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Integrating environmental variability to broaden the research on coral responses to future ocean conditions

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Abstract

Our understanding of the response of reef-building corals to changes in their physical environment is largely based on laboratory experiments, analysis of long-term field data, and model projections. Experimental data provide unique insights into how organisms respond to variation of environmental drivers. However, an assessment of how well experimental conditions cover the breadth of environmental conditions and variability where corals live successfully is missing. Here, we compiled and analyzed a globally distributed dataset of in-situ seasonal and diurnal variability of key environmental drivers (temperature, pCO_2, and O_2) critical for the growth and livelihood of reef-building corals. Using a meta-analysis approach, we compared the variability of environmental conditions assayed in coral experimental studies to current and projected conditions in their natural habitats. We found that annual temperature profiles projected for the end of the 21st century were characterized by distributional shifts

Maren Ziegler, Andrea Anton and Shannon G. Klein contributed equally.

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in temperatures with warmer winters and longer warm periods in the summer, not just peak temperatures. Furthermore, short-term hourly fluctuations of temperature and pCO_2 may regularly expose corals to conditions beyond the projected average increases for the end of the 21st century. Coral reef sites varied in the degree of coupling between temperature, pCO_2, and dissolved O_2, which warrants site-specific, differentiated experimental approaches depending on the local hydrography and influence of biological processes on the carbonate system and O_2 availability. Our analysis highlights that a large portion of the natural environmental variability at short and long timescales is underexplored in experimental designs, which may provide a path to extend our understanding on the response of corals to global climate change.

KEYWORDS
climate change experiments, coral reef, environmental variability, heatwaves, in-situ buoy data, pCO_2, temperature

1 | INTRODUCTION

Coral reefs are one of the most diverse and iconic biomes on Earth, providing ecosystem services and supporting the livelihoods of at least 500 million people (de Groot et al., 2012; Fisher et al., 2015; Wilkinson, 2008). They also rank among the ecosystems most susceptible to climate change (Pandolfi et al., 2011). Record-breaking marine heatwaves in 2015–2016 induced unprecedented global mass coral bleaching, which resulted in a catastrophic die-off of corals that transformed reefs worldwide. While global warming is a main driver of reef degradation (Hughes et al., 2018; Hughes, Kerry, et al., 2017), coral reefs are also vulnerable to concomitant ocean acidification, O_2 depletion, and other anthropogenic stressors (Albright et al., 2016; Andersson & Gledhill, 2013; Anthony et al., 2008; Hughes et al., 2020; Wiedenmann et al., 2013).

Experimental studies assessing the responses of marine biota to climate change provide a powerful tool to improve our understanding of the consequences of rapidly rising levels of atmospheric partial pressure of CO_2 (pCO_2) and concomitant warming on reef corals (Kroeker et al., 2013). Assessing the response of corals to projected climate impacts is therefore fundamental to predict the future of coral reefs. However, this rapidly expanding body of work often builds upon the response of individual organisms exposed to static ocean temperature, pCO_2, and pH conditions projected for the open ocean by the end of the 21st century (i.e., projections of Atmosphere-Ocean General Circulation Models [AOGCMs] as used by the Intergovernmental Panel on Climate Change [IPCC]).

Most experimental manipulations of corals to ocean warming and acidification are based on mean global projections of the four IPCC's Representative Concentration Pathways (RCPs; 2.6, 4.5, 6.0, and 8.5; Hughes, Barnes, et al., 2017; IPCC, 2014). RCP2.6 is a strong mitigation, low greenhouse gas emission scenario with end of 21st-century atmospheric pCO_2 of 430–480 ppm that gives a two in three chance of limiting global warming to below 2°C above pre-industrial temperatures (van Vuuren et al., 2011). RCP4.5 and RCP6.0 are intermediate pathways that result in pCO_2 between 480 and 637 ppm, and warming between 2.4 and 2.8°C (IPCC, 2014). RCP8.5 represents the most aggressive emission scenario without effective climate change mitigation, resulting in a global pCO_2 of 851–1370 ppm and 3.8–4.8°C warming by the end of this century (IPCC, 2014; Riahi et al., 2011). However, some researchers argue that RCP8.5 represents a "worst possible case" scenario that is unlikely to occur (Hausfather & Peters, 2020) and several assessments indicate that median scenarios (RCP4.5 and 6.0) are far more likely (Hausfather & Peters, 2020; Rogelj et al., 2016) given the policies currently in place around the world to reduce carbon emissions (https://climateactiontracker.org/documents/853/CAT_2021-05-04_Briefing_Global-Update_Climate-Summit-Momentum.pdf).

Levels of ocean pCO_2 and warming estimated by the four RCP scenarios are often provided as global averages, which can therefore misrepresent future climate change conditions of specific coral reef provinces (Geraldi et al., 2020; Hughes, Barnes, et al., 2017). For instance, global projections of warming range from 0.7°C (RCP2.6) to 4.8°C (RCP8.5), whereas projections for the six coral reef provinces located between 30°N and 30°S (i.e., the Western Pacific, Caribbean and Gulf of Mexico, Eastern Indian Ocean, Eastern Pacific, Western Indian Ocean, and the Coral Triangle and Southeast Asia) range from 0.3 to 0.7°C under RCP2.6, and 2.7 to 3.1°C under RCP8.5 and may thus overestimate mean temperatures for these provinces. Furthermore, region-specific projections represent plausible outcomes for open-ocean systems within these provinces, but these estimates likely do not account for the substantial heterogeneity of temperature and pCO_2 conditions within particular coral reef ecosystems or coastal environments (Duarte et al., 2013). Importantly, higher frequency and severity of extreme warming events, not just average warmer temperatures, will likely contribute to accelerated coral reef

decline on a global scale (Frieler et al., 2013; Frölicher et al., 2018). Such events have been termed marine heatwaves (MHWs), which are anomalously warm periods, lasting days to months that are typically defined as daily sea surface temperatures (SSTs) exceeding certain percentiles (e.g., 90th, 95th, or 99th) relative to their probability of occurrence in historical baseline periods (Frölicher et al., 2018; Hobday et al., 2016).

