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# Thresholds and drivers of coral calcification responses to climate change

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## Abstract

Increased temperature and $CO_2$ levels are considered key drivers of coral reef degradation. However, individual assessments of ecological responses (calcification) to these stressors are often contradicting. To detect underlying drivers of heterogeneity in coral calcification responses, we developed a procedure for the inclusion of stress–effect relationships in ecological meta-analyses. We applied this technique to a dataset of 294 empirical observations from 62 peer-reviewed publications testing individual and combined effects of elevated temperature and $pCO_2$ on coral calcification. Our results show an additive interaction between warming and acidification, which reduces coral calcification by 20% when $pCO_2$ levels exceed 700 ppm and temperature increases by 3°C. However, stress levels varied among studies and significantly affected outcomes, with unaffected calcification rates under moderate stresses ($pCO_2 \leq 700$ ppm, $\Delta T < 3$°C). Future coral reef carbon budgets will therefore depend on the magnitude of $pCO_2$ and temperature elevations and, thus, anthropogenic $CO_2$ emissions. Accounting for stress–effect relationships enabled us to identify additional drivers of heterogeneity including coral taxa, life stage, habitat, food availability, climate, and season. These differences can aid reef management identifying refuges and conservation priorities, but without a global effort to reduce $CO_2$ emissions, coral capacity to build reefs will be at risk.

**KEYWORDS**
anthropogenic $CO_2$, climate change, coral calcification, effect size meta-analysis, elevated temperature, interactive effect, meta-regression, ocean acidification

## 1 | INTRODUCTION

Climate change and associated ocean acidification and warming (OAW) have been linked to some of the major coral reef crises in Earth's history (Pandolfi, Connolly, Marshall, & Cohen, 2011). The current anthropogenic increase in atmospheric $CO_2$ concentrations is causing environmental change at an unprecedented rate (IPCC, 2014), with deleterious repercussions for coral reef communities (Baker, Glynn, & Riegl, 2008; Hoegh-Guldberg, Poloczanska, Skirving, & Dove,

2017). One potential repercussion is the decline in calcification rates of scleractinian corals (Anthony, Kline, Diaz-Pulido, Dove, & Hoegh-Guldberg, 2008; Dove et al., 2013; Schoepf et al., 2013), which could shift coral reef carbon budgets from net growth to net dissolution (Dove et al., 2013), leading to substantial ecological and socioeconomic impacts throughout the tropics (Moberg & Folke, 1999). Proper management and conservation of coral reef ecosystems in the 21st century therefore requires determining threshold levels for $pCO_2$ and temperature elevations at which corals will lose their capacity to

compete for space, resist waves, and create complex habitats for other reef organisms. However, predicting these thresholds is difficult owing to very heterogeneous and often contradicting outcomes of laboratory assessments. This is partly due to the limited scope of individual studies, which use small sample sizes, and often focus on just one life stage and a limited number of species. Further, the experimental methodologies applied vary greatly in magnitude and duration of exposure of the stressors (Pandolfi et al., 2011). Finally, the heterogeneity of results of existing studies may also be due to natural variation among corals in response to OAW. Some suggested drivers of heterogeneity are differences between life stages (Albright & Langdon, 2011; Loya et al., 2001), growth rates (Comeau, Edmunds, Spindel, & Carpenter, 2014; Rodolfo-Metalpa, Martin, Ferrier-Pages, & Gattuso, 2010), growth forms (Fabricius et al., 2011; Gates & Edmunds, 1999), skeletal densities (Jokiel, 2011), genotypes (Barshis et al., 2010), species (Comeau, Edmunds, Spindel, & Carpenter, 2013c), latitudes (Hoegh-Guldberg, 1999), and preexisting environmental conditions, such as abiotic variability (McClanahan & Maina, 2003) and food availability (Cohen, McCorkle, de Putron, Gaetani, & Rose, 2009). So far, only life stage (Harvey, Gwynn-Jones, & Moore, 2013) and methodology (Chan & Connolly, 2013) have been confirmed as generalizable drivers regulating differential coral calcification responses to climate change; the other potential drivers remain untested.

Effect size meta-analysis has been commonly used to synthesize empirical stress responses into overall effects and general patterns, particularly for calcification responses to climate change (Chan & Connolly, 2013; Harvey et al., 2013; Hendriks, Duarte, & Álvarez, 2010; Kroeker, Kordas, Crim, & Singh, 2010; Kroeker et al., 2013); however, previous analyses failed to determine the drivers of heterogeneous responses of corals to OAW. These analyses generated effect sizes as summarized metrics of laboratory responses without consideration of the magnitude of stress imposed in individual treatments (Chan & Connolly, 2013), leading to large statistical uncertainties. Further, the variation of stress levels across studies may induce false or mask existing differences in comparative analyses; that is, a higher average stress level in one group of studies may lead to a larger effect size for that group, while a smaller effect size of another group of studies may be simply due to a lower average stress level among those studies. Similarly, a real difference between two groups of studies can be masked if the more resistant group is subjected to higher stress levels. This form of research bias could explain why ecological meta-analyses so far have failed to define drivers of heterogeneity in coral calcification responses to climate change, which are required for better understanding why some corals are more affected by climate change than others.

This study aimed at elucidating thresholds and drivers of climate change effects on coral calcification using a novel statistical procedure that improves ecological research syntheses by incorporating stressor–effect relationships. Since researchers conduct stress response experiments under a range of stress levels, the inclusion of study-specific variation in ecological meta-analysis is a promising tool to generate more accurate summary statistics and identify drivers of heterogeneity. We applied our meta-analysis to a dataset containing 294 coral calcification responses from 62 peer-reviewed studies testing the effects of elevated temperature and/or pCO$_2$. Specifically, we performed weighted meta-regression to describe the average relationship between calcification response and the magnitude of temperature/pCO$_2$ elevations. We used this relationship to standardize calcification responses and partitioned them into subsamples based on 22 separate categories (e.g., feeding regime: fed vs. starved). Finally, we compared effect sizes for these subsamples from standardized responses using weighted *mixed-effects* meta-analysis to identify general drivers of heterogeneity in coral calcification responses to climate change.

