



The Future of Coral Reefs Subject to Rapid Climate Change: Lessons from Natural Extreme Environments

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Global climate change and localized anthropogenic stressors are driving rapid declines in coral reef health. *In vitro* experiments have been fundamental in providing insight into how reef organisms will potentially respond to future climates. However, such experiments are inevitably limited in their ability to reproduce the complex interactions that govern reef systems. Studies examining coral communities that already persist under naturally-occurring extreme and marginal physicochemical conditions have therefore become increasingly popular to advance ecosystem scale predictions of future reef form and function, although no single site provides a perfect analog to future reefs. Here we review the current state of knowledge that exists on the distribution of corals in marginal and extreme environments, and geographic sites at the latitudinal extremes of reef growth, as well as a variety of shallow reef systems and reef-neighboring environments (including upwelling and CO₂ vent sites). We also conduct a synthesis of the abiotic data that have been collected at these systems, to provide the first collective assessment on the range of extreme conditions under which corals currently persist. We use the review and data synthesis to increase our understanding of the biological and ecological mechanisms that facilitate survival and success under sub-optimal physicochemical conditions. This comprehensive assessment can begin to: (i) highlight the extent of extreme abiotic scenarios under which corals can persist, (ii) explore whether there are commonalities in coral taxa able to persist in such extremes, (iii) provide evidence for key mechanisms required to support survival and/or persistence under sub-optimal environmental conditions, and (iv) evaluate the potential of current sub-optimal coral environments to act as potential refugia under changing environmental conditions. Such a collective approach is critical to better understand the future survival of corals in our changing environment. We finally outline priority areas for future research on extreme and marginal coral environments, and discuss the additional management options they may provide for corals through refuge or by providing genetic stocks of stress tolerant corals to support proactive management strategies.

Keywords: extreme, ocean acidification, marginal, refuge, review

INTRODUCTION

Coral reef ecosystems and the services they provide sustain half a billion people on Earth, but are deteriorating under the effects of climate change (Cinner et al., 2016; Hughes et al., 2017). Accumulation of greenhouse gases in the atmosphere (primarily carbon dioxide, CO₂) is resulting in warmer sea surface temperatures (SST) and rising seawater acidity; processes that are predicted to intensify under current climate change projections (van Hooidonk et al., 2014). Even if carbon emissions were to stabilize today, the world's oceans will experience prolonged warming and inevitable change in carbonate chemistry, due to the lag time that oceans re-equilibrate with the atmosphere (IPCC, 2014). Further changes in other physicochemical conditions, such as reduced oxygen levels (Schmidtke et al., 2017), are accompanying ocean warming, creating a complex suite of environmental factors that coral reefs will need to overcome in order to persist into the future. Understanding whether and how corals can physiologically or genetically adjust to keep pace with environmental change, has therefore become a global research priority.

A key challenge for researchers studying how future projected climates will impact reef form and functioning, is to consider the influence of local scale environmental conditions, including natural diel and seasonal fluctuations (Guadayol et al., 2014). It is imperative to understand the ecological limits to coral distributions by resolving their fundamental niche (the range of conditions an organism can physiologically survive and reproduce under in the absence of biotic interactions, Hutchinson, 1959), relative to their realized niche [determined by other biological pressures, such as competition, (Morin and Thuiller, 2009)], thereby addressing the impact of climate stressors on community reorganization in response to the prevailing conditions (Doney et al., 2012). Natural environments where corals live at the periphery of their environmental tolerance, such as CO₂ vent sites, have therefore become increasingly popular to study corals free of the constraints imposed by *in vitro* experimentation. Such natural extreme and marginal environments have conditions close to the perceived thresholds of coral growth (Kleypas et al., 1999), but support corals that have clearly acclimated and/or adapted to more extreme environments (e.g., Palumbi et al., 2014). Thus, an important role of these environments is that they can offer insight into how corals and coral reefs may survive into the future (Perry and Larcombe, 2003), as they are continuously subjected to more extreme environmental conditions through climate change. The insight provided by these environments will depend in part on the dispersal of adults and juveniles, with sessile brooding species more likely to exhibit adaptation to extreme environments over multiple generations, compared to broadcast spawning species that may recruit into the extreme environment as progeny from “parents” in less stressful environments. Ultimately, no single site studied to date provides a “perfect” analog to future environmental conditions projected for coral reefs. However, a collective assessment of such sites can provide essential information on the ability of corals and coral reefs to persist according to different scenarios, in terms of intensity of stressor

and/or combination of stressors at play. Until now, no such collective assessment has been undertaken.

Here, we review and synthesize information across a range of extreme and marginal coral environments, to: (i) demonstrate the extent of abiotic scenarios under which corals can persist, (ii) explore whether there are commonalities in coral taxa able to persist in such extremes, (iii) provide evidence for key mechanisms required to support survival and/or persistence under sub-optimal environmental conditions and, (iv) evaluate the potential of current sub-optimal coral environments to act as potential refugia under changing environmental conditions. We undertake a synthesis of the abiotic variability documented for the different extreme environments, to provide a collective assessment of these systems. Finally, we draw on the findings from the review to explore how these systems may support corals tolerant of stress that could be utilized in proactive reef management, and outline key areas for future research.

MATERIALS AND METHODS

To begin, we review the current state of knowledge of coral environments that are considered marginal or extreme in relation to one or more abiotic factor, notably, seawater pH, temperature, low light (including highly turbid environments), and oxygen. We use case studies of some well-documented sites within each environment to quantify the extreme abiotic conditions experienced and provide examples of the mechanisms that have been reported to support coral survival. We also consider the ability of these different environments to act as potential coral refugia. Refuge environments are areas that maintain favorable conditions being lost elsewhere (*sensu* Keppel and Wardell-Johnson, 2012). These could vary across temporal scale, with some environments providing short-term refuge against acute stress (e.g., turbid reefs reducing irradiance during a bleaching event) vs. long term chronic changes (e.g., the potential buffering ability of seagrass systems). As coral reefs globally are forced to acclimatize to changing environmental conditions, utilization of refuge environments becomes an important alternative solution to aid survival.

We then conduct a quantitative synthesis of information from 285 studies (**Supplementary Table 1**) that have considered extreme, marginal or refuge coral environments. To parameterize the literature included in the quantitative synthesis, only studies that considered scleractinian corals or the physicochemical conditions of coral systems were included. Studies were collected for analysis until the 3rd August 2017. The collection of studies was identified from ISI Web of Science database or Google Scholar searching relevant keywords, e.g., the type of extreme coral environments (high-latitude, CO₂ vent, mangrove system, seagrass, macro-tidal, ojos (low pH springs), upwelling, turbid reefs, mesophotic, deep reefs, hot seas, tide-pools) with the following words: refuge, coral, thermal tolerance, bleaching, ocean acidification. We also searched the literature cited in all studies identified during that search. Review of this current literature quickly demonstrated that there were not enough data available to compare biological metrics (e.g.,

calcification rates) across these environments, and as such, we used the quantitative synthesis to: (i) identify knowledge gaps, and (ii) compare the range of abiotic conditions corals are currently able to persist under.

To identify knowledge gaps, the work undertaken in each study was grouped into eight categories: community composition, experimentation, health, holobiont community, physicochemical conditions, physiology, population biology and structural properties, each of which had sub-categories that are illustrated in a heat-map (Figure 1). The heat-map is based on the proportion of studies within a given environment that measured any given parameter.

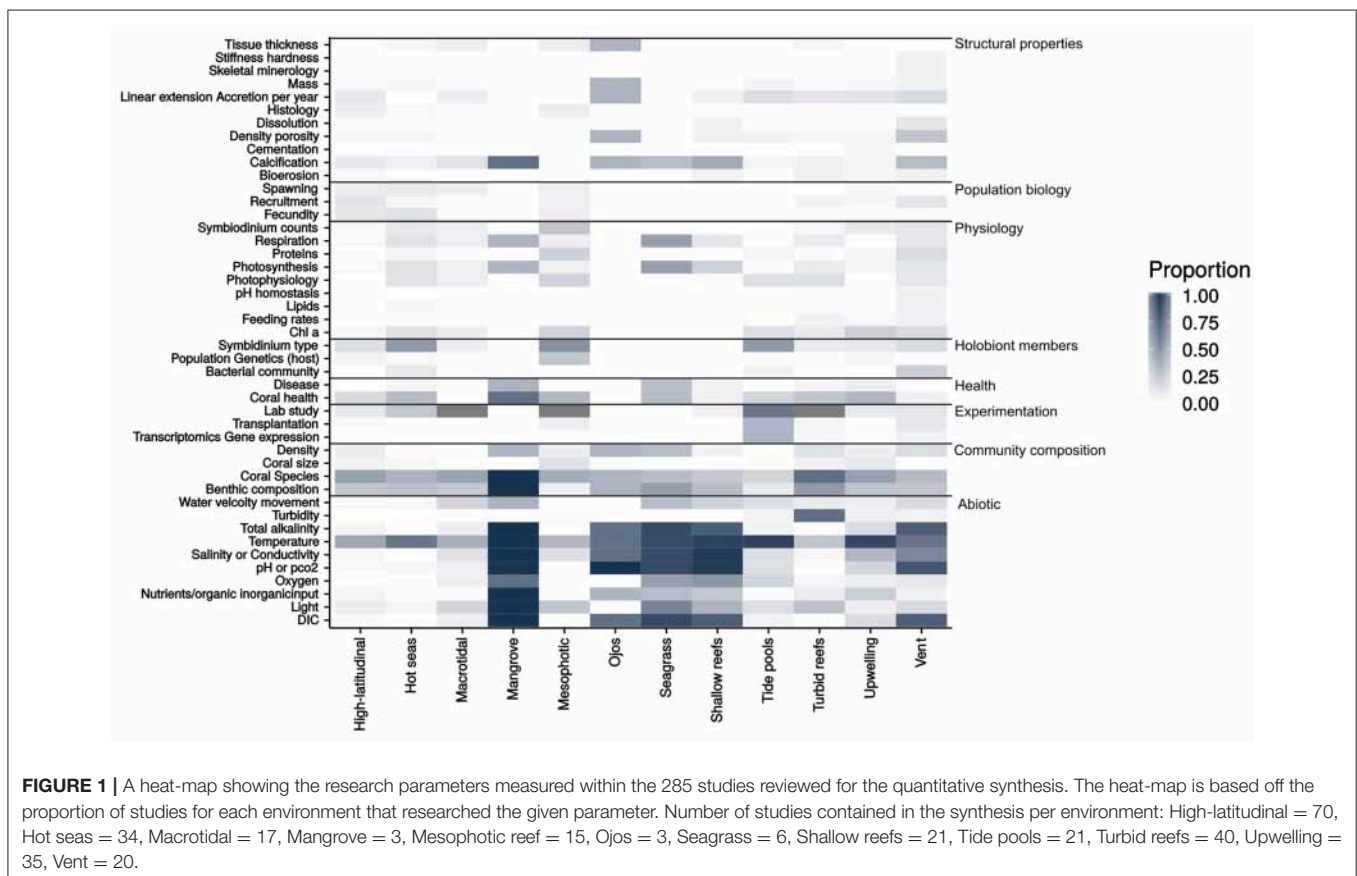
To compare the abiotic parameters (pH, temperature, oxygen, total alkalinity (A_T) and salinity) of sites within different environments, studies that included the maximum and minimum abiotic values for a minimum of one seasonal period (dry season/wet season) were included. Due to the limited data available across temporal scales (e.g., day, week, month, season, years), data were used as long as a minimum of one diurnal cycle was available for that season. Once additional high-resolution abiotic datasets are available for these environments, comparisons across different temporal scales should be conducted (Table 1). Raw data were used or extracted from primary literature using WebPlot Digitizer (Rohatgi, 2017). Unfortunately, the synthesis quickly revealed that the comparison of multiple abiotic variables across all extreme and