While large-scale projections give useful guidance, they provide an incomplete representation of environmental conditions that corals experience today and even less so for conditions expected within this century. There is a growing appreciation that marine habitats are naturally variable environments with consequences for the environmental tolerance and performance of the inhabiting organisms (Kroeker et al., 2020). For instance, natural variability within reef sites can greatly influence accretion potential, thermal tolerance, and coral bleaching trajectories (Ainsworth et al., 2016; Dove et al., 2013; Voolstra et al., 2020). In addition, corals within any individual coral reef ecosystem experience a range of conditions depending on hydrodynamic flows, depth, bathymetry, wind, and currents. Experimental variability among populations of marine organisms can be high in response to projected future average conditions, revealing the potential role of local adaptation and/or phenotypic plasticity to local extremes in increasing resilience of species to environmental change (Osman et al., 2018; Vargas et al., 2017). To assess the environmental conditions that corals experience in their natural habitat, we analyzed high-resolution, long-term in-situ data from five coral reef moorings distributed around the world for seasonal and diel variability in temperature and pCO_2. We then used a global database of published studies on corals (Klein et al., 2021) to compare in-situ environmental variability to that used in climate change experiments on corals and highlight how extant variance in space and time can enhance our understanding and improve future research on coral responses to future ocean conditions.

2 | MATERIALS AND METHODS

2.1 | Time-series data from buoys

The seawater temperature, pCO_2, and O_2 data series logged at 3 h intervals for the period 01.2011–12.2013 were obtained from the moored autonomous pCO_2 buoys ($MAPCO_2^{TM}$) of the global network of CO_2 time-series observations (NOAA coral reef moorings global network; Sutton et al., 2019) in Bermuda (Crescent Reef; 32.40°N, 64.79°W; SCRIPPS), the Florida Keys (24.90°N, 80.62°W; Cheeca Rock; NOAA), the Great Barrier Reef (Heron Island; 22.46°S, 151.93°E; CSIRO), Hawaii (CRIMP2; 21.46°N, 157.80°W; SOEST), and Puerto Rico (La Parguera Natural Reserve; 17.95°N, 67.05°W; NOAA). This time period was chosen because it is representative of non-bleaching years and because it has the highest data coverage between locations.

2.2 | Long-term environmental ranges on coral reefs and experimental treatments

To compare experimentally simulated temperature and pCO_2 treatments in light of local annual profiles, we identified studies involving experimental temperature and/or pCO_2 manipulations with corals collected within a 40 km radius around the data buoys mentioned above (median distance: 4.1 km, average distance: 8.4 km; Table S1). While local-scale variability will differ a lot between any two reef locations, the long-term temperature regimes within regions tend to converge. Therefore, we can be relatively confident in the validity of this comparison. This approach aimed for reasonable proximity while maximizing the number of included studies, and it resulted in a dataset of 38 studies (Bermuda: 4, Florida: 5, Great Barrier Reef: 21, Hawaii: 7, Puerto Rico: 1); we included 31 of these 38 studies that conducted experiments that lasted longer than 24 h (Klein et al., 2021; Table S1). Studies using short-term experiments (<24 h) were excluded, because they tend to exert extreme (unrealistic) conditions and are unsuitable to quantify the effects of recurrent diel variability. The studies were selected from a large-scale global literature search that included a total of 1059 papers (details provided below). Temperatures of control and heat-stress conditions in local experiments were compared to annual temperature profiles of regular non-bleaching years (2011–2013) and to simulated end of 21st-century temperature and pCO_2 under two future greenhouse gas emission scenarios: RCP2.6 and RCP8.5. Annual profiles of RCP2.6 and RCP8.5 scenarios were computed for the daily means of the baseline period 2001–2020 and the end-of-century period 2081–2100. The difference between baseline and end-of-century values was then calculated for each day of the year as delta value. These delta values were calculated for each buoy location separately based on daily mean data from each of nine climate models for sea surface temperature (CanESM2, CSIRO-Mk3-6-0, GFDL-CM3, GFDL-ESM2G, GFDL-ESM2M, IPSL-CM5A-LR, IPSL-CM5-MR, MPI-ESM-LR, and MPI-ESM-MR) that participated in the Coupled Model Intercomparison Project 5 (CMIP5; Taylor et al., 2012) (Supplementary raw data file). We then averaged these daily delta values over the nine climate models to create a daily consensus delta value. Ocean surface pCO_2 projections were based on daily data from GFDL ESM2M (Dunne et al., 2012, 2013) simulations as described in Burger et al. (2020) (Supplementary raw data file). The daily consensus delta values of temperature and the daily delta values of pCO_2 were then added to daily values of in-situ data for the observation period (2011–2013). Therefore, changes in the long-term mean and the daily-to-interdecadal variability are taken into account.

2.3 | Analysis of short-term environmental variability

The 3-hourly variability of temperature and pCO_2 from buoy data for the period 01.2011–12.2013 was obtained after transforming

the data with a 24 h centered moving average to remove seasonal signals. Times were converted to mean solar times (MST) using the R package SolaR (Perpiñán Lamigueiro, 2012).

2.4 | Comparison of in-situ and experimental variability

To compare exposures to environmental stressors between experimental conditions and those in situ, we categorized the magnitude and duration of each stressor (temperature and pCO_2) into 10 distinct groups. A broad range of categories were chosen to represent the distribution of observations in experiments and in situ. For example, an in-situ record of pCO_2 at 3 h intervals would be evaluated in sequence and the duration summed until the magnitude of pCO_2 had changed sufficiently to enter a different bin (e.g., 301–400 ppm for 12 h before switching to 401–500 ppm). Evaluating the durations of exposures from experimental studies was simpler because most studies fixed the magnitude of treatments for a constant period of time. Once every experimental treatment and every sequence of in-situ data had been placed into a category of magnitude and duration, we then calculated the frequency of values for each magnitude/duration combination. Based on these calculations, we created a surface plot of the duration (*x*-axis), magnitude (*y*-axis), and frequency (*z*-axis) of observations, for both in-situ and experimental data. The heat maps compare the relative frequency of stress exposures across a range of temperature and pCO_2 conditions and timescales.

