symbionts [39]. Nielsen *et al.* [40] later found that bleaching independent of ROS can also occur under light. Although ROS were produced in the symbiont, they were not released to the host tissues and no attributable physiological effects were detected in either host or symbiont [40], corroborating field observations that coral superoxide production is unrelated to bleaching status [145]. Furthermore, corals can expel healthy symbiont populations during thermal stress [146–149], highlighting that bleaching does not require photo-oxidative stress and could instead result from a need to eject dividing symbionts [150].

Coral bleaching can also occur solely from the disruption of the coral nutrient metabolism [18,35,38,41]. Corals kept under phosphate limitation sustain only minimal symbiont communities, with corresponding reductions in host biomass [18,38,41]. Furthermore, increasing the severity of phosphate limitation by increasing environmental N:P ratios (nitrate enrichment) results in moderate photodamage [18,38]. This pathway to bleaching can also originate internally, for example when N:P ratios are skewed by increased microbial nitrogen fixation within the coral holobiont [35].

It is important to note that these examples are not mutually exclusive to the extensively characterized photo-oxidative mechanisms of bleaching [37]. Rather, they point to nutritional mechanisms of bleaching which exacerbate a later photo-oxidative response under heat and/or light stress [18,35,49].

nutritional status of corals, driven by external conditions and internal metabolism, can have a profound influence on bleaching susceptibility.

The Impacts of Nutrient Availability on Coral Health and Thermal Tolerance

The direct impacts of nutrient enrichment on coral holobiont physiology (Figure 1, Key Figure) were initially controversial since coral reefs exist in a wide range of nutrient environments and experimental studies failed to yield consistent results [62]. However, recent laboratory studies have clearly linked declines in coral holobiont health to specific nutrient sources and the ratios they occur in [12,23,63]. These studies have primarily focused on three dissolved inorganic nutrient forms present in reef waters (ammonium, nitrate, and phosphate) [12] and organic nutrients in the form of particulate food [23]. Ammonium (NH_4^+) is derived from metabolic processes of the coral host [13] and other reef organisms [14] and is the preferred inorganic nitrogen source of the algal symbionts [64]. In contrast, nitrate (NO_3^-) produced from anthropogenic sources is less favoured [64], perhaps because its utilization diverts electrons away from photosynthesis [61]. Phosphate (PO_4^{3-}) is supplied through a mixture of natural and anthropogenic sources [22].

Particulate food and moderate levels of ammonium and phosphate tend to benefit coral holobiont health (Figure 1B) and increase thermal tolerance [20,23,42,63,65], whereas nitrate negatively impacts the coral holobiont (Figure 1D) and reduces thermal tolerance unless accompanied by phosphorus [12,18,38,63]. Corals with larger algal symbiont populations due to enrichments of nitrogen (N) and phosphorus (P) are usually healthy [63], despite some evidence that dense populations can become parasitic (Figure 1C) [61,66,67] and reduce coral thermal tolerance [68–70]. Therefore, the effects of nutrient enrichment on the coral holobiont are mixed, but negative impacts are largely attributed to increased N:P ratios [12,63].

Symbiodiniaceae Growth Rates and Coral Thermal Tolerance

Worldridge [71] expanded the carbon limitation model of coral bleaching, suggesting that growing algal symbiont populations under nutrient and thermal stress become parasitic and induce

Glossary

Acclimation: the biochemical, epigenetic, and morphological processes by which a biological organism adjusts to maintain health following changes to its environment.

Adaptation: the evolutionary process by which a biological organism becomes better suited to live in its local environment.

Adenosine triphosphate (ATP): an organic chemical which provides energy to cellular processes.

Carbon limitation: the limitation of available carbon within the coral holobiont, brought about by parasitism of the algal symbionts. Carbon limitation can lead to coral bleaching.

Coral bleaching: the loss of the algal symbionts and/or their pigmentation from the coral holobiont.

Coral holobiont: the meta-organism composed of the symbiotic relationships between corals, their algal symbionts, and their associated microbiome (including bacteria, archaea, fungi, protists, and viruses).

Diazotrophs: bacteria and archaea that can fix atmospheric dinitrogen into more bioavailable forms, such as ammonium.