marginal coral environments would not be possible due to a lack of data. As such, abiotic comparisons were made across environments on the most commonly reported abiotic variables: pH and temperature. A further Principle Component Analysis (PCA) was conducted on pH (total scale), temperature ($^{\circ}\text{C}$), total alkalinity (A_T ; $\mu\text{mol kg}^{-1}$ SW), salinity and oxygen (mg L^{-1}) for 14 studies, spanning five environments to demonstrate the need to consider multiple abiotic variables within these systems. The PCA was performed in R (R Core Team, 2017) using the `prcomp` function. To avoid scale change sensitivity in the PCA (Everitt and Hothorn, 2011) variables were rescaled (Härdle and Simar, 2012) to have a mean of zero and a standard deviation of one.

REVIEW OF THE CURRENT STATE OF KNOWLEDGE

Low pH/High CO_2 Environments

Absorption of excess atmospheric CO_2 by the world's oceans lowers seawater pH and re-organizes the composition of carbonate species of seawater, resulting in reduced saturation states of calcium carbonate minerals [e.g., aragonite (Ω_{arag})]. This phenomenon, termed ocean acidification, threatens to impact many marine processes (Kroeker et al., 2013) notably through reduced growth and physical integrity of marine



calcifiers (Guinotte and Fabry, 2008). CO₂ vent sites and ojos (low pH springs) are natural extreme environments where the seawater carbonate chemistry (low pH and low Ω_{arag}) provides comparative conditions to ocean acidification scenarios.

CO₂ Vents

Underwater volcanic vents emit CO₂ (along with other trace gases, e.g., N₂, O₂, CH₄, **Figure 2**) into the adjacent seawater, reducing the Ω_{arag} and creating seawater conditions similar to those predicted to occur under ocean acidification. Local hydrology and variations in gas release can create large diel oscillations in $p\text{CO}_2$ at vent sites relative to adjacent control sites (Enochs et al., 2015). Even so, vent sites offer a unique natural environment to study ecosystem changes in response to frequent, low pH (Hall-Spencer et al., 2008). In the Mediterranean, the release of CO₂ at vent sites has been shown to alter a variety of ecosystems, including seagrass beds (Martin et al., 2008), rocky-reef systems (Hall-Spencer et al., 2008), and vermetid reefs (Milazzo et al., 2014). These temperate studies all report adverse effects of elevated $p\text{CO}_2$, including loss of diversity of marine calcifiers (Martin et al., 2008; Kroeker et al., 2011), reduced calcification (Milazzo et al., 2014), shifts from calcareous dominated systems to a state lacking scleractinian corals (Hall-Spencer et al., 2008) and reductions in trophic groups (Kroeker et al., 2011).

To date, there have only been three regions where vent systems have been described adjacent to coral reefs: Iwotorishima Island, Japan (Inoue et al., 2013), Papua New Guinea (PNG; Fabricius

et al., 2011) and Maug, in the Commonwealth of the Northern Mariana Islands (Enochs et al., 2015). Findings from these vent sites have been variable, likely due to site-specific pH gradients, hydrology and conditions such as nutrient availability (Enochs et al., 2015). For example, in Iwotorishima, communities shifted from hard coral to soft coral as seawater acidified, with all corals absent from the highest $p\text{CO}_2$ zone (1,465 μatm , Inoue et al., 2013). In contrast, coral dominated sites at Maug (mean pH = 8.04 ± 0.016 , min pH = 7.98) transitioned to macroalgal dominance (mean pH = 7.94 ± 0.051 , min pH 7.72).

A common feature across the various vent sites are changes in community structure, where only a few acidification-tolerant species thrive under high $p\text{CO}_2$ (e.g., Hall-Spencer et al., 2008; Fabricius et al., 2011, 2015; Kroeker et al., 2011, 2013). There is also evidence that the structural integrity of any reef framework is compromised due to a loss of architectural complexity (Fabricius et al., 2011), increased rates of bioerosion (Enochs et al., 2016a,b), reductions in coral growth (Fabricius et al., 2011) and reduced skeletal density (Fantazzini et al., 2015; Strahl et al., 2015b).

The ability of corals around vent sites to maintain calcification under elevated $p\text{CO}_2$ appears to be species-specific (Rodolfo-Metalpa et al., 2011; Inoue et al., 2013). Both in laboratory work (Venn et al., 2011; McCulloch et al., 2012) and field investigations (Wall et al., 2016) species-specific abilities to buffer internal-pH have been recorded. There do appear to be defined physiological limits under which calcification can occur (McCulloch et al., 2012; Wall et al., 2016), and physiological plasticity appears important in supporting calcification at high $p\text{CO}_2$. For example,

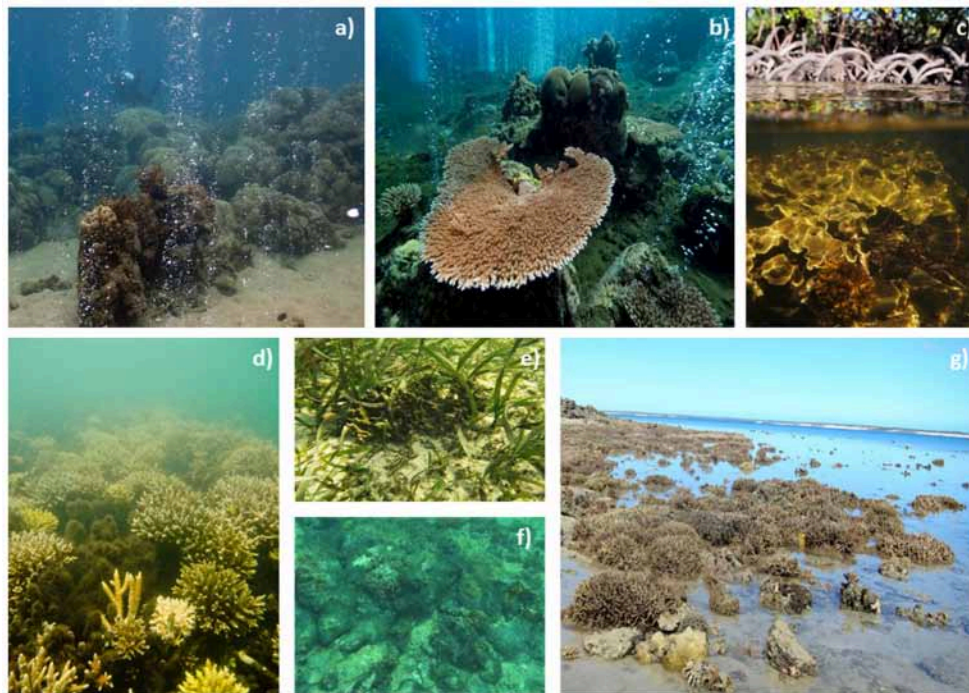


FIGURE 2 | Photographs from different extreme and marginal coral environments. **(a,b)** Vent sites in Papua New Guinea (photo credit R. Rodolfo-Metalpa and J.M. Boré), **(c)** mangrove system Great Barrier Reef (photo credit E. Camp), **(d)** mangrove system New Caledonia (photo credit E. Camp), **(e)** seagrass bed the Cayman Islands (photo credit E. Camp), **(f)** turbid reef Salvador Brazil (photo credit E. Camp), **(g)** Kimberley reef flat (photo credit V. Schoepf).