2.5 | Literature search and data recording from peer-reviewed publications

We used the literature database of calcifying corals from Klein et al. (2021), but included additional experiments that measured any biological response and also included non-calcifying cnidarian taxa that inhabit coral reefs. The search was conducted in September 2017 using the Web of Science® database to obtain published literature on experimental responses of benthic cnidarian taxa to the singular and combined effects of ocean warming and acidification (characterized by elevated pCO_2). The search produced 1059 papers and used the following search term: (coral OR octocoral OR anemone OR cassiopea OR scleractinia* OR corallimorpharia* OR gorgonia*) near/10 (impact OR effect OR response OR affect OR stress*) near/10 (temperature OR warming OR heat OR thermal OR "climate change" OR acidification OR *CO2 OR pH OR hypercapnia OR acidosis) NOT fish.

To be included in the database, each published study had to (1) measure the response of benthic cnidarian taxa known to inhabit coral reef ecosystems, (2) report measurable responses to either the singular or combined effects of warming and acidification relative to responses measured in ambient (control) conditions, and (3) report a mean biological response, a metric of dispersion (e.g., standard error), and sample size. For this study, we extracted the temperature and pCO_2 levels tested, the duration of experimental ramping and exposure, and recorded ambient levels of other environmental parameters (e.g., salinity, light intensity, O_2), when available. We classified control (ambient) and treatment (elevated temperature and/or pCO_2) conditions as those defined by the authors of the published studies. The database included published studies of manipulative laboratory experiments, and also included empirical observations from "model" ecosystems (e.g., CO_2 vent sites), providing the study reported responses of benthic cnidarian taxa from both control and treatment sites and the study included efforts to limit the influence of potentially confounding variables between sites. Laboratory experiments that reduced pH using acid–base manipulation (i.e., manipulated total alkalinity rather than dissolved inorganic carbon) were excluded from the dataset because this method does not accurately replicate changes to ocean carbonate chemistry (Gattuso & Lavigne, 2009) and did not permit the comparison between experimental and environmental pCO_2 levels. The final dataset assessed 3323 independent, replicated experiments of 130 benthic cnidarian taxa from 251 published studies (Figure S1), of which 219 assessed responses of reef-building corals.

3 | RESULTS

3.1 | Temperature ranges on coral reefs and climate change experiments

Based on time-series data from five globally distributed moorings (in: Bermuda, Florida, GBR, Hawaii, Puerto Rico representing the Atlantic, Caribbean, Coral Sea, and Pacific Ocean) that cover coral reef locations between the latitudes of 32°N and 23°S (NOAA—Pacific Marine Environmental Laboratory; Sutton et al., 2019), seawater temperature in coral reefs have a minimum and maximum annual range of 4.2°C (Puerto Rico) and 11.9°C (Bermuda and Florida; Figure 1a; Table S2; Figure S2), respectively. We also compared current annual temperature ranges with end of 21st-century conditions under two future greenhouse gas emission scenarios: the RCP2.6 and RCP8.5 (Figure 1a). We found that peak summer temperatures are projected to increase in most locations under RCP2.6 (i.e., the upper ranges of violin plots as projected for Florida, Bermuda and the GBR in Figure 1). Furthermore, the models project warmer winters (i.e., retraction of lower ranges of violin plots) for all locations except Florida under RCP2.6 (Figure 1a).

We further compared temperature ranges and maxima in coral reefs with those used in global change experiments and, although some experimental temperature treatments were in the range of +1 to +2°C of the local summer maximum, the majority of treatments

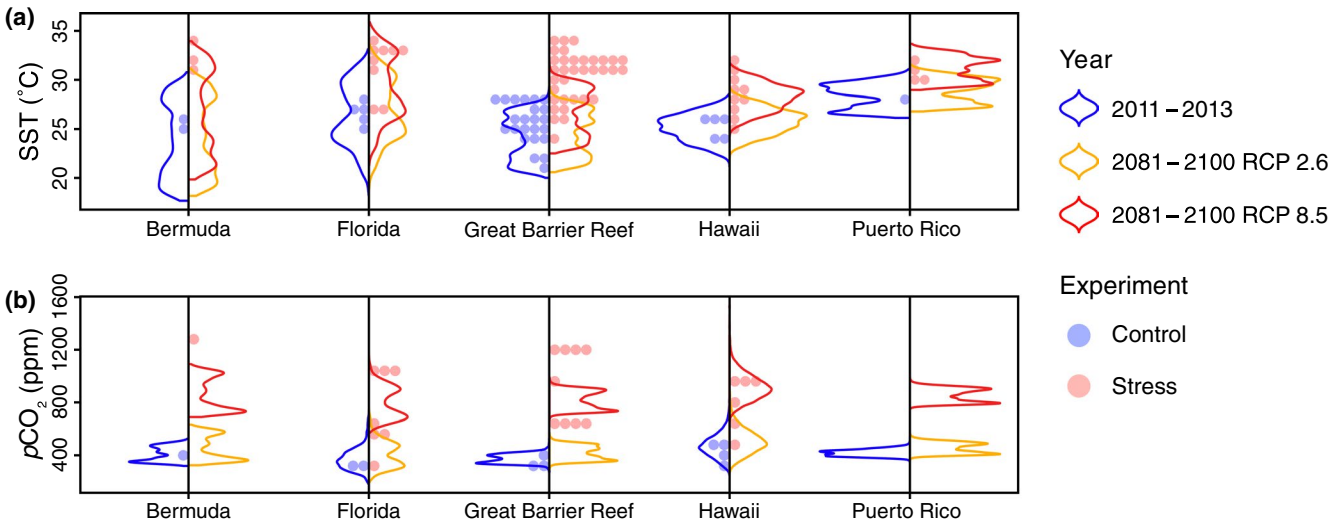

FIGURE 1 Annual range and distribution of (a) seawater temperature and (b) pCO_2 from data buoys at five coral reefs across the globe (Bermuda, Florida, GBR, Hawaii, and Puerto Rico) and control and stress levels from experimental studies. Density histograms depict prevailing environmental conditions during non-bleaching years without thermal stress (2011–2013 in blue) and under ocean warming and acidification conditions projected for the period 2081–2100 under RCP2.6 (in yellow) and RCP8.5 (in red). As a comparison, data points indicate experimental treatments conducted with corals from within 40 km of each buoy (blue = control, red = heat stress/ocean acidification)

applied temperatures +2°C and higher to mimic end-of-century conditions under a high emission scenario (Figure 1a). In addition, the relationship between experimental and natural temperature regimes varied among coral regions. For instance, experiments from Florida and Puerto Rico were testing stress temperatures below conditions projected by the end of the 21st century while stress temperatures in the GBR often exceeded projections of even the RCP8.5 scenario (Figure 1a).