Dissolved organic carbon (DOC): organic carbon compounds, which dissolve in water. DOC includes sugars, which can stimulate microbial activity, for example, in corals.

Microbial dysbiosis: imbalance of the microbiome, often caused by environmental stress.

Microbiome: the assemblage of microorganisms and their genes in an environment, organism, or part of an organism. The coral holobiont is one example of an organismal microbiome.

Nitrogen fixation: the biological conversion of atmospheric nitrogen into ammonium.

Nutrient enrichment: the exogenous enrichment of one or more nutrients above regular concentrations through anthropogenic, biological, and/or physical processes.

Nutrient limitation: the exogenous reduction of one or more nutrients below regular concentrations through biological and/or physical processes. Additionally, imbalanced nutrient enrichment can result in nutrient limitation.

Oxidative stress: the overproduction of reactive oxygen species to a level

Key Figure

Impacts of Inorganic Nutrient Availability on Coral Autotrophic Carbon Metabolism

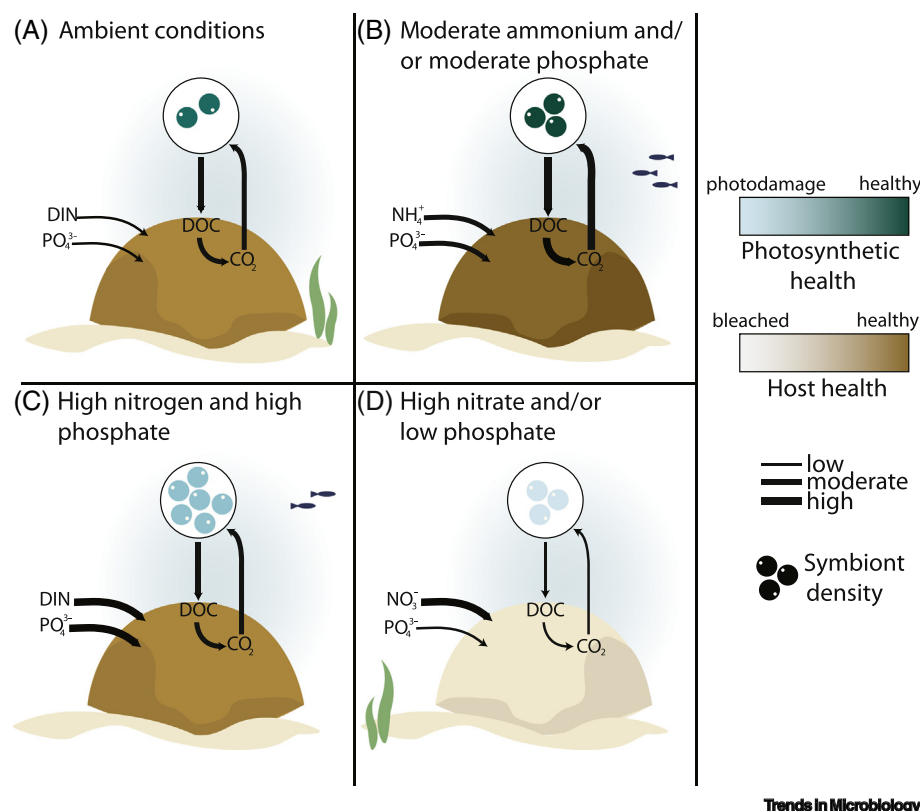


Figure 1. Carbon metabolism and the health of the coral-Symbiodiniaceae endosymbiosis under different inorganic nutrient scenarios. (A) Oligotrophic conditions constrain Symbiodiniaceae growth which stimulates carbon translocation to the host [61]. The translocation of photosynthates as dissolved organic carbon (DOC) facilitates the reverse translocation of inorganic carbon (CO_2) and is hypothesized to be integral to the stability of the symbiosis [49]. (B) Moderate enrichments of ammonium (NH_4^+) and/or phosphate (PO_4^{3-}) can increase Symbiodiniaceae abundance and promote photosynthetic health, enhancing total carbon translocation and coral health [42,61]. (C) High dissolved inorganic nitrogen (DIN) and phosphate enrichments stimulate rapid Symbiodiniaceae population growth, resulting in competition for resources, which lowers photosynthetic performance and carbon translocation per cell [61]. (D) Nitrate (NO_3^-) enrichment and/or phosphate limitation can damage photosynthesis which greatly reduces total carbon translocation and coral health [18,38,61]. Nutrient conditions which weaken the symbiosis (C,D) can be expected to act synergistically with thermal stress to further reduce translocation and induce bleaching [18,30,77]. Conversely, nutrient conditions which strengthen the symbiosis (B) may ameliorate reductions in translocation to increase coral thermal tolerance [42,65].