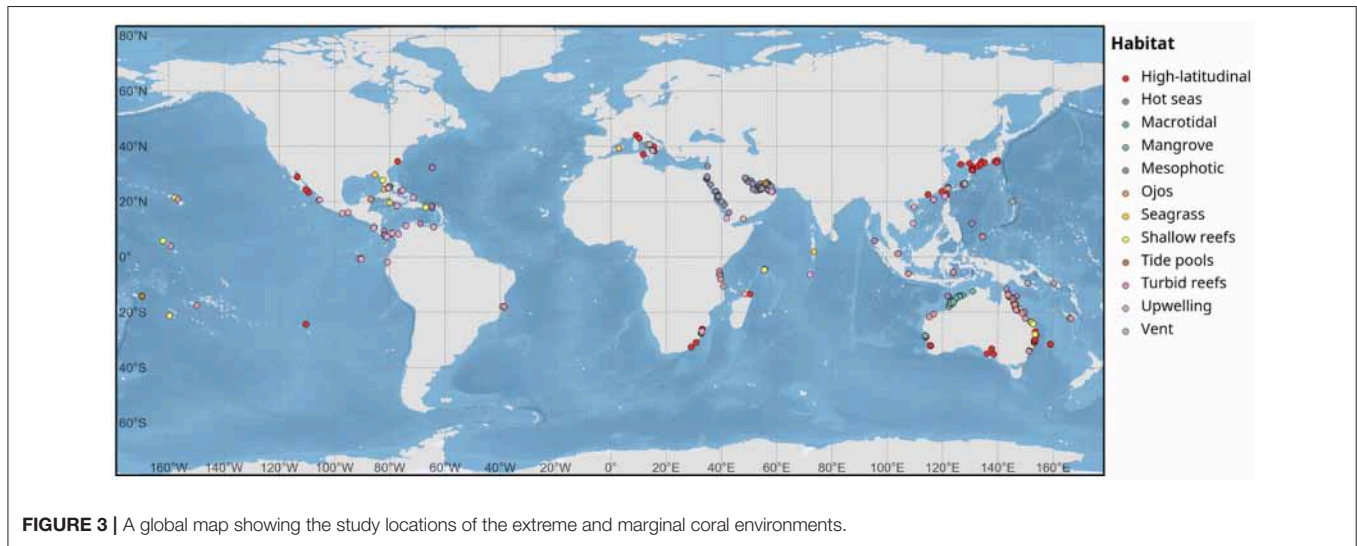


FIGURE 3 | A global map showing the study locations of the extreme and marginal coral environments.

increased rates of calcification (Rodolfo-Metalpa et al., 2011), or the utilization of elevated external dissolved inorganic carbon (DIC) can fuel photosynthesis (Inoue et al., 2013; Strahl et al., 2015a) and offset the higher energetic cost of calcification under acidification. For soft corals (Inoue et al., 2013), sea anemones (Suggett et al., 2012a), and scleractinian corals (Strahl et al., 2015a), success at high $p\text{CO}_2$ seems to be driven by their capacity to enhance, or at least sustain, photosynthesis under elevated $p\text{CO}_2$. Other physiological processes such as higher cell protective capacities, total lipid content, tissue biomass (Strahl et al., 2015b) and changes in fatty acid metabolism (Kenkel et al., 2017) may also promote resistance to environmental stress at low pH.

Alongside physiological plasticity, live-tissue coverage (Rodolfo-Metalpa et al., 2011), and changes in microbial taxa (Morrow et al., 2014) can support species survival under elevated $p\text{CO}_2$. Variable changes in gene expression of *Symbiodinium* at the PNG vent system suggest population-specific responses to low pH (Kenkel et al., 2017). The collective response of the animal host, symbiotic algae and other microbial taxa demonstrate that fully considering the holobiont (i.e., the coral host, algal symbionts and microbiome) is important in determining success and survival under high $p\text{CO}_2$.

Low pH Springs (ojos)

Underwater seeps (ojos) of the Yucatan Peninsula (Mexico) have physicochemical conditions entirely unique to the local area. Here, water that has associated with soil and limestone mixes with high CO_2 groundwater resulting in seawater that has a low pH (6.70–7.30), low Ω_{arag} (0.3–0.97 at the center of the seep), and high DIC, A_T , Ca^{2+} and nutrients (Crook et al., 2012). Although the combined physicochemical conditions differ from potential future ocean acidification scenarios and vent environments (e.g., low pH accompanied by high DIC, A_T , and Ca^{2+}), the site provides insight into how coral diversity and growth are impacted when corals are exposed to low pH for an extended period of time [high CO_2 water has discharged for

millennia, (Beddows et al., 2002)]. Crook et al. (2012) found that only three coral species (*Porites astreoides*, *P. divaricata*, and *Siderastrea radians*) persisted close to the ojos where the Ω_{arag} was <2.5 . Further analysis of the growth rates of *P. astreoides* showed no change in linear extension rates, but a fall in skeletal density (ca. 40%) and calcification (ca. 30%) when Ω_{arag} was below 2.0, relative to an adjacent control site where Ω_{arag} was >3.5 (Crook et al., 2013). The ojos sites can experience changes in temperature, salinity and light that may in part explain the reduced calcification rates (Iglesias-Prieto et al., 2014), although the collective assessment from the laboratory and field experimentation suggests low pH is largely responsible for the reductions in calcification measured (Paytan et al., 2014). To date for this site, no molecular data or information on other life-history traits (e.g., metabolic properties) have been published, making it difficult to assess whether this reduction in density does indeed demonstrate a lack of acclimation ability for *P. astreoides* (Crook et al., 2013) or rather highlights a potential survival process to persist in adverse conditions (e.g., phenotypic or metabolic plasticity, see Pigliucci et al., 2006). Either way, these findings corroborate results from the vent sites that coral calcification will likely be compromised under low pH.

Highly Variable pH/ CO_2 Environments

Similar to corals, seagrasses (Figure 2) are ecosystem engineers given that they modify their local physical and geochemical conditions (Duarte et al., 2013). During daylight hours, seagrass photosynthesis removes CO_2 lowering DIC, while at night, respiration dominates in the absence of photosynthesis, increasing DIC. This metabolic activity in seagrass meadows has been documented to cause large diurnal variation in local seawater carbonate chemistry conditions that can alter the saturation state of carbonate minerals (Schmalz and Swanson, 1969). For example in the Cayman Islands, pH varied by 0.3 units over a diel-cycle (Camp et al., 2016b). Daytime drawdown of CO_2 has resulted in seagrass meadows having elevated pH during the day across several regional locations, e.g., Spain

(Invers et al., 1997), Florida (Manzello et al., 2012), the Cayman Islands, Indonesia, and the Seychelles (Camp et al., 2016a) that can create an inshore-to-offshore carbonate chemistry gradient (Manzello et al., 2012; Camp et al., 2016a). The capability of seagrasses to elevate local mean pH has led to them being described as potential refugia under ocean acidification (Manzello et al., 2012), since they buffer resident species from rising seawater acidity (Hofmann et al., 2011; Manzello et al., 2012; Hendriks et al., 2014). Unsworth et al. (2012) proposed that the photosynthetic activity of seagrass meadows in the Indo-Pacific could enhance seawater physicochemical conditions to increase coral calcification downstream by as much as 18%. However at night, high respiration rates can lead to seagrass meadows becoming a source of CO₂ (Schmalz and Swanson, 1969), causing large drops in local seawater pH, that at several locations have caused pH to fall below 7.8 (Camp et al., 2016a,b), creating conditions predicted under future ocean acidification (Feely et al., 2004).

The ability of seagrasses to modify the local environment may result in non-genetic ecological inheritance (Bonduriansky and Day, 2009), influencing the evolutionary selection pressure on themselves and other local taxa (Mumby and Van Woeseik, 2014). Seagrass meadows have not typically been considered important coral habitats due to a lack of solid substrate (Jackson, 1986; Manzello et al., 2012). However, corals can recruit into seagrass systems; for example in the Cayman Islands where 14 coral taxa (primarily *P. astreoides* and *Siderastrea* sp.) were found to recruit into seagrass beds (Lohr et al., 2017). The ability of seagrasses to moderate the local seawater carbonate chemistry has resulted in an increased interest in their role as a coral habitat and potential coral refugia, although, the latter role is still unclear. Increased availability of CO₂ and HCO₃⁻ under ocean acidification is predicted to enhance photosynthetic rates of carbon limited seagrasses (Durako, 1994; Buapet et al., 2013; Hendriks et al., 2014) and increase the growth and biomass of seagrass beds (Zimmerman et al., 1997). Research from high CO₂ systems has provided compelling evidence that seagrasses will flourish (Hall-Spencer et al., 2008; Fabricius et al., 2011; Duarte et al., 2013), sustaining their ability to modulate pH (Duarte et al., 2013). Furthermore, low night-time pH could result in chemical conditions where carbonate-sediment dissolution occurs (Yamamoto et al., 2012), increasing local A_T and pH, thus creating a self-buffered system (Andersson et al., 2014). However the shallow nature of seagrass systems means they also experience variability in other parameters such as oxygen (Hendriks et al., 2014), salinity (Manzello et al., 2012), temperature (Manzello et al., 2012; Camp et al., 2016a,b), and light (Hendriks et al., 2014). Work from seagrass habitats in the Cayman Islands suggests that if future diel-oscillations in pH and temperature change at an equivalent magnitude as predicted for the open-ocean, seagrass systems could be limited in their ability to buffer resident species, due to the extreme low night-time pH and elevated daytime temperatures they experience (Camp et al., 2016b). Consequently, the interactive effect of local physicochemical conditions, and the magnitude of diurnal and seasonal variance, will likely control whether any protective services are provided by seagrass systems in the future.

High Temperature Environments

Tropical corals live close to their upper thermal limits and are therefore highly sensitive to periods of elevated SST and ocean warming (Heron et al., 2016). Coral bleaching occurs when corals lose a significant portion of their algal endosymbionts and/or photosynthetic pigments in response to heat stress, and can result in widespread coral mortality on regional-to-global scales. Global interest in elevated temperature effects on corals has peaked recently due to the increasing frequency and intensity of thermally-induced mass bleaching events (Hughes et al., 2017). This has led to research efforts that focus on identifying maximum, and variations in thermal tolerance across coral species and regions, as well as identifying potential coral refugia to future ocean warming.

During the summer season, the Persian-Arabian Gulf (PAG) experiences the highest sea temperatures in the world, yet still houses a significant number of coral species (55–60 species) despite the most extreme temperature conditions ever recorded for extant coral reefs (Sheppard, 2009; Riegl and Purkis, 2012). Shallow (generally <30 m) water depth and restricted water exchange with the Indian Ocean, requires that resident corals must not only endure the highest maximum SSTs (>35°C in summer) recorded for extant coral reefs, but also the largest seasonal range of >20°C (Sheppard, 2009; Riegl and Purkis, 2012). In addition, high evaporation rates in the PAG result in unusually high salinity, regularly exceeding 40 psu (Sheppard, 2009; Riegl and Purkis, 2012). Since the PAG was only formed about 15,000 years ago, and shifted toward the present temperature regime only 3–6,000 years ago (Sheppard, 2009; Purkis et al., 2010), Gulf corals have adapted to these extreme environmental conditions over only the last few millennia. As such, the PAG has become a popular area to better understand the mechanisms corals have evolved to thrive under warmer climates.