3.2 | pCO_2 ranges on coral reefs and climate change experiments

Similar to temperature, annual pCO_2 ranges in coral reefs vary substantially between summer and winter (Figure 1b), depending on location and oceanographic condition. For example, in Puerto Rico, annual ranges are small (100 ppm) relative to the high pCO_2 variability in Florida (417 ppm; 1st to 99th percentiles; Figure 1b; Table S2; Figure S2). Following this, the pCO_2 levels that are reached regularly (75th percentile) and those considered extreme (99th percentile) vary among locations. Reefs in Florida, the GBR, and Puerto Rico regularly experienced pCO_2 values near to the lower limit of end-of-century levels projected for RCP 2.6 (~430 ppm). Meanwhile, values in Bermuda (459 ppm) approach mid-point RCP 2.6 projections, and those in Hawaii (523 ppm) regularly reach end-of-century levels projected between RCP 4.5 and 6.0 for the global ocean (Table S2). Ocean acidification treatments used in climate change experiments often mimicked end-of-century high emission scenarios and, in some cases, exceeded plausible ranges by several hundred ppm, particularly in the GBR (Figure 1b). Over shorter timescales, daily pCO_2 concentrations on coral reefs mostly stayed within 10–30 ppm of the daily mean, but they could be an order of magnitude higher and reach daily variations of up to ~200 ppm (e.g., Hawaii in Figure 2).

3.3 | Environmental conditions assayed in coral experimental studies

Across the studies in our database, only 8 (~4%) of the 219 published studies testing coral responses to climate change scenarios (warming, ocean acidification, or both) explicitly assessed the impact of short-term environmental variability. Of the 31 studies (lasting >24 h) that were conducted with specimens from within 40 km of each data buoy considered in this study, only 10 (32%) mentioned temperature variability as part of their treatments and none tested variability as a separate factor. Thus, a majority of climate change experiments employed long-term stable treatments that differed from short-term in-situ variability at large (Figure 3; Figure S3). While in-situ conditions were variable on a scale of hours to one day (Figure S3), experimental treatments maintained stable conditions for time frames in the order of weeks to months (Figure 3).

The majority (77%) of experimental studies assessed here ran from 1 day to 11 weeks (overall mean duration: 4.5 weeks). Ramping times, that is, the time until treatment levels were reached starting from baseline values, were usually much shorter (overall mean duration: 1.4 weeks). Only 31%, 69%, and 3% of heat stress studies reported ambient salinity values, light regimes, and dO_2 levels, respectively.

