



Global coral reef ecosystems exhibit declining calcification and increasing primary productivity

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Long-term coral reef resilience to multiple stressors depends on their ability to maintain positive calcification rates. Estimates of coral ecosystem calcification and organic productivity provide insight into the environmental drivers and temporal changes in reef condition. Here, we analyse global spatiotemporal trends and drivers of coral reef calcification using a meta-analysis of ecosystem-scale case studies. A linear mixed effects regression model was used to test whether ecosystem-scale calcification is related to seasonality, methodology, calcifier cover, year, depth, wave action, latitude, duration of data collection, coral reef state, Ω_{ar} , temperature and organic productivity. Global ecosystem calcification estimated from changes in seawater carbonate chemistry was driven primarily by depth and benthic calcifier cover. Current and future declines in coral cover will significantly affect the global reef carbonate budget, even before considering the effects of sub-lethal stressors on calcification rates. Repeatedly studied reefs exhibited declining calcification of $4.3 \pm 1.9\%$ per year ($\bar{x} = 1.8 \pm 0.7 \text{ mmol m}^{-2} \text{ d}^{-1} \text{ yr}^{-1}$), and increasing organic productivity at $3.0 \pm 0.8 \text{ mmol m}^{-2} \text{ d}^{-1}$ per year since 1970. Therefore, coral reef ecosystems are experiencing a shift in their essential metabolic processes of calcification and photosynthesis, and could become net dissolving worldwide around 2054.

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The ability for coral reefs to maintain critical ecosystem functions and services is under threat^{1,2}. Global climate change is affecting coral ecosystems disproportionately, with waters surrounding coral reefs acidifying faster than the open ocean^{3–5}. Steadily increasing thermal stress is triggering major bleaching events and lowering coral reef resilience^{6–8}. Predicting the future of coral reef persistence relies heavily on understanding the key processes driving ecosystem functionality, such as calcification and productivity⁹.

Assessments of net ecosystem calcification (G_{net}) and organic productivity (P_{net}) in coral reefs provide valuable information about stress responses and reef longevity. Organic productivity (P_{net}) is the net balance between photosynthesis and respiration, and gives insight about algal versus coral dominance, short- versus long-term carbon fluxes, and photosynthetic efficiency in aquatic ecosystems^{10,11}. Pre-1975, P_{net} in coral reefs was estimated to be net-zero or ‘slightly’ positive¹¹. Recent observations of P_{net} indicate a response of coral reefs to stress events and changing environmental conditions^{9,12}. Increasing P_{net} relative to G_{net} also indicates a shift from coral to algal dominated ecosystems^{13–15}. G_{net} is the net balance between calcification and dissolution, which quantifies the productivity of all calcifiers within an ecosystem. Changing rates of G_{net} and P_{net} can indicate growth⁹, degradation^{16–18} or phase shifting^{16,19,20}. Higher rates of G_{net} tend to indicate reefs with higher coral cover^{9,21,22}, and ecosystems which have not been impacted by significant stressors^{23–26}, whereas declining and net-dissolving calcification rates indicate stressed corals^{16,18,27} or ecosystems which have little to no live corals^{25,28}. Therefore, G_{net} and P_{net} are increasingly used as proxies for coral reef ecosystem health^{10,29,30}.

Community census and hydrochemistry are the most widely used approaches to estimate coral reef ecosystem calcification³¹. Community census techniques estimate G_{net} by multiplying calcifier growth rates with biotic abundances³¹, while hydrochemical methods derive G_{net} and P_{net} rates from changes in seawater carbonate chemistry³². Census investigations can resolve the relative contribution of different species of calcifiers, but often rely on growth rates from literature approximations rather than in situ observations. Data obtained from corals studied with different methodologies, locations, depths, stressors, seasons, and years can introduce errors in taxon-specific calcification rates >10-fold³⁰, making accurate reflections of ecosystem-scale conditions difficult. In contrast, hydrochemical methods for measuring G_{net} and P_{net} of coral reefs have the benefit of being spatially and temporally specific, and integrate coral reef calcification at the ecosystem scale without resolving individual or species scale processes^{11,33}. Therefore, ecosystem-scale calcification investigations using hydrochemical methods are the basis for the present meta-analysis.

Potential influences on coral reef G_{net} (e.g. depth, temperature, coral cover) have been identified in many case studies^{33–35}, but there is currently no overarching consensus about the critical drivers at the global scale. Manipulative mesocosm experiments have quantified the relative importance of key factors such as light availability, the aragonite saturation state (Ω_{ar} , as a proxy for ocean acidification), and coral assemblages on metabolic rates^{36–38}. However, mesocosms may not reflect in situ conditions because they cannot capture the rich natural complexity inherent in coral reef ecosystems^{39,40}. Predicting G_{net} as a function of environmental parameters is difficult, and relationships produced at local scales or in mesocosm experiments may not be accurate at broader spatial scales or over time^{9,29,41,42}. Thus, a meta-analysis approach can help to elucidate key drivers of global coral ecosystem calcification and understand how G_{net} may respond to changing environmental conditions.