Corals within the PAG have the highest upper temperature thresholds for bleaching (~35–36°C; Riegl and Purkis, 2012; Coles and Riegl, 2013), but still remain highly susceptible to bleaching when temperatures exceed their local maximum summer temperatures (Coles and Riegl, 2013; Kavousi et al., 2014). For example, five times from 1995 to 2010, temperatures exceeded normal summer temperatures, reaching 35–37°C for extended periods of time, which resulted in extensive bleaching and mortality (Coles and Riegl, 2013; Kavousi et al., 2014). These disturbances resulted in a decline of branching species and rise of massive faviid corals. It is well-known that massive coral species are typically more tolerant to light and heat stress, and such shifts from more heat-sensitive, branching coral communities to more heat-tolerant, massive communities are commonly observed after bleaching (e.g., Loya et al., 2001). In contrast to branching corals, massive corals have skeletons that are less efficient in enhancing the internal light field of the coral (Enríquez et al., 2017), which appears to be a key factor in enabling their higher tolerance to light and heat stress. Although less diverse and spatially complex, the new poritid- and faviid-dominated communities in the PAG appear to be relatively resilient to ongoing disturbances in the region (e.g., Bento et al., 2016) and could represent future coral communities

under continued climate change and increasing anthropogenic stressors.

Extensive research into the biology of corals surviving in the warm waters of the PAG has revealed mechanisms for survival, such as metabolic trade-offs (e.g., reduced fecundity Howells et al., 2016a), and unique physiological and genetic signatures, notably a regionally prevalent heat-specialist algal endosymbiont, *Symbiodinium thermophilum* (Hume et al., 2015; Smith et al., 2017a) belonging to a highly diverse ancient group of symbionts cryptically distributed outside the PAG (Hume et al., 2016). *S. thermophilum* occurs in high temperature, high saline environments, and as such, the benefit of a temperature stress-resistant phenotype, comes with a fitness-trade off of existing in high saline systems (D'Angelo et al., 2015). In addition to the algal endosymbiont species, PAG corals appear to have evolved genetic hardware at both the level of host and host associated bacteria in heat stress resistance, for example, the coral *Platygyra daedalea* exhibits superior ability to cope with oxidative stress in the PAG compared to conspecifics from the cooler Gulf of Oman (Howells et al., 2016b). Unusual patterns in the coral microbiome of PAG corals were also recently observed, as bacterial microbiome composition was found to be similar in bleached and healthy *Porites lobata* corals (Hadaidi et al., 2017), which is in contrast to studies from other coral reef regions (e.g., Bourne et al., 2007).

The PAG is arguably the world's hottest sea supporting coral reefs; however, other hot seas exist (e.g., the Red Sea) that support corals potentially more tolerant of thermal stress events (Fine et al., 2013; Grottoli et al., 2017; Krueger et al., 2017). The hot, southernmost end of the Red Sea acts as a selective thermal barrier favoring heat-resistant genotypes; once these genotypes spread to the northern, cooler Red Sea, they live well below their bleaching threshold (Fine et al., 2013). Consequently, elevated temperatures of 2°C above average thermal maxima did not result in any coral bleaching in northern Red Sea corals in laboratory studies (Fine et al., 2013; Krueger et al., 2017), and for three coral species, *Stylophora pistillata*, *Pocillopora damicornis*, and *Favia fava*, coral bleaching did not occur until 6°C above average thermal maxima (Krueger et al., 2017). Furthermore, the coral *S. pistillata* has shown resistance to the combined effects of ocean acidification (pH 7.8) and elevated temperatures (Krueger et al., 2017). The unique evolutionary history of northern Red Sea corals highlights the key role of broad latitudinal temperature gradients in promoting adaptation to high temperatures and providing genetic rescue via the exchange of heat-resistant genotypes across latitudes. However, high connectivity across latitudes is critical for the establishment of high temperature high-latitude coral reef environments as refugia from climate change.

Highly Variable Temperature Environments

Alongside environments that experience persistently high temperatures, environments that have variable temperature regimes can provide information on the heat-tolerance, and acclimation/adaptation potential of coral species. Variations in temperature regimes can occur due to local (e.g., tide pools) conditions, or can result from temporal differences (e.g., high-latitude corals).

Back Reef Tide Pools

Elevated temperatures become particularly pronounced as reefs shallow and flushing becomes restricted. One key system that has been extensively studied since the early 2000s is the back reef tide pools on Ofu Island, American Samoa. The back reef tide pools harbor diverse coral communities (Craig et al., 2001) and feature distinct thermal regimes, governed by the thermal dynamics of pools of different sizes (Smith et al., 2007; Oliver and Palumbi, 2011b; Koweek et al., 2015); specifically, smaller high-variance (HV) pools where SST can briefly reach 35°C during strong noontime low tides (exceeding the local critical bleaching temperature of 30°C) and fluctuate by up to 6°C daily, vs. larger moderately variable (MV) pools, where SSTs rarely exceed 32°C and exhibit a more stable thermal environment.

Corals within the HV pool appear to have acquired putative heat tolerance through genetic, physiological, and ecological adaptations. For example, phenotypic plasticity of skeletal characteristics (Smith et al., 2007) that could potentially be linked to optimization of skeletal optical properties (Enriquez et al., 2017), a switch in symbiont type that is considered more heat-tolerant (Smith et al., 2008; Oliver and Palumbi, 2009, 2011a,b), enhanced thermal tolerance when exposed to heat stress (Oliver and Palumbi, 2011b; Palumbi et al., 2014), higher transcription of heat responsive genes than MV corals (Barshis et al., 2013) and a reservoir of alleles pre-adapted to high temperatures (Bay and Palumbi, 2014). Changes in the microbiome have also been demonstrated with bacterial communities changing in response to transplantation between the MV and HV pools (Ziegler et al., 2017). Higher heat tolerance of HV corals was found to be the result of both local acclimatization and fixed effects such as adaptation, with acclimatization in <2 years achieving the same heat tolerance that would be expected from strong natural selection over multiple generations (Palumbi et al., 2014). This unique system has thus provided critical insights into the mechanisms underlying coral heat tolerance, particularly of host-based contributions to holobiont heat tolerance. Nevertheless, it is currently unclear whether even naturally heat tolerant corals can continue to improve their heat tolerance fast enough to keep pace with global warming, with locations within American Samoa recently experiencing severe bleaching (Eakin et al., 2016).

High-Latitude Environments

Corals from high-latitude environments are functionally different to tropical corals, having traits that may facilitate their survival under climate change (Beger et al., 2014). High-latitude, cooler water (sub-tropical) coral environments have received increasing attention as potential refugia from climate change and ocean warming for tropical coral reef organisms (Beger et al., 2014; Muir et al., 2015b). They currently exist at the environmental limits for growth, in terms of temperature, salinity and Ω_{arag} , where conditions are also highly seasonally variable (Kleypas et al., 1999; Guinotte et al., 2003). Well-studied locations include: Lord Howe Island and the Solitary Islands (30–32°S), Sydney Harbour (34°S) in eastern Australia, the Abrolhos Islands (28°S) and Rottneest Island (32°S) in Western Australia, Sodwana Bay in South Africa (28°S), several islands

in temperate Japan (32–34°N), and Bermuda (32°N). Due to the marginal environmental conditions (particularly at more extreme high-latitudes), they can be considered natural extreme coral reef environments which differ from their tropical counterparts in many aspects. For example, the unique diversity of high-latitude reefs is due to the overlap of tropical and temperate species ranges, species that are rare or absent at lower latitudes and species endemic to these environments (Beger et al., 2014 and references therein). Species temporal turnover can be high depending on larval supply and recruitment from lower latitudes and fluctuations in environmental conditions. Whilst coral cover (Harriott et al., 1994; Thomson and Frisch, 2010; Denis et al., 2013) and even coral growth rates can be high (e.g., Ross et al., 2015), reef accretion and development are nevertheless often limited, with corals sometimes only forming living veneers on rocky substrate (Beger et al., 2014 and references therein). Furthermore, future reef accretion could become increasingly challenged with the percent changes in Ω_{arag} predicted to be greater at high-latitude reefs relative to their tropical counterparts (Hooionk et al., 2014).

Greater fluctuations in environmental conditions at high-latitude coral reefs have been hypothesized to increase the environmental tolerance of high-latitude species as observed in tropical corals (Oliver and Palumbi, 2011b; Schoepf et al., 2015), thus potentially increasing their ability to cope with climate change. In high-latitude corals, phenotypic plasticity may support their survival, through diverse coral symbiont communities (Wicks et al., 2010b), enhanced symbiont tolerance to extreme (low) temperatures (Wicks et al., 2010a), enhanced heterotrophic plasticity (Bessell-Browne et al., 2014) and evidence of shifted thermal optima for calcification at cooler temperatures (Ross et al., 2015). High-latitude coral communities around the world have also been found to reproduce sexually and are therefore not solely dependent on recruitment from tropical region coral stocks (e.g., Babcock et al., 1994; van Woeseik, 1995; Wilson and Harrison, 2003; Miller and Ayre, 2004; Madsen et al., 2014).

As predicted, corals have already extended their latitudinal range pole-wards in several locations such as Japan and eastern Australia (Booth et al., 2007; Yamano et al., 2011; Baird et al., 2012), although range expansion can be accompanied by reduced symbiont diversity (Grupstra et al., 2017). The ability and rate of this range expansion will be key in determining the ability of high-latitude locations to act as refugia. Furthermore, high-latitude corals themselves are increasingly threatened by climate change and ocean warming, as bleaching events have also occurred in many high-latitude locations in recent years (Celliers and Schleyer, 2002; Harrison et al., 2011; Thomson et al., 2011; Abdo et al., 2012; Smale and Wernberg, 2012). In addition, several other factors specific to high-latitude coral reefs, such as latitudinal light attenuation (Muir et al., 2015a), geographic isolation and small population sizes combined with greater predicted ocean warming and generally lower Ω_{arag} of cooler waters, could make high-latitude coral communities particularly susceptible to climate change (Beger et al., 2014). It is therefore currently unclear whether and to what extent high-latitude corals can in fact serve as refugia from continued climate

change, despite evidence for some adaptations to their marginal, more extreme environments.