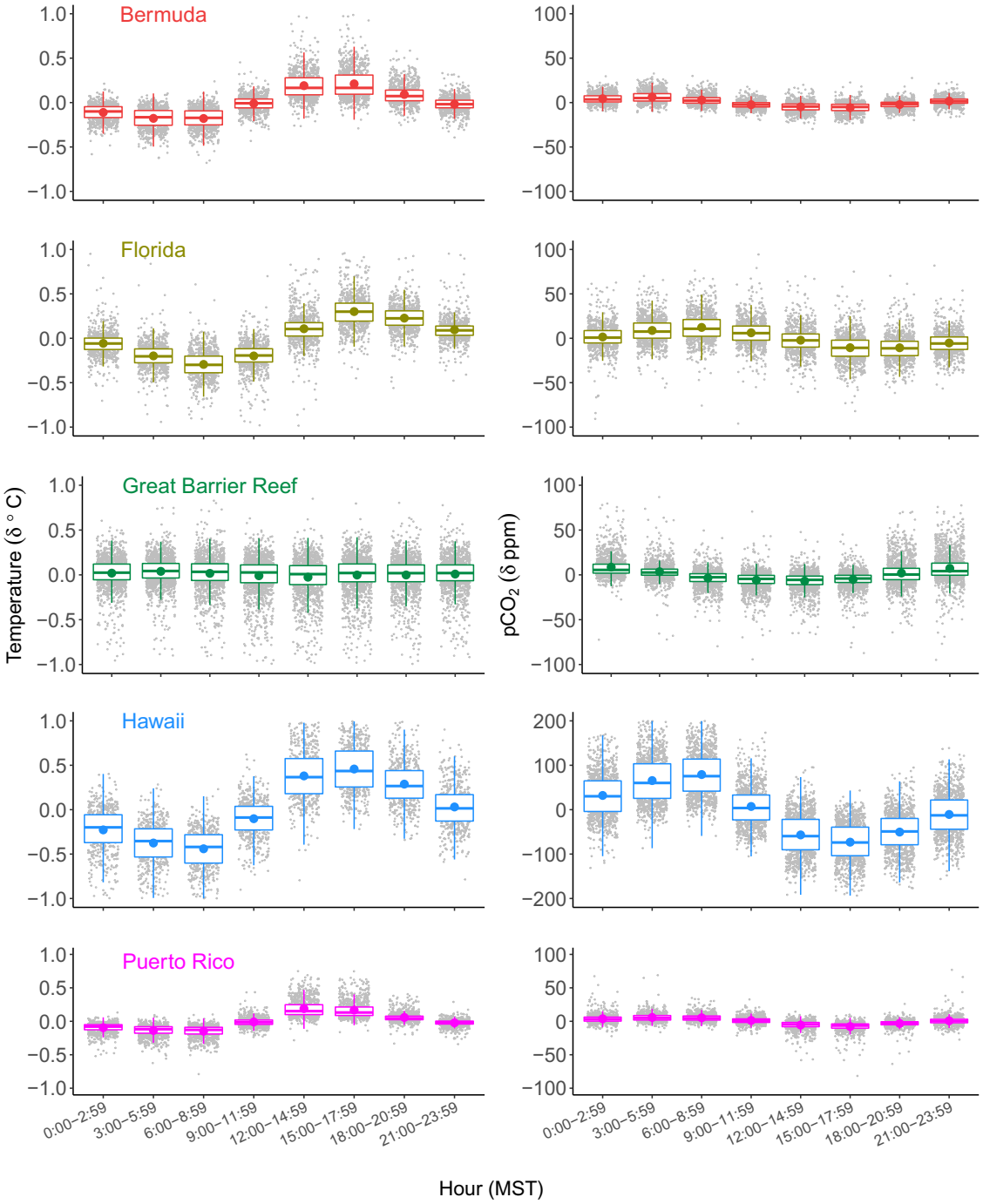

FIGURE 2 Diel variability of temperature and pCO_2 at five coral reef locations across the globe. The 3-hourly variability for the years 2011–2013 (all seasons) was obtained after filtering the data with a 24 h centered moving average to remove seasonal signals. Filled circles in the box plots denote mean values, lines are median values, the box represents the interquartile range (IQR or middle 50% of scores) with the lower and upper quantiles representing 25% and 75% of the scores (Q1 and Q3, respectively), and the lower and upper whiskers representing the minimum (Q1 − 1.5*IQR) and maximum (Q3 + 1.5*IQR) scores. Grey dots represent raw data points, with points outside the whiskers as outliers. Please note that the *y*-axis scale for pCO_2 conditions at Hawaii is larger than for the other four locations

3.4 | Correlated changes between physicochemical parameters on coral reefs

The coral reef mooring sites in Bermuda and Puerto Rico showed tight coupling among physical parameters, indicating well-flushed, open-ocean conditions at these sites. In contrast, sites at Florida and Hawaii showed less coupling among parameters (Figure 4). Specifically, the correlation between dO_2 and pCO_2 and between temperature and pCO_2 at these sites is weak, indicating systems that are influenced by community metabolism.

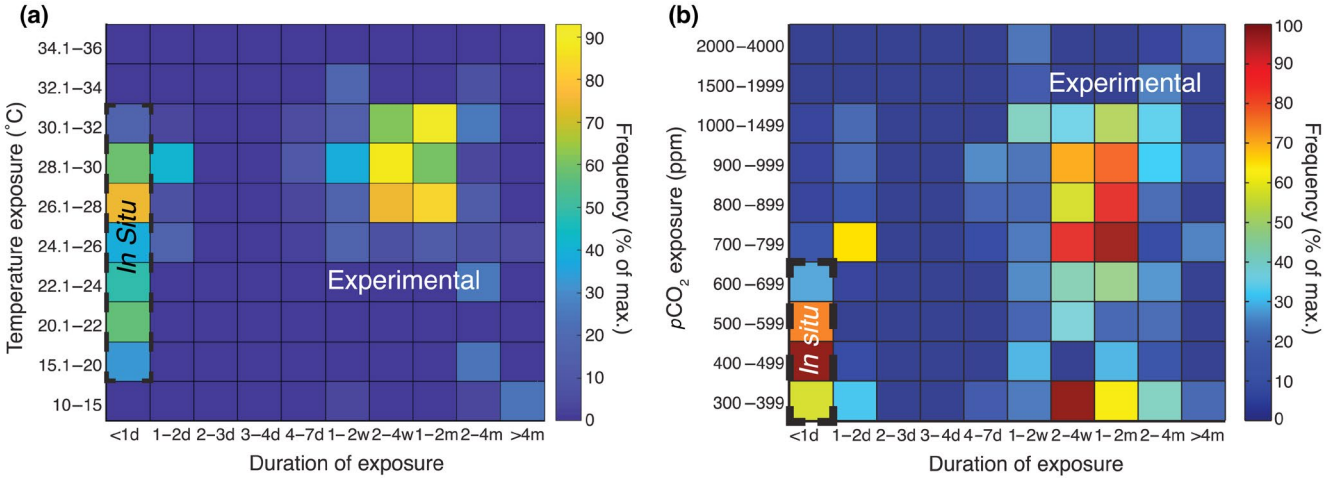

FIGURE 3 Heat map illustrating the contrast between the frequency and levels of in-situ temperatures (a) and pCO_2 (b) at coral reef buoys in Bermuda and Hawaii and experimental temperature and pCO_2 treatments during climate change experiments from the meta-analysis by Klein et al. (2021). Warmer colors represent more frequently reached levels and time frames. *X*-axis labels for time frames: d, days; m, months; w, weeks

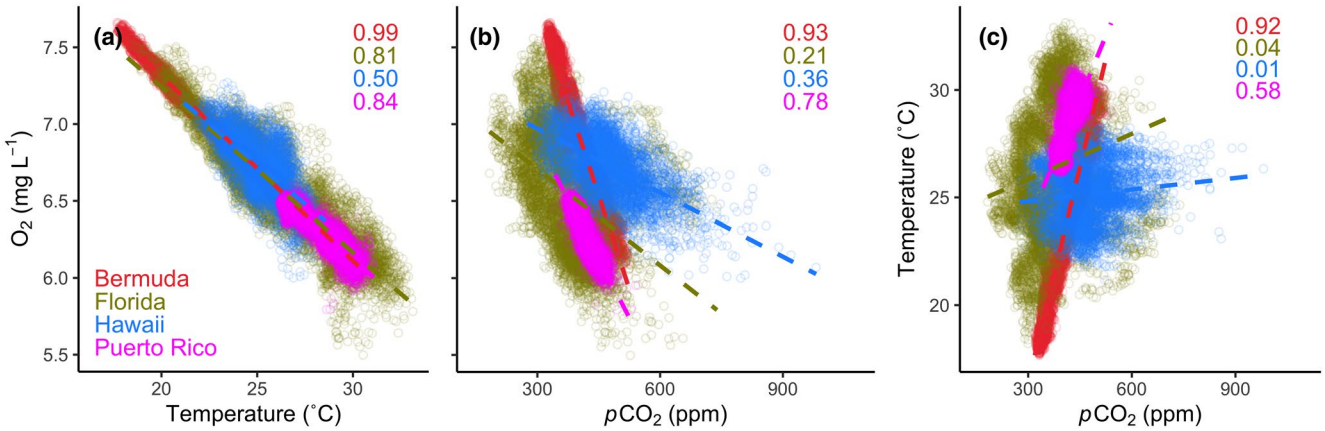

FIGURE 4 Relationships between dissolved O_2 levels and temperature (a) and pCO_2 (b), and between pCO_2 and temperature (c) in global coral reef locations. Data extracted from 3-hourly time-series data between 2011 and 2013 from four NOAA coral reef moorings; colored numbers depict strength of relationship between variables at each site (R^2)