## 2 | MATERIALS AND METHODS

### 2.1 | Data preparation

Peer-reviewed articles on laboratory experiments were assembled from the Web of Science database (search terms: "coral" AND "calcification" AND ["Climate change" OR "Ocean warming" OR "Ocean acidification"]) (Appendix S1: Table S4). The study was limited to reef-building corals that live in shallow waters due to their socio-economic importance (Moberg & Folke, 1999) and particular sensitivity (Carpenter et al., 2008; Hoegh-Guldberg et al., 2017). Initially, all studies published until December 31, 2015, that reported effects of elevated temperature and pCO$_2$ on net coral calcification were collected. Studies published after this date were therefore not considered here but should be considered in future meta-analyses. To generate summary statistics of predicted effects, experiments with stress levels above currently predicted ranges for 2100 (i.e., "Representative Concentration Pathways" [RCPs], +4.4°C or 1370 ppm) (IPCC, 2014) were excluded from the dataset. These data were reintroduced at a later stage and combined with our standardization procedure (see Section 6) to identify drivers of heterogeneity in coral calcification resistance. Most studies included in this analysis investigated zooxanthellate corals. However, two suitable temperature experiments contrasted presence and absence of endosymbiotic algae within the same coral species (Holcomb, Cohen, & McCorkle, 2012; Inoue et al., 2012), and one study investigated the effects of OA on the azooxanthellate coral *Balanophyllia elegans* (Crook, Cohen, Rebolledo-Vieyra, Hernandez, & Paytan, 2013). These data were included in our dataset based on their potential for investigating isolated effects of symbionts (temperature experiments) and similarity to calcification responses of symbiont-bearing corals (OA experiment). All studies included in our analysis are listed in Appendix S1 (Tables S1 and S2).

One calcification response was extracted from summary plots for each treatment at ambient levels of any additional stress (e.g., irradiance or oxygen saturation) using the software application Datathief (http://www.datathief.org). Suitable measurements included mean response, sample size, and some form of variance (standard error, standard deviation, or 95% confidence interval) of experimental and control treatments. Mean responses of experimental ($\bar{X}_E$) and control ($\bar{X}_C$) treatments were combined and log transformed according to Hedges, Gurevitch, and Curtis (1999):

$$L = \ln\left(\frac{\bar{X}_E}{\bar{X}_C} + C\right) \quad (1)$$

with $C$ ensuring that all values for $L \geq 0$:

$$C = 1 - \min\left(\frac{\bar{X}_E}{\bar{X}_C}\right) \quad (2)$$

Standard errors (*SE*) and 95% confidence intervals (CI) were transformed into standard deviations (*SD*) according to:

$$SD = SE\sqrt{n} = \frac{CI}{1.96}\sqrt{n} \quad (3)$$

where $n$ represents the number of replicates.

Levels of temperature, salinity, $pCO_2$, pH, $CO_3^{2-}$, $HCO_3^-$, dissolved inorganic carbon [DIC], alkalinity [$a_T$], and aragonite saturation state [$\Omega_A$] were recorded and the difference between experimental and control treatments computed (e.g., $\Delta pH = pH_E - pH_C$). Carbon chemistry parameters were calculated using the *seacarb* package in R (R Development Core Team 2010) to substitute for missing data. Whenever available, up to 22 biological, environmental, and methodological factors (Appendix S1: Table S7) potentially driving variations in coral ability to maintain calcification under elevated temperature or $pCO_2$ were also extracted. The resulting datasets are provided in Appendices S2–S4.

## 2.2 | Statistical analysis

Analyses were carried out in software R (R Development Core Team 2010) using the packages *devtools, broom, ggplot2, forestplot, akima, R.basic, doBy, lme4, lmtest, lattice, lsmeans, bear,* and *xlsx*. A schematic diagram of the statistical model is given in Appendix S1: Figure S1. As a preliminary analysis, conventional effect sizes of coral calcification responses to individual and combined effects of elevated temperature and $pCO_2$ were computed. To examine statistical properties of the datasets, a Shapiro–Wilk normality test was used, QQ plots and histogram plots were visually inspected, and kurtosis, skewedness, and suitability of individual responses were estimated. Suitability ratios $s_{iC}$ (control treatment) and $s_{iE}$ (experimental treatment) were obtained from:

$$s_{iC} = \sqrt{n_C}\frac{\bar{X}_C}{SD_C} \quad \text{and} \quad s_{iE} = \sqrt{n_E}\frac{\bar{X}_E}{SD_E} \quad (4)$$

If these ratios fall below 3 in more than 30% of the data, meta-analytical results may be misleading (Hedges et al., 1999). The data were normally distributed (Appendix S1: Figure S2), and parametric calculations were used to estimate overall means and CIs. Random variance was tested by comparing the heterogeneity statistics $Q$ against a chi-square distribution with $n - 1$ degrees of freedom:

$$Q = \sum_{i=1}^n \lambda_i (L_i)^2 - \frac{\sum_{i=1}^n (\lambda_i L_i)^2}{\sum_{i=1}^n \lambda_i} \quad (5)$$

with subscript $i$ referring to the individual sample and $\lambda$ as the reciprocal of the given within-study variance $v_w$. If the null hypothesis (i.e., observations share a common effect) could not be rejected, no random variation was assumed and the dataset was analyzed using a *fixed-effects* model with $\lambda_i$ as statistical weights. In case of significant random variation, a *mixed-effects* model was used and between-study variance $v_b$:

$$v_b = \frac{Q - (n - 1)}{\sum_{i=1}^n \lambda_i - \frac{\sum_{i=1}^n \lambda_i^2}{\sum_{i=1}^n \lambda_i}} \quad (6)$$

was added to calculate statistical weights [$\lambda_i^* = 1/(v_w + v_b)$]. Overall means $\bar{L}$ (i.e. effect sizes) were estimated from:

$$\bar{L}_{fix} = \frac{\sum_{i=1}^n \lambda_i L_i}{\sum_{i=1}^n \lambda_i} \quad \text{or} \quad \bar{L}_{mix} = \frac{\sum_{i=1}^n \lambda_i^* L_i}{\sum_{i=1}^n \lambda_i^*} \quad (7)$$

with the subscripts fix and mix denoting the model type (*fixed effects* and *mixed effects*, respectively). Standard error estimates (*SE*) were obtained from:

$$SE = \sqrt{\frac{1}{\sum_{i=1}^n \lambda_i}} \quad \text{or} \quad SE_{mix} = \sqrt{\frac{1}{\sum_{i=1}^n \lambda_i^*}} \quad (8)$$