bleaching. Elevated temperatures can directly stimulate cell division (through increased metabolism) and the reductions in algal symbiont density during bleaching may free up resources, including inorganic nitrogen, for the remaining population to grow [13,31,43,72]. At the same time, the dividing algal symbiont populations may retain more photosynthates for their own growth [43,71], which could prevent the host from actively controlling the supply of nitrogen to the symbionts [13,73]. However, this hypothesis contradicts the finding that ammonium enlarges algal symbiont populations whilst also increasing thermal tolerance, whereas nitrate increases

which overwhelms the antioxidant capabilities of a biological organism.

Photo-oxidative stress: oxidative stress resulting from damage to photosynthesis.

Reactive oxygen species (ROS): chemically reactive molecules which contain oxygen and damage cellular components.

Scleractinian corals: stony corals, which build their polyps upon an aragonite skeleton and often form reef ecosystems.

Super-quenching: the diversion of electrons away from photosynthesis through reconfiguration of the photosynthetic membranes to avoid photo-oxidative stress.

Symbiodiniaceae: the family containing the algal symbionts of corals. The Symbiodiniaceae currently separate into 15 distinct lineages of which corals typically associate with 4 genera: *Symbiodinium*, *Brevium*, *Cladocopium*, and *Durudinium*.

Water quality: the chemical, physical, and biological characteristics of water. In the context of coral reefs, water quality is used to describe the concentrations of anthropogenic pollutants such as nutrients, sediments, and pesticides which impact coral reef organisms.

bleaching susceptibility without prior enlargement of symbiont density (Figure 1) [63]. It is important to note that nitrogen enrichments may not result in increased algal symbiont cell division *per se* [72,74], but rather changes to the stable density of symbiont populations [63]. Therefore, coral holobionts could simply reach a new and healthy equilibrium that balances nutrient availability, symbiont growth, and carbon translocation under nutrient enrichment.

The opposing impacts of ammonium and nitrate on coral thermal tolerance are better explained by their relative effects on holobiont carbon metabolism and oxidative stress. Ammonium stimulates photosynthesis and allows the algal symbionts to maintain photoprotective pigmentation and carbon translocation to the host under thermal stress (Figure 1B) [20,61,65]. In contrast, increased nitrate assimilation, due to external enrichment and/or thermal stress, encourages symbiont parasitism (Figure 1D), where the algal symbionts pass the energetic costs of nitrate utilization onto the coral host [43,61,75]. Therefore, nitrogen enrichment mediates coral bleaching through the carbon limitation model. However, this is realized through direct impacts on photosynthesis rather than symbiont growth.

Symbiodiniaceae Density and Coral Thermal Tolerance

An extension to the carbon limitation bleaching model is that very dense algal symbiont populations become parasitic due to intercellular competition and thereby reduce coral thermal tolerance [76,77]. In this case, excess nutrients which enlarge algal symbiont populations to levels at which other resources (e.g., CO₂ and light availability) limit photosynthetic output are linked to parasitism [76]. Indeed, some studies correlate algal symbiont density with coral bleaching susceptibility under ambient nutrient conditions [60,68–70], citing increased oxidative stress. However, this is contradicted by others, who suggest that coral holobiont genetic identity is more important, or that self-shading within dense algal symbiont populations protects against photo-oxidative damage [78,79]. The impact of symbiont abundance on coral bleaching susceptibility therefore remains difficult to resolve.