Broad Temperature Gradients

Reef systems that extend across broad latitudes and temperature gradients have provided evidence of juvenile (Woolsey et al., 2015) and adult corals with enhanced thermal tolerance (Ulstrup et al., 2006; van Oppen et al., 2011; Howells et al., 2012, 2013). On the Great Barrier Reef (GBR), mean summer maximum temperatures have been reported to have nearly 2°C difference at reefs 250 km apart (South Molle Island to Magnetic Island; Howells et al., 2013). Different thermal histories on the GBR have been found to influence bleaching susceptibility (Ulstrup et al., 2006; Ainsworth et al., 2016) and the physiological performance of a generalist coral symbiont (Howells et al., 2012). Warmer latitudes have also been shown to enhance heritable thermal tolerance, up to 10-fold in *Acropora millepora* from the GBR (Dixon et al., 2015). Such latitudinal gradients thus provide important information over the spatial scales through which thermal tolerance can be achieved, and opens discussion on the ability for more “tolerant” species to provide “genetic rescue” through the exchange of more tolerant larvae across latitudes (Ingvarsson, 2001). That said, studies of the coral *Oculina patagonica* in the Mediterranean across locations with different thermal temperature regimes demonstrated limited capacity to acclimate to conditions comparable to future warming (Rodolfo-Metalpa et al., 2014). Thus, the ability for corals to inherit thermal tolerance is likely to be species-specific, and highly-dependent on the dynamics of local temperature regimes. Costs may also be associated with greater thermal tolerance, for example, a thermo-tolerant symbiont, *Symbiodinium trenchii* (D1a), has been shown to reduce host mortality rates by 30% under thermal stress; however, that is accompanied by a reduction in growth rates of 50–60% (Little et al., 2004; Smith and Iglesias-Prieto, 2010; Pettay et al., 2015). Energetic trade-offs need to be considered alongside the benefit of tolerance to assess whether coral reef form and function can be maintained.

Low Light Environments

Limitations in light availability can be fundamental in restricting scleractinian coral distribution (Yentsch et al., 2002; Muir et al., 2015a). However, during thermal stress events, solar radiation can act synergistically to intensify the impact on corals (Mumby et al., 2001; Anthony et al., 2007). Consequently, shaded (Coelho et al., 2017) and low-light environments (e.g., turbid reefs and mesophotic reefs) that are typically considered marginal for coral growth, could become increasingly valuable for corals under climate change and ocean warming.

Turbid Reefs

Inshore turbid environments (Figure 2) often have a suite of extreme conditions, such as low light and elevated water temperatures, and thus have historically been overlooked as important coral environments. Corals employ physiological plasticity to persist in turbid waters, including flexible photosynthetic properties, which may include a change of algal endosymbiont genetic type, and/or enhanced host

heterotrophy (Anthony, 2000; Anthony and Fabricius, 2000; Hennige et al., 2008, 2010; Suggett et al., 2012b). Morgan et al. (2016) recently described over 21 genera of coral surviving in muddy waters on the inshore GBR suggesting that turbid systems may afford important range (niche) extension beyond that currently considered for many key “blue water” tropical oligotrophic reef-forming coral taxa.

High irradiance exacerbates susceptibility to coral bleaching, and thus turbid reef environments where irradiance is reduced could act as potential refugia during bleaching events. Cacciapaglia and van Woesik (2015) predicted that 9% of coral environments previously considered uninhabitable under ocean warming, due to the combination of elevated temperatures and high irradiance, would be protected by the mitigating effect of shading in high turbid sites. Studies in Palau (van Woesik et al., 2012), Florida (van Woesik and McCaffrey, 2017), and on the GBR (Morgan et al., 2017) have all provided compelling evidence that coral bleaching can be reduced at high-turbidity sites. Consequently, as the oceans warm and bleaching events become more frequent, there could be a direct selection of corals able to survive in inshore turbid environments (van Woesik and McCaffrey, 2017). Potts and Jacobs (2000) propose that turbid inshore habitats have provided ecological and evolutionary continuity and refugia for scleractinian corals during non-reefal periods when environmental conditions have been too extreme for reef growth.

Mesophotic Reefs

High-anthropogenic stress experienced by shallow reefs has seen deeper reefs proposed as potential refugia (Glynn and Morales, 1997; Riegl and Piller, 2003; Armstrong et al., 2006). Under this hypothesis, deeper reefs are able to: (i) protect or reduce the disturbances faced on shallower reefs, and (ii) provide a genetic stock of corals that can re-seed shallower reefs after a disturbance. Supporting this theory are studies evidencing reduced bleaching on deeper coral reefs (e.g., Riegl and Piller, 2003; Bridge et al., 2014). However, this bleaching pattern is not always observed; for example, with deeper corals in the Seychelles bleaching first, and more severely, than shallow corals during the 1997–1998 bleaching event (Spencer et al., 2000). Smith et al. (2016) demonstrated that deep (30–75 m) coral reefs have lower bleaching threshold temperatures than shallow-reefs, and that any increase in temperature above the local mean can result in stress and bleaching. Furthermore, deepwater generally has lower pH and Ω_{arag} than shallow-water, complicating the ability of these systems to act as refugia.

Capacity for deep reefs to act as potential refugia remains debated and depends in part on the connectivity of shallow and deep coral populations (Bongaerts et al., 2011). van Oppen et al. (2011) found evidence of deep-to-shallow coral recruitment for some reefs (Scott’s Reef) on the GBR, but not others (Yonge Reef). Similarly, Serrano et al. (2014) found geographic differences in vertical connectivity due to local geophysical conditions. Species-specific differences in population connectivity with depth have also been reported in the Caribbean (Bongaerts et al., 2017).

Low-light conditions of deeper reefs are considered sub-optimal, and may select against some corals that do not have the physiological plasticity to survive. For example, Smith et al. (2017b) identified the importance of photoconvertible red fluorescent proteins (pcRFPs) to support coral adaptation/acclimation to deeper waters, while Cooper et al. (2011) showed that both the host and symbiont needed to have photobiological flexibility to survive across light regimes. Similarly, Lesser et al. (2010) found for the coral *Montastrea cavernosa* in the Bahamas that both physiological and morphological adaptation was required to survive in depths down to 91 m. Changes in the endosymbiont community (e.g., Frade et al., 2008; Lesser et al., 2010; Bongaerts et al., 2015) and density (Frade et al., 2008) have also been reported with depth. Specialization of deeper coral communities suggests plasticity will be required for species to survive across depths and ultimately utilize these systems as potential refugia.

Multiple Stressor Environments

Under climate change, multiple environmental factors such as temperature, pH, and oxygen, are predicted to co-vary (Bijma et al., 2013). Understanding how these changes will co-occur and influence biological processes is one of the hardest challenges facing researchers. Natural extreme environments where multiple factors co-vary, e.g., mangrove systems (Yates et al., 2014; Camp et al., 2016a), shallow reef habitats (e.g., Price et al., 2012), macrotidal reef environments (e.g., Schoepf et al., 2015) and upwelling environments (Riegl and Piller, 2003) offer natural laboratories to address these more complex environmental questions. Notably in these systems it can be difficult to assess the relative importance of individual factors for the observed response; thus, a collective assessment with systems where one abiotic variable primarily changes is essential to advancing our understanding of how corals will survive into the future.

Mangrove Habitats

Mangroves are widespread reef-associated environments that have recently received attention for their potential services to corals threatened by climate change (e.g., Yates et al., 2014; Camp et al., 2016a). Mangrove systems have dynamic temperature, pH and oxygen profiles, and as such, expose resident corals to very different physicochemical conditions than neighboring reefs (Camp et al., 2017). Mangroves are highly heterogeneous in nature, with freshwater input, organic content, system size and consequently water residency time, along with other benthic components (e.g., seagrass composition) influencing the local physicochemical conditions. As such, mangrove systems appear to offer a range of potential services to corals, dependent on local spatial and temporal biogeochemical conditions. For example, work in the Caribbean (Yates et al., 2014) suggested that mangroves could act as a potential refuge for corals, through physical shading and the elevation of downstream A_T as a result of carbonate-sediment dissolution (i.e., buffering potential similar to seagrass habitats), as well as frequent exposure to more variable temperatures. In other locations [e.g., the Seychelles, Indonesia (Camp et al., 2016a) and New Caledonia (Camp et al., 2017)] mangrove systems have exposed corals to simultaneously

low pH, low oxygen and warmer waters relative to adjacent reefs. As such, these mangrove systems may precondition corals to future climates (Camp et al., 2016a) or house corals more resilient to future climate conditions (Figure 2, Camp et al., 2017). In New Caledonia, over 20 coral species were regularly exposed to pH as low as 7.3, temperature 1–2°C higher than adjacent reefs, and oxygen levels below 3 mg L⁻¹ (Camp et al., 2017). Initial research at this site suggests that physiological plasticity (e.g., enhanced respiration indicative of increased heterotrophy) is facilitating survival of diverse coral communities, which include numerous species typically thought to be more sensitive to stress, e.g., *Acropora* spp.

Shallow In-shore Variable Reef Habitats

Physicochemical conditions of shallow reef systems are dynamic and highly influenced by their coastal interface, ecosystem structures and local metabolic activity. Across global locations, there are reports of shallow in-shore reef systems being regularly exposed (albeit for different durations) to conditions predicted for the open-ocean under climate change by the end of the century (e.g., Hofmann et al., 2011; Price et al., 2012; Albright et al., 2013; Guadayol et al., 2014; Kline et al., 2015). The shallow water depth and reduced residency time of inshore waters can create an inshore to offshore carbonate chemistry gradient (Manzello et al., 2012; Shamberger et al., 2014; Camp et al., 2016a). Nutrient run-off and freshwater input can influence A_T , while the metabolic activity of local benthos can change $p\text{CO}_2$ levels. Sites in Palau (Shamberger et al., 2014; Barkley et al., 2015), Puerto Rico (Gray et al., 2012), Florida (Millero et al., 2001; Yates et al., 2007), and the GBR (Santos et al., 2011; Shaw et al., 2012, 2015; Kline et al., 2015) have all been characterized as having extreme in-shore low pH reef systems. In the in-shore low pH bays of Palau, coral cover and richness remained similar to control areas, but community composition shifted, with replacement of *Acropora*, *Montipora*, and *Pocillopora* with *Porites* (Barkley et al., 2015). For the abundant *Porites* sp. skeletal extension and density remained unchanged but macrobioerosion increased at the lower Ω_{arag} sites (Barkley et al., 2015). Interestingly, one of the low pH Palau communities was not dominated by *Porites* but instead, *Leptastrea*, *Platygyra*, *Favites*, and *Dipsastraea*, contributing to the emerging evidence that a range of species are tolerant to low pH conditions. These findings suggest that acidification conditions are not deterministic, and that other local factors are also important in shaping coral community composition under low pH and low Ω_{arag} (Barkley et al., 2015).