However, small sample sizes can lead to inaccurate estimates of standard errors using equation 8. Standard errors of small parametric samples ($n < 50$) were estimated from:

$$SE = \sqrt{\frac{1}{\sum_{i=1}^n \lambda_i^*}\left(1 + 4\sum_{i=1}^n \frac{1}{df_i}\left(\frac{\lambda_i^*}{\lambda_i}\right)^2 \frac{\lambda_i^*[(\sum_{i=1}^n \lambda_i^*) - \lambda_i^*]}{(\sum_{i=1}^n \lambda_i^*)}\right)} \quad (9)$$

with $df_i$ denoting the degrees of freedom in the $i$th study, which was obtained from sample sizes of experimental ($n_{iE}$) and control ($n_{iC}$) treatments ($df_i = n_{iE} + n_{iC} - 2$). 95% upper and lower confidence intervals ($CI_U$ and $CI_L$, respectively) were estimated according to:

$$CI_L = \bar{L} - \tau SE(\bar{L}) \leq \bar{L} \leq \bar{L} + \tau SE(\bar{L}) = CI_U \quad (10)$$

with $\tau$ as the 97.5% point of the standard normal distribution ($\tau = 1.96$). Effects were considered significant, if the confidence interval did not include zero. Finally, back-transformed effect sizes $\bar{L}_{bt}(= e^{\bar{L}} - C)$ and confidence intervals $CI_{bt}(= e^{CI} - C$ were generated for illustration and interpretation of relative changes in coral calcification (Figure 1a–c).

An essential prerequisite for our comparative analysis is a significant relationship between calcification response and the magnitude of stress. To assess this, the datasets were split into experiments simulating high stress (i.e., RCP8.5, $pCO_2 > 700$ ppm, $\Delta T \geq 3°C$) and low stress (i.e., RCP6.0 or lower, $pCO_2 \leq 700$ ppm, $\Delta T < 3°C$) (IPCC 2014). Separations were based either on experimental treatment condition ($pCO_2$ treatments) or the difference between control and experimental treatment conditions (temperature treatments), based on which parameter produced better fitting linear models of treatment responses. Both subsamples were tested for normality and parametric suitability as described above. If normality and/or suitability assumptions were not satisfied, effect sizes and CIs were computed using weighted percentile bootstrapped intervals (Adams, Gurevitch, & Rosenberg, 1997). For that purpose, statistical weights were transformed into probabilities $p_i$:

$$p_{i_{fix}} = \frac{\lambda_i}{\sum_{i=1}^n \lambda_i} \quad \text{or} \quad p_{i_{mix}} = \frac{\lambda_i^*}{\sum_{i=1}^n \lambda_i^*} \quad (11)$$
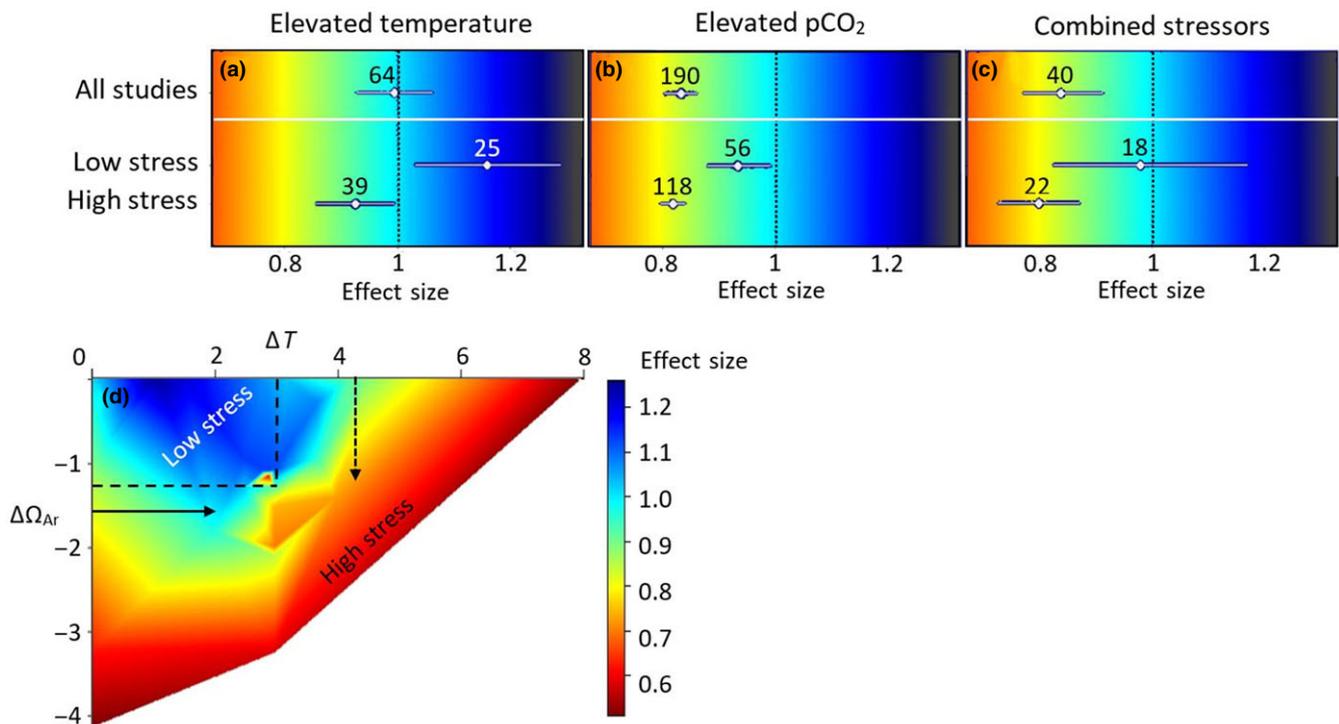
**FIGURE 1** Coral calcification responses to climate change depend on the magnitude of pCO2 and temperature elevations. Shown are back-transformed effect sizes (i.e., relative changes in coral calcification rates) from elevated temperatures (a), declining aragonite saturation (b), and both stressors in combination (c). Effect sizes with 95% CIs and sample sizes are displayed for studies exposing to high stress ($pCO_2$ > 700 ppm, $\Delta T \geq 3°C$), low stress ($pCO_2 \leq 700$ ppm, $\Delta T < 3°C$), and all studies combined. Response ratios of multi-stressor treatments were interpolated with linear models of single-stressor treatments (Appendix S1: Figure S3) to illustrate interactive effects of temperature and $pCO_2$ (d). Note the mitigating effect of moderate temperature increases (solid arrow) and the worsening effect of acidification at higher temperatures (dashed arrow) [Colour figure can be viewed at wileyonlinelibrary.com]