The relationship between algal symbiont abundance and the coral carbon metabolism may better explain the observed impacts on thermal tolerance. Symbiont densities above an optimal range ($\sim 1\text{--}3 \times 10^6$ cells cm⁻² depending on coral host species) have the potential to reduce carbon availability within the coral holobiont [66,67,76]. Balanced nutrient enrichments (nitrogen plus phosphorus) lead to the highest algal symbiont densities but can also reduce carbon translocation per symbiont cell (Figure 1C) [61,63]. However, total carbon translocation to the host is unaffected [60,61,75], indicating that dense populations remain mutualistic. In general, studies which combine nitrate and phosphate enrichments with elevated temperature suggest that balanced nutrient enrichments have little impact on coral thermal tolerance [18,19,80–82], although exceptions can occur [83,84]. Conversely, corals that are depleted in both nutrients take on a relatively bleached appearance [18,38,41] and reduced thermal tolerance [19,20]. Based on these studies, there is equivocal evidence that dense algal symbiont populations increase the susceptibility of corals to thermal stress. No single study thus far has simultaneously linked coral carbon metabolism and thermal tolerance with intraspecific variation in symbiont population size, and/or exposure to balanced nutrient enrichment. This leaves major gaps in our understanding of how algal symbiont density relates to thermal tolerance and should be a focus for future research.

Phosphorus Stabilizes the Coral–Symbiodiniaceae Symbiosis

Phosphorus has beneficial impacts on coral growth [63] and is integral to the stability of the coral holobiont [22]. Without an adequate supply of phosphate, coral holobionts that are enriched with nitrate can suffer reduced health [18,38] and impaired carbon metabolism (Figure 1D) [61,75], negatively impacting their thermal tolerance [18,80]. Corals also require a baseline supply of phosphate (regardless of nitrogen levels) to maintain autotrophy and thermal tolerance [38,42].

A lack of phosphorus limits the synthesis and maintenance of crucial molecules for cellular growth, including phospholipids [18] and DNA [85], which could therefore inhibit cell division in both coral hosts and the algal symbionts [22,86].

The negative impacts of phosphate limitation (relative to nitrate) on the coral holobiont have been mechanistically linked to the substitution of phospholipids with sulfolipids, which compromises the stability of algal symbionts' photosynthetic membranes and renders them susceptible to heat and light stress [18,38]. Furthermore, there is emerging evidence that high N:P ratios inhibit DNA repair in corals during thermal stress [85]. Under the high N:P condition, severe competition for phosphorus can occur where the algal symbionts become parasitic, retain nutrients [38,87], and potentially sequester ATP from their hosts [88,89]. In response, the coral host may digest its symbiont population to recuperate lost nutrients [90,91]. Shifts towards phosphorus limitation of the coral holobiont have the potential to severely compromise the stability of the coral–Symbiodiniaceae symbiosis, leading to carbon limitation, photo-oxidative stress and an increased susceptibility to coral bleaching.

Heterotrophic Feeding Mediates Inorganic Nutrient Availability

Heterotrophic feeding is known to improve the health of corals under ambient conditions [23] and when faced with thermal stress [30,36]. Heterotrophic food sources contain carbon, in addition to providing nitrogen and phosphorus [23], which prevents carbon limitation under thermal stress and enhances coral bleaching resistance [30,36,92]. However, heterotrophic feeding is not always beneficial, particularly under stressful inorganic nutrient conditions [20,41,80] or when food is of poor quality [35,93–97]. When coral holobionts experience stressful inorganic nutrient conditions, heterotrophic feeding can exacerbate the nutrient imbalance [41,80,98], or alternatively, heterotrophic nutrient assimilation may decrease [20]. Changes to the nutritional composition of food may also have negative implications for the coral holobiont, particularly when combined with thermal stress [93–97]. These findings are particularly relevant given that corals on productive nearshore reefs rely more on heterotrophic feeding [99], due to increased organic nutrient availability and/or nutrient stress [20,41,80,100]. Overall, heterotrophic feeding under oligotrophic conditions provides benefits to the coral holobiont, but stressful inorganic nutrient environments may decrease food quality or negatively interact with heterotrophy to impact coral health and thermal tolerance.