Along with environments that have persistently low pH (e.g., Palau), there are highly variable pH habitats that routinely, through tidal and diurnal cycles, experience low pH beyond what is predicted for coastal systems by 2100 (Duarte et al., 2013). For example, the Heron Island reef flat can experience a seasonal range in temperature of 8.1°C (17.9–26°C) and pH of 1.04 (7.57–8.61; Kline et al., 2015). Daytime photosynthesis, and night-time respiration in the absence of photosynthesis, create large diel cycles in pH (0.75 units, Santos et al., 2011) and Ω_{arag} (5.4 units, Shaw et al., 2012). At these highly variable in-shore sites, carbonate chemistry conditions can be optimal

(elevated pH and Ω_{arag}) or sub-optimal (low pH and Ω_{arag}), and the presence of diverse and abundant coral communities at these sites indicates that corals can tolerate, at least periodic, short-term exposure to low pH. It remains unclear whether exposure to periodic low pH and low Ω_{arag} enhances resistance to future ocean acidification. In the Cayman Islands, corals from a naturally variable inshore pH environment experienced no enhanced tolerance when exposed to conditions predicted for 2100 (Camp et al., 2016b). Similarly, three coral species in Florida Bay regularly exposed to seasonal and diel variance in $p\text{CO}_2$ and Ω_{arag} showed no reduced sensitivity to low Ω_{arag} , with calcification rates equivalent to corals from a more stable physicochemical environment (Okazaki et al., 2013). However, the natural oscillations of $p\text{CO}_2$ in these in-shore environments may reduce the negative effects of elevated $p\text{CO}_2$, by ensuring at least periodic conditions for optimal calcification. For example, Comeau et al. (2014) observed calcification rates for *Acropora hyacinthus* that were increased by 21% under 400 to 2,000 μatm oscillatory $p\text{CO}_2$ vs. 1,000 μatm constant $p\text{CO}_2$ treatment. Such heterogeneity of in-shore reef systems, means that some locations dominated by photoautotrophs could in fact see an elevation in mean pH relative to offshore, due to the daytime consumption of CO_2 elevating pH and local Ω_{arag} , as observed for the back reefs of the Cayman Islands (Camp et al., 2016a) and in seagrass dominated environments.

Macrotidal Coral Reef Environments

Coral reefs subjected to large tidal ranges are similarly exposed to extreme environmental conditions. The most extreme macrotidal reef site examined to date is the Kimberley region in northwest Australia, which features the world's largest tropical tides (up to 12 m). Corals on the reef flat of the Kimberley region have to cope with extended aerial exposure during spring low tides (up to several hours, Figure 2) and periods of stagnant water alternating with strong tidal currents (>10 knots). These physical conditions create extreme fluctuations in environmental parameters, such as temperature (e.g., the well-studied Shell Island where temperature can fluctuate by up to 7°C daily, Dandan et al., 2015; Schoepf et al., 2015), pH (e.g., Tallon Island where pH can fluctuate from 7.6 to 8.8 units over a spring low tide, Pedersen et al., 2016), dissolved oxygen (Pedersen et al., 2016; Gruber et al., 2017), unusually turbid waters, and monthly SST exceeding 30°C for several months a year. Despite these extreme conditions, highly diverse coral reefs exist throughout the Kimberley of up to 225 species (Rosser and Veron, 2011; Richards et al., 2015), which are comparable to inshore reefs in the central GBR ~2 decades ago (Richards et al., 2015).

Research is just beginning to uncover the biological properties that allow corals to thrive in this extreme macrotidal environment. Firstly, algal endosymbionts appear to be locally adapted with clade C dominating northern Kimberley *Acropora* assemblages (Thomas et al., 2014) and southern *Acropora* and *Dipsastraea* corals (Schoepf et al., 2015); however, further research is required to determine how *Symbiodinium* diversity within clade C is linked to environmental gradients in this region. Furthermore, thermal history has been shown to influence bleaching susceptibility of corals harboring the same symbiont

type, with more variable temperature environments enhancing heat resistance (Schoepf et al., 2015). During the first documented regional-scale bleaching event in the Kimberley in the austral summer of 2016 (Hughes et al., 2017), corals were more severely bleached (Le Nohaïc et al., 2017) and experienced much greater mortality (V. Schoepf, unpublished data) at the less-variable subtidal site on Shell Island.

Reef flat communities of the Kimberley appear to have adapted their physiology to maintain metabolic balance of photosynthesis-to-respiration (P:R) despite the extreme physicochemical conditions of the reef-flat (Gruber et al., 2017). Furthermore, a seasonal calcification study revealed high resilience of coral calcification to both intertidal and subtidal temperature conditions as branching and massive corals calcified at rates that were comparable to those of similar species at a more typical coral reef 1,200 km to the southwest (Ningaloo Reef; Dandan et al., 2015). Given that rising sea levels are expected to reduce extreme temperature variation on macrotidal reef flats such as Tallon Island (Lowe et al., 2016), reef flat communities might have more time than other reef types to acclimatize and/or adapt to ongoing ocean warming. However, further research is needed on these systems to disentangle the complex interactions of acclimation/adaptation processes that support coral survival under such extreme physicochemical conditions.

Upwelling Environments

Dispersed across the world's oceans are sites where deep, nutrient-rich, cooler ocean water wells-up to the surface through local water circulation. Such waters have been proposed as potential localized coral refugia under times of thermal stress (Riegl and Piller, 2003); however, the cool water is also high in CO_2 and low in Ω_{arag} ; consequently, upwelling environments have the potential to be ocean acidification hot-spots (Feely et al., 2008; Manzello, 2010). Upwelling sites clearly comprise a complex mix of abiotic stressors, with any refuge potentially limited by upwelling time (Chollett et al., 2010). In regions such as the Eastern Tropical Pacific (ETP) and Arabian Sea, marginal coral reef formation has been attributed to the cool upwelled waters creating a "pseudo-high-latitude effect" (Sheppard and Salm, 1988) by reducing reef-building processes (Benzoni et al., 2003). Here, corals do not form a true reef structure, but instead form low-relief coral carpets (often monospecific) or remain as isolated coral colonies that are generally small in size. These locations can illustrate the changes in coral community composition when reef formation ceases, as is predicted to occur in a high CO_2 world.

A unique upwelling system exists in the ETP where high CO_2 water upwells to the surface, resulting in coral reef and coral communities off the coast of the Galápagos Islands having some of the lowest Ω_{arag} documented for modern coral reefs (<2.5 , (Manzello et al., 2008)). Corals of the Galápagos Islands and neighboring Panamá reefs also contend with frequent exposure to the El Niño-Southern Oscillation (ENSO, $+3\text{--}4^\circ\text{C}$ during ENSO events for >2 months), creating a unique opportunity to study the long-term effects of low pH and thermal stress events on corals (Manzello et al., 2014). Only one coral reef exists within the low Ω_{arag} waters of the Galápagos archipelago and it is dominated

by *P. lobata* (Manzello et al., 2014). High bioerosion rates ($>25 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) and low reef cementation are characteristic of sites within the Galápagos region (Manzello et al., 2008).

Upwelled waters of the ETP are also high in nutrients, which may in part have enhanced coral growth rates for four coral species of the ETP (Jiménez and Cortés, 2003). Elevated nutrient levels have the potential to alleviate some of the negative impacts of decreased coral calcification associated with the low Ω_{arag} of the upwelled waters, by potentially enhancing heterotrophy (Langdon and Atkinson, 2005; Cohen and Holcomb, 2009), or increasing inorganic nutrients that can enhance cell growth and proliferate abundance of the algal symbiont (see review by Fabricius, 2005). However, enhanced heterotrophy may not always be an advantage for corals around cooler upwelling sites, with zooplankton feeding rates of three coral species reduced under cooler upwelling conditions in Panamá (Palardy et al., 2005). High nutrients, in particular phosphates, can also reduce skeletal density (Dunn et al., 2012), and may explain why corals around the Galápagos Islands maintain their linear extension rates, but experience reduced skeletal density (Manzello et al., 2014). Increased exposure to nitrogen levels has also been documented to enhance bleaching susceptibility when exposed to heat and light stress (Wiedenmann et al., 2013) and could add to the potential bleaching susceptibility of corals at upwelling sites (D'Croz and Maté, 2004). Clearly the net-gain or cost of elevated nutrients for corals around upwelling sites remains debated and is an area for further investigation. An important consideration with upwelling sites is that the severity or even presence of upwelling is often seasonal (as occurs for sites of the ETP), meaning the physicochemical conditions representative of future scenarios may be limited in duration. Timing of assessment at these sites is therefore important, with seasonal differences having large impacts on the biodiversity recorded (e.g., Diaz-Pulido and Garzón-Ferreira, 2002; Witman and Smith, 2003).

DISCUSSION

What Are the Extreme Abiotic Scenarios Extant Corals Persist under?