and fed into a subsampling command with replacement and 9999 iterations, each time computing the arithmetic mean response. Over-all means and 2.5% and 97.5% points from the resulting distribution were extracted to build 95% confidence intervals. Effects of subgroups were considered significantly different, when their CIs did not overlap. Partitioned heterogeneity statistics to quantify the amount of heterogeneity explained by significant factors were also estimated. Total heterogeneity $Q_T$ and model heterogeneity $Q_M$ were estimated using:

$$Q_T = \sum_{i=1}^{n} \lambda_i (L_i - \bar{L})^2 \quad \text{and} \quad Q_M = \sum_{m=1}^{M} W_m (L_m - \bar{L})^2, \quad (12)$$

respectively, with $M$ as the number of subsamples and $W$ as the sum of weights ($\lambda_i$ or $\lambda_i^*$) in subsample $m$. The residual heterogeneity $Q_E$ resulted from the difference of the two ($Q_E = Q_T - Q_M$).

To quantify the relationship between coral calcification response and the magnitude of stress exposure, weighted meta-regression was performed. First, originally excluded data using unrealistically high in situ stress levels were reintroduced to the dataset. The predictive power of various metrics describing the stressor was quantified by fitting first- and second-order linear models. For heat experiments, experimental temperature ($T_E$) and the difference between experimental and control temperatures ($\Delta T = T_E - T_C$) were compared (unit in °C). For acidification experiments, 14 different carbon chemistry parameters were compared (Appendix S1: Table S5). The best-fitting model was defined based on significance of the relationship ($p$-value) and amount of variation explained ($R^2$ and $Q_M$) (Appendix S1: Table S6). $Q_M$ was obtained from:

$$Q_M = \frac{\beta^2}{SE_{\beta^2}} \quad (13)$$

with $\beta$ as the estimated slope of the relationship and $SE_\beta$ as its standard error. To illustrate the interactive effects of temperature and $pCO_2$ (Figure 1d), the least squares (LS) predictions of the most significant models were back-transformed and interpolated with response ratios of combined stress treatments in R (akima package).

LS were then used to generate standardized log response ratios $L^*$ (Appendix S1: Figure S3):

$$L_i^* = \frac{L_i}{LS_i} \quad (14)$$

that account for variation in the magnitude of stress across samples. Standardized response ratios were partitioned according to biological, environmental, and methodological factors potentially driving variations in observed tolerances (Appendix S1: Table S7), and analyzed using the methods described above. In contrast to our previous effect sizes, corrected effect sizes resulting from this approach do

not display estimated changes in calcification rates. Since individual responses are viewed relative to their stress intensities, corrected effect sizes depict the general resistance of a subsample, thus facilitating comparison between subsamples to identify general drivers of heterogeneity. The correction can also be used to evaluate research bias. If a significant difference between two groups for $\bar{L}$ becomes insignificant for $\bar{L}^*$, the original difference likely resulted from lower stress levels in the apparently better performing group. Alternatively, an insignificant difference for $\bar{L}$ that becomes significant for $\bar{L}^*$ would indicate a type II error. In this case, an actual difference in tolerance was masked in $\bar{L}$ because the better performing group has been subjected to higher stress levels, creating the impression that the two groups perform equally. To detect this type of research bias, we carried out all comparisons with and without prior standardization of individual response ratios (Appendix S1: Figures S4–S11).

## 2.3 | Sensitivity analysis

Sensitivity of the data was analyzed in five separate investigations: (a) a random permutation test was designed to estimate the likelihood of committing type I errors; (b) funnel plots were investigated to assess distribution properties and potential for publication bias; (c) fail-safe analysis (Rosenthal, 1979) was performed to address robustness against publication bias; (d) meta-regression with publication year as independent variable was used to assess whether time-related factors have influenced outcomes; and (e) an exclusion comparison as described by Kroeker et al. (2013) was performed to assess individual contributions of the most significant outcomes.