4 | DISCUSSION

4.1 | Long-term environmental variability in coral reef ecosystems

Natural temperature ranges for coral reef biota vary substantially over seasonal timescales. Based on our analysis of time-series data across the five locations, seawater temperatures in coral reefs ranged annually from 4.2°C in Puerto Rico to 11.9°C in Bermuda and Florida. This seasonality strongly depends on latitude (where higher latitudes typically exhibit larger fluctuations) and depth (as temperature in shallow seas can range up to 17–20°C annually at the most extreme locations in the Persian Gulf; Coles & Fadlallah, 1991; Paparella et al., 2019). For most of the locations examined, our analysis projects that peak summer temperatures, considered the main cause of coral bleaching events, will increase and winters will be warmer. Such temperature increases during winter have been implicated in increasing coral growth rates that may, in turn, offset reduced growth rates during summer in low latitude reefs and hot seas (Anderson et al., 2017; Roik et al., 2016). However, the consequences of seasonal shifts in temperature distribution, such as the effects of warmer winters on bleaching susceptibility in the summer, are not well understood, and require more attention.

By directly comparing temperature profiles present in the reef and those manipulated in the experiments on a local scale, our analysis corroborates previous broad-scale data that show a disparity between experimentally assessed temperatures and projected near-term warming temperatures (Hughes, Barnes, et al., 2017). Such discrepancies lower the ability of experimental findings to accurately forecast responses to global warming over the coming decades. In

addition, most contemporary experiments do not account for potential acclimatization or adaptation of populations or species to future conditions, which will also be fundamental to predicting responses of organisms to climate change (Munday et al., 2013). In the case of pCO_2, we found that annual pCO_2 ranges varied between summer and winter, but the extent of these variations depended on the location and proximity to the open ocean. For instance, reefs in Florida, the GBR, and Puerto Rico regularly experienced pCO_2 values near to the lower limit of end-of-century levels projected for RCP 2.6 (~430 ppm), whereas values in Hawaii (~520 ppm) regularly reach end-of-century levels projected between RCP 4.5 and 6.0 for the global ocean. As such, the present-day coral reef ecosystems assessed here already frequently experience pCO_2 conditions within the range of future global atmospheric CO_2 concentrations expected under the low and intermediate RCPs for the global ocean. These patterns in pCO_2 variability will further be exacerbated by increases in seasonality of ocean acidity under future emission scenarios (Burger et al., 2020; Kwiatkowski & Orr, 2018). Despite the higher pCO_2 ranges in natural coral reefs than commonly assumed, ocean acidification treatments used in climate change experiments often mimicked end-of-century high emission scenarios and some even extended beyond plausible ranges by several hundred ppm (e.g., GBR). Even under these extreme experimental conditions, the impacts of ocean acidification on coral reef biota could be minor when compared to the impacts of intensifying MHWs (Chan & Connolly, 2013; Klein et al., 2021).

4.2 | Short-term environmental variability in coral reef ecosystems

Coral reefs are inherently variable ecosystems, characterized by substantial environmental fluctuations over short (hours and days) and long (annual and decadal) timescales (Kleypas et al., 1999; Waldbusser & Salisbury, 2014). Diel temperature fluctuations in coral reef environments are commonly within 0.5–1°C of the daily mean (i.e., they experience daily variations of 1–2°C, Figure 2), but can reach up to 7°C daily, depending on the oceanography and geomorphology of the site, where upwelling, tidal exposure, or back-reef dynamics leads to large temperature fluctuations (Cyronak et al., 2020; Dandan et al., 2015; Oliver & Palumbi, 2011; Schoepf et al., 2015).

Diel pCO_2 fluctuations are largely driven by metabolic processes involving community primary production, respiration, and calcification that are tied to the organismal community structure and light–dark cycles (Camp et al., 2018; Kleypas et al., 2011; Silbiger & Sorte, 2018), among other physical processes such as the influence of temperature solubility (Takeshita et al., 2018). Daily pCO_2 concentrations on coral reefs mostly stay within 10–30 ppm of the daily mean, but can be an order of magnitude higher and reach daily variations of up to ~200 ppm (e.g., Hawaii in Figure 2), or more, under the influence of upwelling processes (Feely et al., 2008; Shaw, Munday, et al., 2013). Thus, fluctuations of temperature and pCO_2 occur on short timescales within hours and may regularly expose corals to average conditions projected for low and moderate emission scenarios (RCP2.6 and 4.5).