Nutrient Availability and the Coral Microbiome

The coral microbiome (specifically bacteria and archaea) has been implicated in the cycling of essential nutrients within the coral holobiont and may therefore play a role in mediating coral–Symbiodiniaceae metabolic interactions and holobiont responses to environmental stress [24]. However, the microbial metabolic pathways integrated with the coral host and their algal symbionts remain poorly characterized [13,22]. Nitrogen fixation is perhaps the best characterized microbial metabolic function that supports the coral–Symbiodiniaceae symbiosis [13]. Corals harbour a diverse community of diazotrophs [101], and nitrogen fixation has been observed in a range of coral species [25,102] to potentially provide nitrogen to both the host and algal symbiont tissues [26]. Importantly, nitrogen fixation is influenced by environmental conditions [32,35,102,103] and has been suggested to both support and hinder the stability of the coral–Symbiodiniaceae symbiosis [13]. Nitrogen fixation is known to increase in warm summer conditions, when both external nutrient availability and algal symbiont populations are low, and putatively allows the coral holobiont to maintain its productivity through these stressful conditions [32,102,104,105] much like ammonium enrichment [20,61,65]. However, other studies have linked elevated nitrogen fixation to thermal stress and bleaching [32,35,103]. The activity of nitrogen fixers in corals is known to be stimulated by **dissolved organic carbon** (DOC) enrichment, which increases N:P ratios within the coral holobiont and can lead to bleaching through carbon limitation and photo-oxidative stress [35]. In the same way, summer conditions on coral reefs

coupled with increased nitrogen fixation could represent a 'perfect storm' for coral bleaching, where the coral-Symbiodiniaceae symbiosis becomes overwhelmed by a combination of high temperatures, elevated irradiance, and increased N:P ratios. Furthermore, diazotrophs may act as an additional sink of carbon and bypass the host's ability to restrict external nitrogen supply to the algal symbionts, thereby enhancing the likelihood of coral bleaching. Microbial nitrogen fixation therefore represents a highly dynamic pathway by which other coral holobiont members can acquire nitrogen; however, the consequences of this differ depending on the environmental context.

Changes to environmental nutrient conditions may impact the coral microbiome, manifesting as **microbial dysbiosis** [106] and resulting in coral disease [84]. For example, field and laboratory studies have linked nutrient enrichment to coral disease, where enrichments of ammonium, nitrate, and phosphate induced and/or enhanced a range of coral diseases including black band disease [107], yellow band disease [108], and dark spot syndrome [84]. In addition, these combined nutrient enrichments triggered the production of herpes-like viruses in *Porites compressa* [109], while both DOC and nutrient enrichments were shown to shift the microbiome towards a pathogenic state [110]. However, other studies have shown that coral microbiome structure does not consistently respond to nitrate and/or phosphate enrichment [111], nor to DOC or urea enrichment [112]. These latter experiments suggest that coral microbiomes can either shift into unique and random dysbiotic states [111], or remain inflexible [112] under nutrient stress. Therefore, although nutrient enrichment can be broadly associated with coral dysbiosis and disease, relationships with specific nutrient forms are unclear and should be a focus for future study.

Nutrient Availability and Coral Bleaching Recovery

It is well established that particulate nutrients ingested by the coral host promote recovery following thermal bleaching [29–31]. However, information regarding the comparative impacts of inorganic nutrients is lacking. Heterotrophic feeding can promote recovery from bleaching by alleviating coral carbon limitation [30,92], whereas bioenergetic modelling suggests that inorganic nitrogen enrichment has an opposite, detrimental effect [77].

Empirical studies testing inorganic nutrient impacts on corals following thermal stress are few in number, but nitrate enrichment can either trigger the rapid growth of photodamaged algal symbionts [80,113] or prolong coral bleaching leading to increased mortality [111]. Both responses are well explained by a bioenergetic model [77]. Firstly, dense algal symbiont communities can form naturally in corals post-bleaching, owing to a sudden increase in resources per symbiont cell [31,69,77]. Secondly, the growing algal symbiont population retains photosynthates, delaying recovery of the coral host [71,77]. External nitrogen enrichment could therefore be expected to prolong the carbon-limited status of a bleached coral holobiont and increase the risk of mortality through starvation. However, to date, the impacts of inorganic nutrient availability on bleaching recovery have only been tested in experiments that enrich corals throughout entire thermal stress periods [80,111,113]. To fully understand the nutritional processes involved in coral bleaching recovery, future experiments should apply nutrient manipulations following thermal bleaching, rather than before or during bleaching, to explicitly separate pre- and post-bleaching nutrient impacts.