For each dataset, two random subsamples were created without replacement. The sample size of the first subsample $n_1$ was determined randomly to any number between 3 and $n - 3$. The sample size for the second subsample $n_2$ resulted from $n_1$ ($n_2 = n - n_1$). Effect sizes and confidence intervals were estimated using weighted bootstrapping (see above). Then, the distances between confidence interval limits $d_{S1}$ and $d_{S2}$ were computed from the upper and lower confidence intervals $CI_U$ and $CI_L$ as:

$$d_{S1} = \sqrt{CI_{U1}^2 + CI_{L2}^2} \quad \text{and} \quad d_{S2} = \sqrt{CI_{U2}^2 + CI_{L1}^2} \qquad (15)$$

The smaller of $d_{S1}$ and $d_{S2}$ reveals the shorter distance between upper confidence limit of one subsample and lower confidence limit of the other subsample. These confidence limits were used to obtain a measure of significance $D_S$ between the groups:

$$D_S = CI_{Um} - CI_{Lj} \qquad (16)$$

with subscripts $m$ and $j$ referring to the subsamples. If $D_S$ becomes negative, the confidence intervals of the two randomly allocated subsamples do not overlap each other (i.e., type I error). This was done 2,999 times, and the resulting distribution of $D_S$ was examined to extract a $p$-value for the likelihood to commit a type I error:

$$p = \frac{D_0 + 1}{3,000} \qquad (17)$$

where $D_0$ equals the number of permutations with $D_S < 0$ (Adams et al., 1997).

Publication bias results from unequal effect size distribution among published and unpublished data. In ecological response measurements, results are more likely to be published if they show significant effects. Therefore, publication bias may lead to an overestimation of the mean effect. Funnel plots of response ratios over sample sizes and standard errors (Appendix S1: Figure S12) were examined to investigate two sources of bias: unequal source populations and potential for publication bias. If the dataset describes a common mean response, the response ratios should "funnel" in toward that response as sample sizes increase or standard errors decrease. Alternatively, an equal spread of response ratios is indicative of two or more true mean effect sizes within the dataset. Assuming the estimated response ratios derive from an approximate standard distribution, the two sides of the funnel should be equally occupied by empirical data. Publication bias may be pronounced if the response ratios tend to aggregate on one side of the funnel. Rosenthal's fail-safe analysis was also used to estimate the number of insignificant results that would change the mean effect of each subsample into an insignificant result (i.e., $p > 0.05$). The fail-safe statistics $I$ was computed as:

$$I = \frac{n}{2.706} \left[ n(\bar{Z}_n)^2 - 2.706 \right] \qquad (18)$$

with $\bar{Z}_n$ as the $Z$ score obtained by comparing the mean effect size of the subsample with 1 (i.e., no effect). Rosenthal provides a conservative estimate for the minimum value of $I$ ($I_{min} = 5n + 10$) that would render the effect size of the subsample robust against publication bias. We used a slightly less conservative threshold ($I_{min} = 5n$) due to small sample sizes in some factorial comparisons.

Unproportioned contribution of individual responses was tested using the method described in Kroeker et al. (2013). The five most significant responses were selectively excluded, one at a time, and the overall mean effect was re-computed. If the procedure changed the significance of a result for any of the excluded responses, that particular result was omitted.

## 3 | RESULTS AND DISCUSSION

Our modified meta-analysis method allowed us to identify several drivers of heterogeneity in the calcification response of scleractinian corals to OAW. Calcification responses were correlated with the magnitude of temperature/pCO₂ elevations (Appendix S1: Figure S3). After standardizing individual study outcomes to these correlations, we found strong taxonomic variation in the effects of temperature and acidification stress (Figure 2a,d). We also found that temperature stress is more pronounced in adult corals and during summers (Figure 2b,c), whereas juvenile corals are more sensitive to OA (Figure 2e). The adverse effects of OA are further pronounced in subtropical latitudes and on fringing reefs (Figure 2f,g), while particulate food supply can ameliorate these effects (Figure 2h).
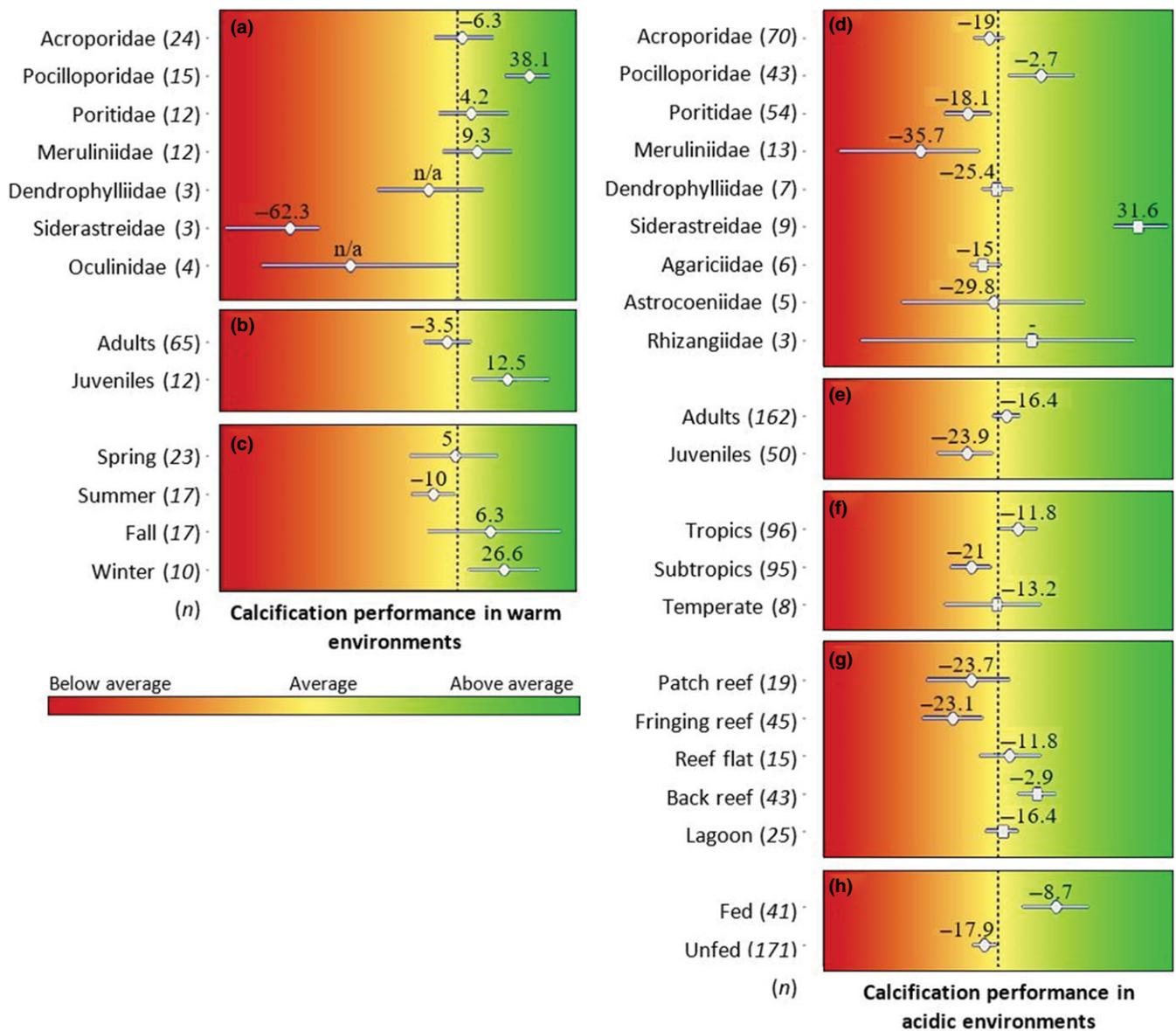
**FIGURE 2** Back-transformed, corrected effect sizes (see Section 6 for definition) with 95% CIs and number of studies (*n*) show coral calcification performance (relative to stress level) of meaningful subgroups under elevated temperatures (a–c) and declining aragonite saturation (d–h). Dotted lines represent average relationships between stress level and calcification response (Appendix S1: Figure S3) with deviations from it illustrating above or below average performances. Numbers on graphs display relative changes in calcification rates (i.e., non-corrected effect sizes) under expected future conditions of ocean acidification and warming. Effect sizes were generated either with a *mixed-effects* (circles) or *fixed-effects* (squares) model. n/a: data not available [Colour figure can be viewed at wileyonlinelibrary.com]