4.3 | Short-term environmental variability in coral reefs drives patterns of tolerance

A common emergent picture from the contemporary literature is that environmental variability influences the stress tolerance of organisms living in a given ecosystem through adaptation (Barshis et al., 2018; Bay & Palumbi, 2014; Herrera et al., 2020; Palumbi et al., 2014) and phenotypic plasticity (Donelson et al., 2019; Kenkel & Matz, 2016; Palumbi et al., 2014). This phenomenon, however, seems to be constrained by the reliability of the environmental variability or its predictability, where large environmental stochasticity (i.e., lower predictability of the variability) limits plasticity (Reed et al., 2010; Sæther & Engen, 2015) and may ultimately lead to population collapse (Botero et al., 2015). The relevance of environmental variability and its predictability is primarily unexplored in coral reef research given the largely consistent conditions applied by many experimental settings (Grottoli et al., 2021; McLachlan et al., 2020). Generally, corals from habitats with higher short-term temperature variability are more heat tolerant than corals from less variable habitats (Kenkel et al., 2013; Oliver & Palumbi, 2011; Safaie et al., 2018; Schoepf et al., 2015). Increasing temperature variability at a site or repeated exposure to sub-lethal stress is associated with increased resistance to coral bleaching (Ainsworth et al., 2016; Langlais et al., 2017; Safaie et al., 2018; Voolstra et al., 2020). Although variations in temperature and pCO_2 in shallow reef ecosystems are often correlated, much less is known about how short-term pCO_2 variability affects the stress response of corals (Ruiz-Jones & Palumbi, 2017). The few studies that tested the effect of pCO_2 variability found positive effects of this variability on coral growth, even at remarkably high pCO_2 ranges (from 366 to 1839 ppm; Comeau et al., 2014; Dufault et al., 2012). The responses of other marine organisms to such changes suggest similar relationships between increased pCO_2 variability and stress tolerance as well as more plastic responses at least for some life stages (Schaum et al., 2016; Vargas et al., 2017). However, such beneficial organismal responses to environmental variability may be limited (Boyd et al., 2016) as found for corals from naturally extreme environments, where future climate scenarios superimposed onto existing large variability do not result in enhanced performance beyond current levels (Camp et al., 2016).

4.4 | Short-term environmental variability and climate change

Despite growing evidence on the relevance of environmental variability for organismal stress tolerance, our knowledge on how climate change will affect this variability, and thus the stress responses, is limited. On a global scale, marine heatwaves will become more frequent, intense, protracted, and geographically widespread (Frölicher et al., 2018). However, it is difficult to project local temperature variability in coastal coral reefs because the resolution of the IPCC-type ocean models is too coarse to accurately simulate these systems.

Nevertheless, it is expected that MHW frequency and intensity will also increase in the tropical oceans, as the increase in MHW characteristic is mainly caused by the long-term increase in ocean temperatures (Frölicher et al., 2018). Similar to MHWs, the number of days with extreme ocean acidity events is also projected to strongly increase due to ocean acidification (Burger et al., 2020). In contrast to MHWs, large increases in the seasonality of pCO_2 will further exacerbate the increases in ocean acidity extremes due to mean ocean acidification. For example, due to changes in variability alone, ocean acidity extremes are projected to increase by a factor of 14 by the end of the 21st century (RCP8.5), with threefold longer duration and fivefold higher intensity of events (Burger et al., 2020). The daily variability of pCO_2 and its influence on seawater pH is difficult to predict, but an increase in atmospheric CO_2 could also be accompanied by a nonlinear (3- to 4.5-fold) increase in daily CO_2 variability in some coral reef locations (Jury et al., 2013; Shaw, McNeil, et al., 2013). The magnitude of this variability may vary across locations, as it depends on a number of factors that will be differentially affected by climate change, including benthic community composition and seawater buffering capacity (Jury et al., 2013; Takeshita et al., 2018). These considerations on increasing environmental variability become important in the light of irreversible tipping points that may be reached with increasing extremes and require attention in future research (Helmuth et al., 2014; Shaw, Munday, et al., 2013).

4.5 | Environmental variability is only partially reflected in experimental approaches

To date, most experiments on responses of coral reef taxa to ocean warming and acidification have employed static experimental levels often equivalent to mean global projections of the commonly used RCP scenarios (Klein et al., 2021). Only 8 of the 219 studies examining the responses of reef-building corals to climate change scenarios (warming, acidification, or both) explicitly included short-term variability (Klein et al., 2021). While the cautious application of static experimental scenarios has facilitated comparisons among coral reef taxa in response to global change (e.g., Kroeker et al., 2010; Okazaki et al., 2017), such scenarios fail to consider the substantial environmental heterogeneity in reef ecosystems and the consequential local response. Current research only measures a small space of the actual environmental ranges and these simplistic conditions are not necessarily representative of natural reef conditions. However, there are some notable exceptions that incorporate natural variability in their experimental designs that were not included in the Klein et al.'s (2021) meta-analysis (among others Camp et al., 2016; Dove et al., 2013; Langdon et al., 2018; Putnam & Edmunds, 2011).

Studies that investigate the role of environmental variability on coral reef biota can yield surprising results that illustrate the biological complexity of these systems. For example, in the intermediate and high emission scenarios, growth of the coral *Acropora hyacinthus* was consistently equal or higher in the variable treatment compared to the stable controls (e.g., 400–2000 μatm vs. 1000 μatm; Comeau et al., 2014). However, differences in the response to environmental variability are apparent among taxa (Cornwall et al., 2018; Johnson et al., 2019). Thus, to accurately predict coral reef responses to climate change, experimental designs should consider current and future short-term environmental variability (Box 1).

BOX 1 Research priorities to broaden the research on coral responses to future ocean conditions

- Quantify expected changes to short-term environmental variability of temperature, the carbonate system (pCO_2), and O_2 owing to changes in future reef metabolism and seawater chemistry under scenarios of global change.
- Test predictability and stochasticity of environmental variability in coral reefs and investigate its potential to shape organismal phenotypic plasticity and adaptation.
- Improve understanding of how current and future short-term environmental variability across diverse reef settings affects organismal susceptibility to climate change.
- Resolve latitudinal and regional effects on annual environmental ranges and shifts in seasonality under climate change scenarios.
- Determine how annual environmental ranges and seasonality, and future shifts in winter temperatures affect summer bleaching susceptibility and experimental thermal tolerance.
- Expand routine monitoring of reef conditions to incorporate measurements of O_2 conditions and the characterization of pCO_2 to improve the capture of baseline environmental variability, including multiple monitoring stations at the scale of one reef ecosystem to compare local (forereef and backreef) versus global variability.
- Investigate the role of non-climatic environmental variables (e.g., O_2, light, salinity, and nutrients among others) in shaping the responses of coral reef biota to global change scenarios.