Inorganic Nutrient Metabolism Underpins Coral Stress Tolerance

Evolutionary theory predicts that the stability of nutritional symbioses is controlled by finely balanced conflict mediation between partners [114]. The same theory can be applied to the coral holobiont, where selection favours symbiont cells which retain photosynthates for their own growth, yet the coral host requires symbionts to translocate photosynthates or else they are eliminated [115]. Genetic and phenotypic variation underpins the environmental stress tolerance of coral holobionts and may manifest in processes such as the control of inorganic nutrient

metabolism, which mediates whether it is the coral host or the algal symbionts that benefits from autotrophic carbon fixation [13,28,43,115].

The processes that regulate the supply of nutrients to the algal symbionts and the subsequent translocation of carbon are still poorly understood [13,21]. However, some coral hosts can actively decrease the N:P ratio of nutrients supplied to the algal symbionts when at risk of bleaching [20,35,42,116]. Combined transcriptome–metabolome analyses in *Exaiptasia diaphana* anemones (common name Aiptasia) also suggest that coral hosts may use photosynthates to sequester their own ammonium wastes into amino acids [73]. Both of these actions may represent host-derived mechanisms that act to maintain the algal symbionts in a nitrogen-limited state and, in turn, prevent carbon limitation of the holobiont. However, the algal symbionts have evolved to counteract nitrogen limitation [117], rendering corals susceptible to symbiont parasitism under nitrate enrichment and thermal stress [43,61,75]. Despite this, interspecific differences in the nutrient acquisition and utilization of the symbionts offer a potential avenue to holobiont stress tolerance [28,117].

Metabolic Compatibility between Coral and Symbiodiniaceae Lineages

Coral holobionts containing high-performance ‘generalist’ algal symbionts (e.g., *Cladocopium goreaui*) often outperform more ‘specialized’ stress-tolerant symbionts (e.g., *Durussdinium trenchii*) in terms of key traits such as photosynthesis and host growth [118–121]. This can be attributed to the greater fixation and translocation of inorganic carbon and nitrogen by generalist types [44,120,122,123]. However, these trends are reversed at elevated temperatures where stress-tolerant types outperform generalists [70,124,125]. These observations may be related to differences in nutrient metabolism, where thermally tolerant types upregulate their nitrate intake to maintain carbon translocation [44]. Hence, thermally tolerant algal symbiont species may convey resistance to nutrient and/or thermal stress, whereas corals hosting other algal species become carbon-limited [30,36,43,45,47,61,75]. Furthermore, increased nitrogen availability per symbiont following bleaching can promote recovery of corals with stress-tolerant types [31]. It is possible that thermally tolerant species direct additional nitrogen towards carbon translocation, as their growth rates are low and stable across environmental conditions compared with other species [126], which may proliferate and subsequently reduce overall holobiont health [112]. Therefore, the identity of the algal symbionts appears to alter holobiont tolerance to nutrient and thermal stress through differences in inorganic nutrient metabolism, although this remains to be fully determined.

Evidence from Aiptasia suggests that both host and algal symbiont identity mediate inorganic nutrient metabolism and thermal tolerance. The photosynthetic response of Aiptasia to thermal stress depends on both the host strain and algal symbiont genus: where heterologous (‘novel’) holobionts outperform those that are homologous (‘normal’) at elevated temperatures [127]. Similar host–symbiont interactions can occur in corals, where host species impacts the relative thermal tolerance of holobionts containing different, yet homologous, algal symbiont genera [128]. At the nutritional level, carbon fixation and nitrogen assimilation by the algal symbionts in Aiptasia have been shown to depend solely on symbiont identity, whereas host benefits through carbon translocation are codependent on host genotype [27]. In this case, the algal symbionts retained a constant amount of fixed nutrients regardless of their host [27]. In general, homologous holobionts outperform heterologous holobionts as evidenced by reduced carbon translocation [27,129–131] and growth [132] in heterologous symbioses. Furthermore, novel symbionts may sustain themselves by manipulating host nitrogen cycling [130]. Although the later observations appear to contradict earlier findings [127], it remains to be seen how nutrient and thermal stress impact host–symbiont interactions in nutrient metabolism.