## 3.1 | Complex interactions between OA and warming drive multi-directional changes in coral calcification

Coral calcification responses in laboratory experiments displayed a significant relationship with the magnitude of stress (Appendix S1: Figure S3) for both ocean acidification ($R^2 = 0.22$, $p = 5.6 \times 10^{-12}$) and warming ($R^2 = 0.16$, $p = 3 \times 10^{-4}$). The effect of moderate OA (≤700 ppm) reduced coral calcification by 7% (CIs = 12%–1%), compared to 18% (20%–16%) from high acidification stress (>700 ppm, Figure 1a). The underlying mechanisms of OA-induced reductions in coral calcification are not fully understood, but some progress has

been made in recent years. Corals secrete their skeletons by elevating pH within their calcifying compartments to shift the carbonate system in favor of carbonate ions ($CO_3^{2-}$) over bicarbonate ions ($HCO_3^-$), although the relative importance of $CO_3^{2-}$ and $HCO_3^-$ for coral calcification is still in debate (Comeau, Carpenter, & Edmunds, 2013a,b; Jokiel, 2013; Jokiel, Jury, & Kuffner, 2016; Jury, Whitehead, & Szmant, 2010). This shift in carbonate chemistry increases the saturation state of aragonite, which drives its precipitation (Cohen & Holcomb, 2009; DeCarlo et al., 2017; Ross, Schoepf, DeCarlo, & McCulloch, 2018). Although the calcifying fluid is likely supplied by seawater (Tambutte et al., 2012), these changes can make the $CO_2$ system less dependent from ambient conditions (McCulloch,

D'Olivo, Falter, Holcomb, & Trotter, 2017; Venn, Tambutte, Holcomb, Allemand, & Tambutte, 2011). Therefore, it remains questionable to which extent predicted shifts toward aragonite dissolution via input of atmospheric $CO_2$ (Roleda, Boyd, & Hurd, 2012) translate into the coral calcifying compartment, and to which extent this increases the energetic cost of calcification (Cohen & Holcomb, 2009). Our overall results indicate that atmospheric $CO_2$ concentrations of more than 700 ppm will shift carbon ion concentrations in shallow waters to unfavorable levels, at which most corals will not be able to maintain existing calcification rates. Some corals, however, maintain calcification rates despite shifts in their calcifying fluid carbonate chemistry (Comeau, Cornwall, & McCulloch, 2017), which is supported by concordant species-specific heterogeneities found in this study (Figure 2d).

In contrast to OA, moderate temperature elevations (<3°C) increased coral calcification by 16% (3%–29%), while stronger heat exposure (≥3°C) led to a reduction in calcification of 8% (15%–1%, Figure 1b). This threshold response to increasing temperature is well described for many ecological traits (Dell, Pawar, & Savage, 2011) and illustrates the tight coupling of calcification rate and metabolism in corals (Al-Horani, Al-Moghrabi, & de Beer, 2003). All subject species in our temperature study obtain energy via respiration and photosynthesis (from endosymbiotic dinoflagellates *Symbiodinium*), except for two studies that contrasted symbiont presence and absence in the same species (Holcomb et al., 2012; Inoue et al., 2012). Both processes scale with temperature (Clarke & Fraser, 2004), which accelerates chemical reactions involved in calcification at elevated temperatures (Castillo, Ries, Bruno, & Westfield, 2014). If temperatures continue to rise, intermolecular interactions become destabilized and corals start to bleach (i.e., expulsion of *Symbiodinium*) (Brown, 1997). The resulting lack of phototrophic energy likely decreases calcification rates. Our data suggest that the "tipping point" between positive and negative effects of temperature averages around +3°C above annual mean water temperature. However, it is important to consider that our overall effect sizes lack accurate representation of seasonality and spatial heterogeneity, as their underlying response ratios are derived from studies conducted across all seasons and regions. Whereas small increases in maximum summer temperatures for elongated durations can already exceed the tolerance threshold of most corals (Hughes, Barnes, et al., 2017), similar heat addition in winter likely remains within coral temperature limits, leading to enhanced or unchanged calcification rates (Schoepf et al., 2013) from increased metabolic activity (Rodolfo-Metalpa et al., 2010). Likewise, corals that experience small seasonal temperature ranges, predominantly found in tropical regions, are particularly prone to bleaching from heat exposure (Hughes et al., 2018), whereas corals experiencing fluctuating thermal regimes are usually unaffected by temperature increases larger than +3° (Oliver & Palumbi, 2011). Our data support these paradigms, showing increased calcification performance in experiments conducted in winter seasons, while summer experiments display negative effects (26.6% increase and 10% reduction, respectively, Figure 2c). Although not significant, the same is true for tropical (negative

effects) vs. subtropical (positive effects) corals (Appendix S1: Figure S8). The spatial and temporal variation of thermal tolerance in corals creates a complex range of calcification responses and should be carefully evaluated when making inferences from our overall temperature responses.