Review of the current literature on extreme and marginal coral environments demonstrated that coral populations presently thrive under different combinations of extreme abiotic conditions that are comparable to, or even exceed, predictions for the open-ocean under future climate change (Figures 3, 4). For example, corals around ojos experienced persistently low pH below 7.7 (Crook et al., 2013), while corals of the PAG in summer experienced temperatures exceeding 35°C (Sheppard, 2009); these are conditions that are not predicted for the tropical open-ocean to well beyond 2100 (IPCC, 2014). The predictability and duration of the extreme environmental conditions experienced by corals are important considerations when assessing the role these environments can play in coral reef research and management. For example, regular exposure, rather than periodic pulses of extreme conditions may be required to facilitate acclimation and/or adaptation (e.g., Oliver and Palumbi, 2011a; Howells et al., 2012). Alternatively, fluctuating

abiotic conditions, such as pH, may offer periods of time when physiological processes (e.g. calcification) can occur at less of an energetic cost. A key question is therefore how species will respond to stress according to different exposure time-frames (Mumby and Van Woesik, 2014). To better resolve how environmental history influences the survival of extreme and marginal corals, continuous, multi-physicochemical data sets are required that show both the mean and range of environmental conditions. As demonstrated in **Figure 4**, clustering of sites varied depending on the metric considered, e.g., mean or range. When reporting environmental conditions, there is also a need to provide both the immediate and historical context. As such, it is recommended that actual abiotic measurements (both mean and variance) are reported alongside historical datasets.

The current review highlighted that few studies reported multiple physicochemical conditions. For example, a seasonal comparison of pH, temperature, A_T , salinity, and oxygen was only possible at a total of 14 sites spanning five environments (**Figure 4**). The limited data collected on multiple abiotic parameters fundamentally restricts our ability to: (i) determine how extreme some coral environments are, and (ii) understand the different biogeochemical responses reported across sites. The PCA highlights that for many environments multiple parameters interact within these extreme systems (**Figure 4**), thus emphasizing the need to collect a full suite of abiotic parameters to provide context for biological assessments (**Table 1**). Whilst such a recommendation is not trivial, it becomes increasingly important as we begin to resolve the complex abiotic interactions that regulate many biological processes.

Are There Commonalities in Coral Taxa of Extreme Environments?

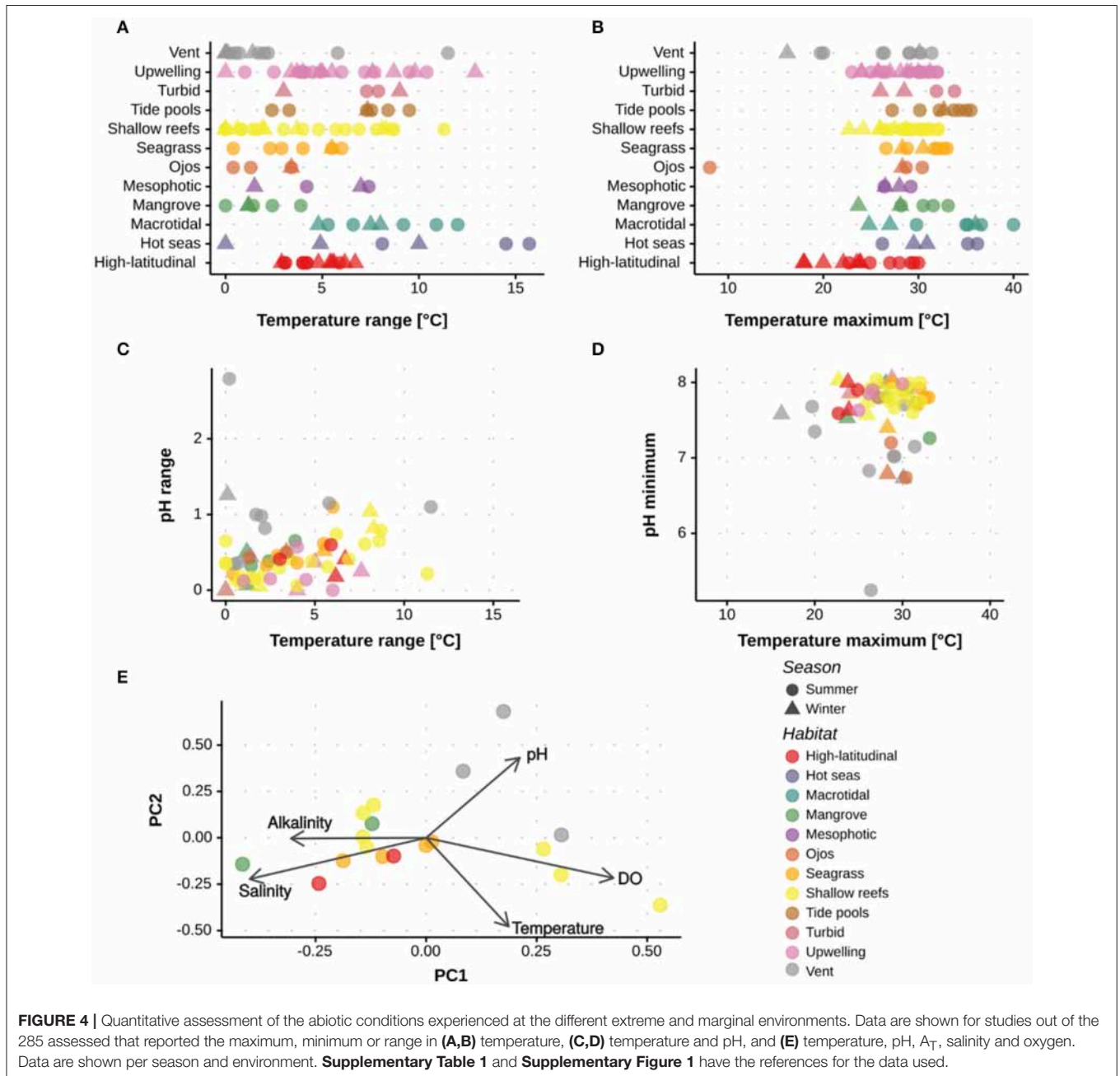
Review of the current literature suggests that the capacity for coral taxa to persist in sub-optimal environments is species-specific, and largely dependent on local factors, e.g., nutrient availability. Despite a lack in common coral taxa across extreme environments, critical thresholds in community structure do appear to exist as abiotic conditions become increasingly less optimal: (i) an initial reduction in species diversity (e.g., Craig et al., 2001; Fabricius et al., 2011; Enochs et al., 2015) with specialist species often able to survive and potentially even thrive within the new environmental niche (e.g., Kroeker et al., 2011; Fabricius et al., 2014; Dandan et al., 2015; Schoepf et al., 2015), followed by, (ii) a “lethal” threshold beyond which survival ceases (e.g., Inoue et al., 2013). For example, in the vent sites of Japan, hard corals dominate at 225 μatm , become limited at 831 μatm and are absent at the highest $p\text{CO}_2$ sites (1,465 μatm , Inoue et al., 2013). Similarly, in the Kimberley region, diverse coral communities dominated by branching *Acropora* exist in tide pools characterized by large diurnal temperature but not pH fluctuations (Dandan et al., 2015), whereas coral cover drops to <10% and *Acropora* ceases to exist on reef flats where extreme temperature, pH and oxygen fluctuations create a much more extreme environment (Gruber et al., 2017).

Changes in the ecological success of coral taxa can result in shifts in coral community composition that can change the entire reef function. For example, the reduction in coral diversity and dominance by a single taxa, *Porites* of the PNG vent site have reduced architectural complexity compared to adjacent reefs, where multiple coral species with a range of growth forms are present. A loss of reef structure and architectural complexity will compromise the ecological services provided (Rogers et al., 2015). The ability for coral taxa to provide reef accretion is a clear difference between several of the extreme and marginal coral environments; some have diverse coral reef systems e.g., the reef flats of Kimberley (Richards et al., 2015) and American Samoa (Craig et al., 2001), deep-reefs (Glynn and Morales, 1997) and reefs of the PAG (Sheppard, 2009). These environments demonstrate that the realized niche for many corals can in fact span a broad range of abiotic conditions (Schoepf et al., 2015). However, in some environments, non-framework building coral populations are described, e.g., in seagrass habitats of the Cayman Islands and the mangroves of the Seychelles and Indonesia (Camp et al., 2016a,b).

Understanding the interaction of physicochemical factors that result in critical thresholds is required to better predict, and ultimately manage changes in coral community structure, e.g., from accreting reef structures to isolated coral populations. Greater environmental characterization, along with information on the fitness trade-offs for coral populations to survive in sub-optimal environments (see **Figure 2**), will be needed to better resolve the thresholds and patterns underpinning survival (**Table 1**). Ultimately, it is likely that moving to a framework that considers the key functional traits conferring fitness (Madin et al., 2016; Suggett et al., 2017) may be required to overcome the limitations and complexities in attempting to reconcile commonalities based on taxonomic identity. Understanding mechanisms that confer survival will be necessary to identify the traits of interest (Suggett et al., 2017).

Mechanisms That Support Corals Surviving in Extremes

Some naturally extreme environments are well-studied with regards to the mechanisms that support survival, while other sites have only recently been discovered (**Figure 2**). Nevertheless, across environments various adaptive mechanisms seem evident. For example, genetic and physiological characterization across environments where corals have acquired high heat tolerance have shown it is typically the result of acclimatization and/or adaptation in both the coral host and algal symbionts. For example, many PAG corals host an endemic *Symbiodinium* species with high heat tolerance (Hume et al., 2015), but the coral host also contributes to heat tolerance via a superior ability to cope with oxidative stress (Howells et al., 2016b). Similarly, prevalence of clade D *Symbiodinium* is linked to heat tolerance in corals from American Samoa (Oliver and Palumbi, 2011b), but follow-up genomic and transcriptomic work has again highlighted the critical role of the coral host in terms of higher transcription of heat responsive genes and alleles pre-adapted to high temperatures (Barshis et al., 2013; Palumbi et al.,



2014; Bay and Palumbi, 2015). Around the vent sites of PNG, changes in gene expression of *Symbiodinium* were highly variable across populations of *A. millepora*, whereas the host-response remained consistent (Kenkel et al., 2017). These findings suggest population-specific responses may exist, driven by differences in the holobiont community.