Phenotypic Plasticity in Nutrient Metabolism

The ability of the coral holobiont to activate mechanisms which maintain and enhance metabolic compatibility may be partly determined by **adaptation** or **acclimation** to their environment. For example, algal symbionts in warm-acclimated coral holobionts assimilate less nitrogen and translocate more carbon than their ambient-acclimated counterparts upon acute exposure to thermal stress [46]. Although both sets of coral holobionts were physiologically unaffected by thermal stress in this experiment [46], other studies have found that acclimation to elevated and variable temperatures prior to acute thermal stress reduces the severity of coral bleaching [133–135]. Therefore, as part of, or in addition to observed genetic mechanisms [136], temperature acclimation may help coral hosts to resist bleaching by invoking metabolic processes which act to maintain their symbionts in a mutualistic state.

Prior exposure to different water quality environments may provide another avenue for acclimation. Inshore reefs are often resistant to bleaching, despite their exposure to elevated and variable nutrient and temperature conditions relative to offshore reefs [137–140]. In the Florida Keys, the growth of inshore corals is reduced upon transplantation to new off- or along-shore environments, suggesting that their thermal tolerance is linked to fine-scale nutritional specialization [141–143]. In contrast, the evolved thermal tolerance of corals in oligotrophic regions, such as the Red Sea, may be highly sensitive to even minor increases in nutrient availability [83,144]. Combined, these results suggest that the historical nutrient conditions (over proximate and evolutionarily timescales) can prime coral hosts for the nutritional disruption that occurs during acute stress.

Concluding Remarks

The coral bleaching process is currently understood mainly through photo-oxidative pathways, although recent evidence indicates that nutritional mechanisms are involved. The coral–Symbiodiniaceae relationship is primarily a trophic mutualism and therefore the stability of this symbiosis is dependent on the balance and exchange of nutrients in response to environmental conditions. In this review, we have integrated novel experimental evidence to show how nutrient availability and metabolism can mediate coral bleaching with and without photo-oxidative stress. Nutrient availability has previously been postulated to influence bleaching susceptibility through increasing symbiont growth rates; however, we demonstrate here that bleaching is better attributed to changes to autotrophic carbon metabolism, which depend on nutrient form and ratio. Furthermore, historical nutrient conditions may influence host–symbiont metabolic capability and therefore bleaching susceptibility. Future experiments should determine how nutrient and temperature conditions alter the metabolic cooperation and stability of distinct coral–Symbiodiniaceae combinations (see Outstanding Questions). An added focus should also be placed on understanding how inorganic nutrients mediate the re-establishment of the coral–Symbiodiniaceae symbiosis following bleaching. Nutrient metabolism within the coral holobiont still remains poorly characterized beyond the identification of putative nutritional pathways, and therefore the specific metabolic pathways which destabilize the symbiosis should be elucidated by manipulating the genes which encode enzymes and transporters involved in nutrient cycling. To truly understand the cellular mechanisms leading to coral bleaching, a renewed focus must be placed upon the nutrient metabolism of the coral holobiont.

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Outstanding Questions

How do nutrient and thermal stress interact to mediate algal symbiont parasitism and coral holobiont function? How does this impact coral bleaching susceptibility? Are the impacts related to algal symbiont density?

Do nutrient conditions that increase coral bleaching susceptibility, specifically high N:P ratios, also impact recovery from bleaching? If so, do these facilitate or inhibit coral recovery?

Do natural nutrient subsidies and anthropogenic nutrient pollution influence coral thermal tolerance in similar or different ways? Are the impacts the same even when the nutrients take the same form (e.g., nitrate from runoff versus natural remineralization)?

To what extent does the metabolic compatibility of the coral hosts and their algal symbionts contribute to their thermal tolerance? Are even the most compatible symbioses susceptible to nutrient stress?

Do high-performance generalist symbioses and specialized stress-tolerant symbioses have common metabolic responses to stress? Can nutrient stress be unequivocally diagnosed through specific metabolic biomarkers?

Does coral acclimation or adaptation to environmental stress occur through the reconfiguration of internal nutrient metabolism? Can acclimation/adaptation to nutrient stress also increase resistance to thermal stress, and vice versa?

What are the outstanding mechanisms in which nutrient availability and metabolism mediate coral holobiont health and stress tolerance?

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