Moderate warming can counteract the adverse effects of OA. Our combined effect sizes remained within the confidence intervals for a simply additive interaction between ocean acidification and warming (Figure 1c), which had already been suggested in previous analyses (Kroeker et al., 2013; Przeslawski, Byrne, & Mellin, 2015). In the high-stress scenario (i.e., RCP8.5, $pCO_2 > 700$ ppm, $\Delta T \geq 3°C$), the additive effect of warming and acidification reduces calcification rates by 20% (27%–13%), which would threaten the building capacity of most existing reefs (Kleypas et al., 1999). In the low-stress scenario (i.e., RCP6.0 or lower, $pCO_2 \leq 700$ ppm, $\Delta T < 3°C$), the interactive effect is neutral (18% reduction–17% increase). These findings support the assumption that moderate temperature elevations can mitigate negative effects of seawater acidification on calcification in some corals (Figure 1d, solid arrow) (Cole, Finch, Hintz, Hintz, & Allison, 2018; Harvey et al., 2013; Muehllehner & Edmunds, 2008), whereas more pronounced exposure to heat adds to the negative effects from acidification on calcification, particularly in tropical regions and during summers (Figure 1d, dashed arrow) (Reynaud et al., 2003; Rodolfo-metalpa et al., 2011; Towle, Baker, & Langdon, 2016). The mitigating effect of temperature on calcification could also partly explain why tropical corals, living under higher ambient temperatures, cope better with acidification stress compared to subtropical corals (11.8% and 21% reduction, respectively, Figure 2f). However, the additive negative effect of OA and temperatures past the tolerance threshold implies a notable risk for the world's coral reefs, given the increased prominence of abnormally hot sea surface temperatures in recent years (Hughes, Kerry, et al., 2017, Hughes et al., 2018).

Our overall effect sizes were robust to both publication bias and significant contributions of individual studies; that is, exclusion of the most significant studies as in Kroeker et al. (2013) did not change any of the results. Further, meta-regression revealed no significant trend between response ratios and year of publication, suggesting that the datasets were not influenced by changes in methodology or assumptions (Appendix S1: Table S3).

## 3.2 | Why some corals cope better with climate change than others

The use of corrected effect sizes (see Section 6) increased our ability to detect drivers of heterogeneity in coral calcification responses to elevated temperature and $pCO_2$. Rosenthal's fail-safe numbers (Rosenthal, 1979) were low for some comparative analyses, indicating that publication bias may have affected certain results. We therefore limited our discussion to results that were robust to publication bias, and found eight distinct differences between ecologically relevant groups, compared to only three using conventional effect sizes (Appendix S1: Figures S4–S11). The likelihood to obtain a

significant difference by chance remained within tolerable limits (<5.4%) for both datasets (Appendix S1: Table S3). The differences discussed below provide the opportunity to investigate how divergent factors and assumptions affect coral vulnerability to climate change.

Coral calcification resistance to OAW differs between taxa (Figure 2a,d) (Loya et al., 2001; van Woesik, Sakai, Ganase, & Loya, 2011). Branching Pocilloporids and massive Siderastreids showed the highest resistance to OA, while calcification in other massive corals (*Porites* and Merulinids) appears more vulnerable. These findings are in contrast with some field studies. While De'ath, Lough, and Fabricius (2009) reported a 14% decline in *Porites* calcification on the Great Barrier Reef since 1990, which may be due to OA or ocean warming, Cooper, O'Leary, and Lough (2012) presented long-term data that indicate no effect from OA. Fabricius et al. (2011) found major *Porites* dominance on reefs around $CO_2$ seeps, where surrounding waters are naturally acidified. They concluded that elevated $pCO_2$ levels could reduce the structural complexity of coral reefs by giving massive corals a competitive advantage over more susceptible branching corals. However, these field observations may also be associated with the increased spatial heterogeneity of $pCO_2$ around $CO_2$ seeps, and may not allow prediction of effects of future global OA on coral reef communities. In this study, growth form was not a significant driver of coral calcification responses to OA (Appendix S1: Figure S6), which is corroborated by accumulating reports of highly diverse coral reefs under chronically acidified conditions in semi-enclosed bays (Camp et al., 2017; Golbuu, Gouezo, Kurihara, Rehm, & Wolanski, 2016; Shamberger et al., 2014). The above average calcification performance of Pocilloporids under increased $pCO_2$ is supported by recent experiments (Comeau et al., 2017; Edmunds & Burgess, 2018), while the exceptional performance in siderastreid corals (90%–120% of control calcification at $pCO_2$ = 2553 ppm, $\Omega_{Ar}$ = 1.1) and their susceptibility to elevated temperatures result from a single study (Castillo et al., 2014) and should be interpreted with caution. Pocilloporid corals also displayed the highest resistance to elevated temperatures. This coral family was subject to severe population declines during the 1998 global bleaching event (Loya et al., 2001; Marshall & Baird, 2000), while more recent experimental observations suggest increased thermal tolerance in this family (Manzello, 2010; Schoepf et al., 2013). One possible explanation for this may be natural selection from previous bleaching events (Guest et al., 2012), but other potential driving factors include colony size and turbulent water flow (Edmunds & Burgess, 2018), ambient thermal variability (Tortolero-Langarica, Rodriguez-Troncoso, Cupul-Magana, & Carricart-Ganivet, 2017), and ambient carbonate chemistry (Bahr, Jokiel, & Rodgers, 2016).