4.6 | Experimental time frames and long-term variability

The majority (77%) of experimental studies assessed here ran from 1 day to 11 weeks and ramping times (defined here as the time until treatment levels were reached starting from baseline values) lasted only 1.4 weeks on average. These experimental rate changes of temperature and pCO_2 exceed natural environmental variability and, therefore, likely assess short-term responses that may give insights into compensatory principles to short-term stress rather than acclimation and adaptation scenarios that we might expect from climate change. Such short-term exposures also hamper the investigation of

seasonality and changes to annual ranges. In addition to increased peak summer temperatures, another trend uncovered in our analysis was that many locations under RCP scenarios (Figure 1) had warmer winters and longer warm periods that fell within the ranges experienced during regular non-bleaching years today—a pattern worth exploring further during future long-term exposure experiments (Box 1).

4.7 | Integrating 'variance space' to broaden coral reef resilience research

To study climate change impacts on coral reef ecosystems, multifactorial experimental designs quickly become impractical. Thus, reductionist approaches represent a first step to gain a mechanistic understanding of the main drivers (Boyd et al., 2018; Boyd & Hutchins, 2012). However, with a focus on ocean warming and ocean acidification, other contributing variables may be less well understood. For instance, local salinity (Gegner et al., 2017, 2019), light (Fitt et al., 2001; Lesser, 1996), and dissolved O_2 (dO_2; Hughes et al., 2020) influence coral heat stress tolerance, but baseline values for these parameters were seldom reported for published experiments. Another environmental factor that is not commonly incorporated into such studies is the nutrient regime, even though high or imbalanced nutrient levels can cause bleaching alone or aggravate thermal bleaching outcomes (DeCarlo et al., 2020; Pogoreutz et al., 2017; Wiedenmann et al., 2013). Thus, underlying environmental drivers that may lead to complex biological response patterns remain unreported and may lead to conflicting findings (McLachlan et al., 2020). These environmental drivers are highly connected within coral reefs and can operate synergistically or antagonistically in regulating coral physiological performance (Suggett & Smith, 2020).

Climate change also contributes to an increase and severity of O_2-depleted ocean dead zones (Altieri & Gedan, 2015). Deoxygenation can cause coral bleaching and massive mortality of corals (Altieri et al., 2017), and is emerging as a poorly studied but major threat to coral reefs (Hughes et al., 2020). As shown here, long-term in-situ data on dO_2 in coral reefs are available. Our analysis illustrates that the variability of dO_2 can be tightly linked to that of pCO_2 in the framework of biological metabolism, physicochemical dynamics, temperature-dependent solubility (Figure 4; Camp et al., 2018; Nelson & Altieri, 2019), and thermal enhancement of metabolic rates (Brown et al., 2004; van der Meer, 2006). These data further underline the heterogeneity of processes that lead to variability in environmental conditions among coral reef sites and may guide different research approaches for sites with tightly coupled parameters compared with those where community metabolism plays a larger role.

Studies that investigate O_2 as a driver of coral performance are generally limited to singular ecological scales (e.g., coral boundary layers; Marshall & Clode, 2003) or processes (e.g., respiration; Dodds et al., 2007; e.g., calcification; Wijgerde et al., 2014) and seldom consider the outcomes of O_2 depletion in combination with other stressors (Hughes et al., 2020; Nelson & Altieri, 2019). Of the 219 published studies that experimentally applied climate change scenarios to corals, not one tested parallel changes in O_2 regimes (but see Lunden et al., 2014; Weber et al., 2012). Findings from studies assessing the impact of deoxygenation and acidification on other marine taxa indicate that these dual stressors typically impart negative, largely additive responses (Gobler & Baumann, 2016; Steckbauer et al., 2020) or, in the case of a non-calcifying cnidarian, deoxygenation can play an antagonistic role to the positive influence of higher CO_2 (Klein et al., 2017). Importantly, it is well established that marine taxa will likely be more susceptible to deoxygenation in the presence of thermal stress (Alderdice et al., 2021; Pörtner & Farrell, 2008; Vaquer-Sunyer & Duarte, 2011), while greater O_2 availability (oxygen supersaturation) may promote thermal resilience when internal O_2 production is impaired (Giomi et al., 2019). Similar assumptions on the manifestation of local dO_2 variability to that of pCO_2 can probably be made, that is, larger daily fluctuations are predicted with climate change (Shaw, McNeil, et al., 2013; Shaw, Munday, et al., 2013). There is clearly an urgent need to investigate the role of O_2 decline as a potential driver of future coral reef performance alongside warming, acidification, and other major threats causing coral reef degradation (Box 1).

5 | CONCLUSIONS

Including the variability of environmental conditions in coral reef ecosystems in experimental approaches is integral towards comprehensively understanding responses of reef organisms to climate change. The type of environmental variability to take into consideration will depend on the environment from which the study organisms are collected, as well as the spatial and temporal scale of the research question under study. Based on our examination of in-situ conditions and experimental treatments, our analyses highlight that long-term environmental ranges (minima and maxima) and the extent of short-term daily variability differ between geographic locations. Experimental designs should consider these multifaceted conditions and incorporate long- and short-term environmental variability into study designs, both in terms of control and treatment levels. Notably, marine heatwaves and pCO_2 variability have been projected to increase with progressing atmospheric CO_2 levels and climate change by the end of the century. As such, it may become important to include future environmental variability in experimental treatments. Incorporating these considerations into experimental coral reef approaches requires future experimental designs to explore responses to projected, correlated combinations of temperature, pCO_2, and dO_2 across Representative Concentration Pathways (Geraldi et al., 2020), allowing the examination of coherent fluctuations mimicking natural oscillations.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

AA, NG, SK, JP, SSR, CV, and MZ conceptualized this study, AA, NG, SK, SSR, and MZ obtained funding and initiated the underlying dataset. All authors refined the study design during a workshop; AA, SK, PM, NR, VS, and MZ analyzed and plotted environmental data; TLF provided output from GCMs; MZ wrote the manuscript with AA, SK, and contributions from all authors. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The buoy data are freely available at their online sources (Sutton et al. 2019). The meta-analysis data are available in the supplement of Klein et al. (2021). The climate data projections for sea surface temperature and pCO_2 (delta values) are included with this publication as raw data file.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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