Capacity for phenotypic plasticity is also clearly critical in response to naturally extreme environmental conditions. For example, corals across high temperature, low pH, and multi-stressor sites were able to maintain high calcification rates (e.g., Dandan et al., 2015; Wall et al., 2016), enabled via mechanisms

such as unimpaired pH-homeostasis at the site of calcification (Wall et al., 2016) or increased photosynthesis rates to supply the required energy demand (Strahl et al., 2015a). Although this is sometimes associated with trade-offs such as lower skeletal density and increased bioerosion (Smith et al., 2007; Crook et al., 2013), other corals are able to do so without indication of compromised energy budgets (Strahl et al., 2015a). Similarly, corals in mangrove habitats appear to enhance respiration rates indicative of increased heterotrophy, to facilitate survival in this challenging habitat (Camp et al., 2017). Traits that can facilitate energy acquisition appear beneficial across environments as

TABLE 1 | Future research priorities.

- Collection of longer-term, high-resolution abiotic data sets that include multiple parameters, across different temporal scales.
- Reporting of both mean and variance, and the time-frames over which data were collected to allow better cross-comparison between studies and environments.
- Utilization of multi variant analysis to consider the influence of several abiotic variables on the biological responses reported for corals in extreme systems.
- Ground truth satellite data by deployment of *in situ* loggers.
- Research that considers multiple members of the coral holobiont.
- Research on physiological traits beyond photosynthesis and calcification rates, particularly related to energy budgets.
- Research into the fitness trade-offs associated with surviving in sub-optimal conditions.
- Research into the connectivity of extreme coral populations relative to adjacent, optimal reef environments.
- Understanding the interaction of multiple-stressors, across varying temporal scales.

corals persist toward the tails of their fundamental niche (Sommer et al., 2014). Currently it is still being resolved how the long-term ability to cope with one stressor could impact the ability of corals to deal with other chronic stressors. For example, in the coral *A. millepora* at the PNG vent site, a downregulation of chaperones could increase its vulnerability to temperature stress (Kenkel et al., 2017). Understanding the interaction of multiple-stressors, across varying temporal scales, should be a research priority (Table 1).

For many environments significant knowledge gaps exist regarding the adaptive capacity of their coral population (Figure 2), and further research is required to identify how widespread phenotypic plasticity is across these extreme systems. In particular, it is poorly understood whether high physiological plasticity is ultimately an inheritable trait and thus reflects adaptation of specialist populations. In the PAG for example, the algal endosymbiont *S. thermophilum* demonstrated superior heat tolerance but only within the high saline waters of the PAG (D'Angelo et al., 2015), thus demonstrating that adaptation can constrain the acclimatization potential of well-adapted populations. Similar evidence comes from heat tolerant corals in American Samoa, where the genotype of the coral host limits the plasticity of physiological responses when faced with new environmental conditions (Barshis et al., 2010). Such “specialist” restrictions carry critical implications for the ability of naturally stress-resistant corals to cope with future climate change superimposed on already extreme physicochemical conditions. As a consequence, protecting existing biodiversity by maintaining the largest possible pool of potentially stress-tolerant genotypes, rather than solely the best adapted genotypes, will be crucial to provide sufficiently diverse genetic material for evolution to act on, and thus promote rapid adaptation to climate change (Hume et al., 2016).

The Potential of Refuge Environments

Refuge environments are likely to become increasingly important, particularly for species that are less capable of acclimating to environmental change. The current review shows that there are systems that could off set single stressors; for

example, turbid reefs can provide refuge for corals during thermal stress events (van Woesik et al., 2012; Morgan et al., 2017; van Woesik and McCaffrey, 2017) whereas high-latitude reefs can provide refuge from rising ocean temperatures (Beger et al., 2014; Muir et al., 2015a). However, with the exception of the northern Red Sea (Fine et al., 2013), most refuge environments are highly debated, with inconsistent findings across geographic locations. This, in part, results from the heterogeneity of coral environments on the scale of individual reefs. For example, local hydrography likely explains why some deep reefs, but not others, are capable of seeding shallow reefs (van Oppen et al., 2011; Serrano et al., 2014). Similarly, differences in local physicochemical conditions see mangroves of the U.S. Virgin Islands considered a coral refuge, while mangrove systems in the Seychelles, Indonesia and in New Caledonia are not (Camp et al., 2016a, 2017).

Timing of buffering is also an important consideration at these potential refuge environments. Upwelling sites, for example, can only offset thermal stress if the pulse of cool upwelled water coincides with a stress-event, yet this is frequently not the case (Chollett et al., 2010). Similarly, seagrass environments can only positively enhance local seawater pH and Ω_{arag} during the day, with the opposite occurring at night due to the dominance of respiration in the absence of photosynthesis (Schmalz and Swanson, 1969). Furthermore, environments that operate as a refuge against one abiotic variable may also enhance stress from another; for example, cool upwelled water often has a lower Ω_{arag} , which can increase the threat of ocean acidification (Manzello, 2010). Similarly, lower light levels and Ω_{arag} characteristic of high-latitude reefs, particularly during winter, could potentially become limiting for many physiological variables (Beger et al., 2014; Muir et al., 2015a,b).

A further complication of refuge environments is that we currently have only limited information on the ability of non-native coral populations to move into these systems. Although poleward range expansion of tropical coral has been documented in several geographically different locations (e.g., Yamano et al., 2011; Baird et al., 2012), such information for other potential refuge environments is currently lacking. Thus, we do not know if all corals could utilize potential refuge services as they may lack the traits needed to survive. For example, there is evidence that corals surviving on deep reefs require physiological plasticity to survive (Lesser et al., 2010; Cooper et al., 2011; Smith et al., 2017b). An ultimate unknown on the potential of refuge environments is how they will themselves change in the future, and ultimately whether favorable physicochemical conditions can be sustained (Shaw et al., 2013). What we do know is that our understanding of conditions optimal for refugia is increasing, but that the heterogeneous nature of reef systems challenges the ability for environments to act as refuge against multiple abiotic parameters. Effective refugia have recently been described by Kavousi and Keppel (2017) as needing to provide long-term buffering to multiple-stressors. As such, consideration could be given to environmental engineering to facilitate the suite of conditions

required for effective refugia, e.g., artificial shading (Coelho et al., 2017).

CONCLUSIONS

The future structure and composition of coral communities will be shaped by the vulnerability of different species to climate change and local stressors. Protection of existing biodiversity must be a priority to help maintain the greatest pool of stress-resistant genotypes (Hume et al., 2016). Critical thresholds appear to be a commonality for coral populations within extreme coral environments, which could provide valuable information on the tipping-points beyond which coral reefs or coral populations cease to exist. Importantly, corals will need to be ecologically competitive despite the extreme prevailing conditions to maintain their form and function. This could be increasingly challenging if they experience reductions in growth, while other taxa they compete for space with flourish, e.g., photoautotrophs (Durako, 1994; Buapet et al., 2013; Hendriks et al., 2014). Slower growth not only limits reef formation, but it can also compromise recruitment success (Ortiz et al., 2014). The interaction between taxa will be important in shaping the realized niche of corals into the future as environmental conditions change. As such, caution should be taken in making simple projections on future reef form and function when only a limited number of species are considered (Mumby and Van Woesik, 2014).

Our collective assessment of extreme and marginal coral environments highlights that multiple factors appear important to coral survival in sub-optimal conditions, particularly phenotypic plasticity and ecological fitness traits that can facilitate energy acquisition. Consequently, unless corals can be protected by refuge environments, it will be the collective suite of available traits of the coral holobiont that determine its adaptive capabilities and ultimate survival. As such, understanding the full suite of traits available for corals to trade-off for survival is imperative to assessing the future vulnerability of species, and ultimately shifts in community structure and function (**Table 1**) (van Woesik et al., 2012). Caution must therefore be taken in assessing single traits and using these to make statements on acclimation and/or adaptive potential (e.g., Suggett et al., 2017).

While no single environment is a perfect analog to projected future climates (which themselves are uncertain), they consistently provide evidence of corals tolerant to stress conditions that could become the “norm” in the future, and that plasticity is often required to survive. Extreme coral populations provide key additional tools for researchers to use alongside laboratory studies and modeling, to better understand the future survival of coral reefs. Beside the value extreme coral environments offer for research, they may also provide additional management options for corals through refuge systems or by providing genetic stocks of corals preconditioned to extreme physicochemical conditions (Camp et al., 2016a). Current information on coral refuge environments remains highly-debated, but evidence suggests the northern Red Sea could provide some refuge for corals in the future (Fine et al.,

2013). Reduction of emissions, in particular carbon dioxide, is undoubtedly required to preserve the future form, function and ecosystem services of coral reefs (Gattuso et al., 2015; Hughes et al., 2017). But there is also an increasing debate over the need to facilitate coral survival through proactive reef management, e.g., reef restoration and/or assisted evolution processes (e.g., Coles and Riegl, 2013; van Oppen et al., 2015; Oppen et al., 2017). The use of proactive reef management is highly debated and beyond this synthesis (see van Oppen et al., 2015; Oppen et al., 2017), but what is evident from these extreme environments is the presence of corals that have traits highly favorable for future survival. For many environments we still do not know how these traits may be conserved or lost as corals are moved to new environments, however evidence of heritable heat-tolerance (Palumbi et al., 2014) and conserved thermal tolerance (Hume et al., 2013) has been reported.

Despite current knowledge gaps, extreme coral environments may have an unrecognized (and disproportionately) high conservation value, due to the trait selection of resident coral populations adapted to extremes. Furthermore, extreme environments may offer genetic rescue (e.g., heat-tolerant genotypes across latitudes), which again gives them a high research and conservation value. As we move to identifying areas of high conservation priority to better target limited management resources, encompassing areas that have extreme elements may be crucial in maximizing diverse genetic populations.

AUTHOR CONTRIBUTIONS

EC, DSu, and VS conceived the manuscript. EC and VS led the review and quantitative synthesis. LH conducted the data analysis and figure production. EC and VS led the writing of the manuscript with all authors contributing to the final manuscript preparation.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2018.00004/full#supplementary-material>

Supplementary Table 1 | Literature used in the quantitative synthesis for each environment.

Supplementary Figure 1 | Quantitative assessment of the abiotic conditions experienced at the different extreme and marginal environments. Data is shown for studies out of the 285 assessed that reported the maximum, minimum, or range in **(A,B)** temperature, **(C,D)** temperature and pH, and **(E)** temperature, pH, A_T , salinity, and oxygen. Data is shown per season and environment. Numbers correspond to the studies where data was obtained (detailed in **Supplementary Table 1**).

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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