During early life stages, coral calcification is more sensitive to OA (Figure 2e), but more resistant to ocean warming (Figure 2b). Since elevated $pCO_2$ adds energetic costs to the production of $CaCO_3$ (Cohen & Holcomb, 2009), juvenile corals are particularly prone to suffer from OA based on their need for growth despite limited energy (Edmunds, Brown, & Moriarty, 2012). In addition, Moya

et al. (2015) found disruptions of gene expression involved in skeleton production for juvenile corals under elevated $pCO_2$. Decreased thermal thresholds in adult stages may be associated with shape-dependent differences in mass-transfer efficiency (Loya et al., 2001). Adverse effects of temperature are linked to the accumulation of harmful metabolites (e.g., superoxides), which are expelled more efficiently in flat invertebrates (Patterson, 1992). Thus, ensuring colony health under elevated temperatures may become more difficult, as corals grow from two-dimensional recruits to three-dimensional adults.

Coral capacity to maintain calcification under OA is mediated by habitat structure (Figure 2g). Back reef environments appear to inhabit more resistant coral populations compared to fringing reefs. One possible explanation for this may be the relatively stable environmental conditions on fringing reefs, which could make corals more prone to the stresses associated with collection and ex situ acclimatization, leading to lower calcification rates of these corals in subsequent experiments. On the contrary, back reef environments can experience large diel carbon chemistry fluctuations from organismal activity and freshwater input (Gagliano, McCormick, Moore, & Depczynski, 2010). Exposure to this variability may select for more resistant genes or phenotypes and possibly increase tolerance thresholds. Dufault, Cumbo, Fan, and Edmunds (2012) found that coral recruits exposed to fluctuating $pCO_2$ regimes have increased calcification rates, which they attributed to efficient DIC storage mechanisms that could fuel otherwise DIC limited calcification during the day. Kurihara, Takahashi, Reyes-Bermudez, and Hidaka (2018) compared the calcification performance of adult Indo-Pacific *Acropora* living in stable vs. variable carbon chemistry regimes. The latter corals maintained calcification rates at elevated $pCO_2$ levels and showed elevated expression of calcification-related genes, while corals from more stable forereef habitats did not. However, this was not found for Caribbean *Acropora* (Camp et al., 2016). Although fast adaptive abilities have been confirmed in corals (Palumbi, Barshis, Traylor-Knowles, & Bay, 2014), it remains questionable whether they can keep pace with the current rate of anthropogenic $CO_2$ input (Crook et al., 2013).

Heterotrophy can ameliorate adverse effects of OA on coral calcification (Figure 2h). Knowledge of coral energy reserves and their impact on OA resistance is still limited (Schoepf et al., 2013), but heterotrophy appears to mitigate reduced calcification in a high $CO_2$ world (Drenkard et al., 2013; Towle, Enochs, & Langdon, 2015). This is supported by the observation that metabolic $CO_2$ comprises up to 70% of inorganic carbon used in coral biomineralization (Furla, Galgani, Durand, & Allemand, 2000). However, declining feeding rates under OA (Houlbreque et al., 2015) and species-specific variation in coral capacity to offset OA-induced growth limitations via heterotrophic feeding (Drenkard et al., 2013; Edmunds, 2011) emphasize the need for additional research on the relationship between feeding regime and stress resistance in reef-building corals.

We showed that coral reef accretion is likely to decline if current atmospheric trends in carbon dioxide and temperature persist. These trends interact in complex ways to drive coral calcification responses

| Comparison | Ocean acidification | | | Ocean warming | | | Combined | | |
|---|---|---|---|---|---|---|---|---|---|
| | $Q_T$ | $Q_M$ | $Q_E$ | $Q_T$ | $Q_M$ | $Q_E$ | $Q_T$ | $Q_M$ | $Q_E$ |
| Latitude | 174.16 | 7.38 | 166.78 | | | | | | |
| Reef type | 121.88 | 21.42 | 100.47 | | | | | | |
| Food availability | 182.22 | 3.11 | 179.11 | | | | | | |
| Stress level | 182.22 | 4.79 | 177.53 | 78.23 | 11.48 | 66.75 | 59.39 | 4.03 | 55.36 |
| Taxa | 182.22 | 36.75 | 145.48 | 64.49 | 18.20 | 46.29 | | | |
| Life stage | 182.22 | 9.311 | 172.91 | 78.23 | 3.04 | 75.18 | | | |
| Seasons | | | | 61.09 | 10.30 | 50.79 | | | |

**TABLE 1** Heterogeneity statistics of significant factorial analyses on coral calcification responses to ocean acidification, ocean warming, and combined stressors. Listed are total heterogeneity $Q_T$, model heterogeneity $Q_M$, and residual heterogeneity $Q_E$

to climate change, which are further mediated by seasonal effects and differences in morphological plasticity, energetic status, and habitat structure. However, our large residual heterogeneities (Table 1) suggest additional contributing factors. Important physiological aspects such as adaptation and acclimatization (Hume et al., 2016; Palumbi et al., 2014; Pandolfi, 2015), species interactions (Evensen & Edmunds, 2017; Kordas, Harley, & O'Connor, 2011), photosynthesis (Langdon & Atkinson, 2005), coral microbiome stability (Grottoli et al., 2018), and compounding stressors (Carpenter et al., 2008; Comeau, Carpenter, & Edmunds, 2014) can have profound impacts on coral resistance to climate change and were insufficiently represented in our analysis. While the differences in vulnerabilities and environmental circumstances illustrated above can aid coral reef management identifying local refuges and conservation priorities, the main finding of this study illustrates the urgent need for a global effort to reduce carbon emissions or we risk losing major ecosystem services via loss of the ability of corals to build reefs.

### CONFLICT OF INTEREST

The authors declare that there is no conflict of interest regarding this work.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.