Here, we analysed data from 116 hydrochemical case studies quantifying ecosystem-scale coral reef production and calcification. We determined key global-scale biogeochemical drivers of calcification and predicted global G_{net} using linear mixed effects regression models (LMER). We aim to uncover whether overarching trends in ecosystem metabolic rates are related to experimental designs to assess potential methodological biases that can influence the interpretation of long-term trends. We hypothesised that G_{net} is driven by interactive effects of biogeochemical parameters, climate change and reef states. Overall, we expect declines in G_{net} with increasing P_{net} over time due to reductions in coral cover and declining reef condition as previously reported at the local scale^{9,16,17,43}. Our meta-analysis of in situ, hydrochemical, ecosystem-scale calcification rates reveals global patterns and trends, building on the breadth of case study and laboratory-based investigations to pinpoint the drivers of G_{net} and predict the future of coral reefs.

Results

Summary of the literature. A total of 53 publications fit our meta-analysis criteria (see methods), providing 116 unique diel-integrated calcification rates from 36 coral reef sites in 11 countries (Fig. 1, Supplementary Data 1). Australian reefs contributed 35% of studies which mostly occurred on the Great Barrier Reef (GBR) (Fig. 1). Shiraho Reef, Japan, is the most well-studied ecosystem with 12 investigations, followed by Lizard Island⁴⁴ ($n = 9$) and One Tree Island⁹ (GBR, $n = 7$) and Kaneohe Bay, Hawaii⁴¹ ($n = 7$). Reefs in Palau¹⁷, Moorea⁴⁵ and Heron Island⁴⁶ (GBR) also have multiple repeat studies ($n = 4–6$). 51% and 49% of studies occurred in the Northern and Southern Hemispheres, respectively. Although >50% of all coral reefs exist in the 0–15° latitude range⁴⁷, only 20% of ecosystem calcification estimates occurred in low-latitude reefs near the equator. Mid-latitude reefs (15–28°) represented 72% of studied reefs, whereas high-latitude reefs (28–32.5° N and S), which constitute only 1.5% of reefs globally, but are hotspots of change^{20,48,49}, were the focus of 8% of ecosystem metabolism studies (Fig. 1, Supplementary Fig. 1).

Although the methodology and equipment required to estimate hydrochemical coral ecosystem calcification has existed for more than 50 years, 40% of all coral reef metabolism studies have occurred within the past decade. The 1970s and 1980s together produced 15% of studies, the 1990s produced 30%, and the 2000s produced 15%. There were 38% of G_{net} studies that occurred in summer, 21% were undertaken in autumn, 20% in winter, and 18% in spring (with the remaining represented by studies that provided ‘annual’ estimates). The duration of these studies ranged from 1 to 58 days ($\bar{x} \pm \text{SD} = 6.5 \pm 9.0$ days), with the longest continuous study occurring over 28 consecutive days (One Tree Island, GBR⁴³).

G_{net} ranged from -90 to $667 \text{ mmol m}^{-2} \text{ d}^{-1}$, averaging 124.1 ± 106.6 ($\bar{x} \pm \text{SD}$) across all studies. P_{net} rates had a greater range than G_{net} rates and averaged $65.1 \pm 254.3 \text{ mmol m}^{-2} \text{ d}^{-1}$ ($\bar{x} \pm \text{SD}$) (Table 1). Six out of the 116 studies compiled here reported diel net ecosystem dissolution, and 34 investigations determined the ecosystem to be net respiratory (i.e. 32% of studies reported negative P_{net} rates).

Of all reefs studied, 25% were reported as degraded ($n = 9$) from either pollution, dredging, eutrophication, bleaching and/or recent cyclone events. 11% ($n = 4$ reefs) had combinations of stressors (e.g. cyclone damage and bleaching from heat waves). Although reef state was not retained in the LMER (due to potentially confounding locational effects), degraded and recovering reefs had lower G_{net} than healthy/recovered/unspecified reefs ($\bar{x}_{\text{degraded}} = 64.2 \pm 10.5 \text{ mmol m}^{-2} \text{ d}^{-1}$ versus $\bar{x}_{\text{healthy}} = 137.5 \pm 11.7 \text{ mmol m}^{-2} \text{ d}^{-1}$). Globally, 67% of reefs were actively

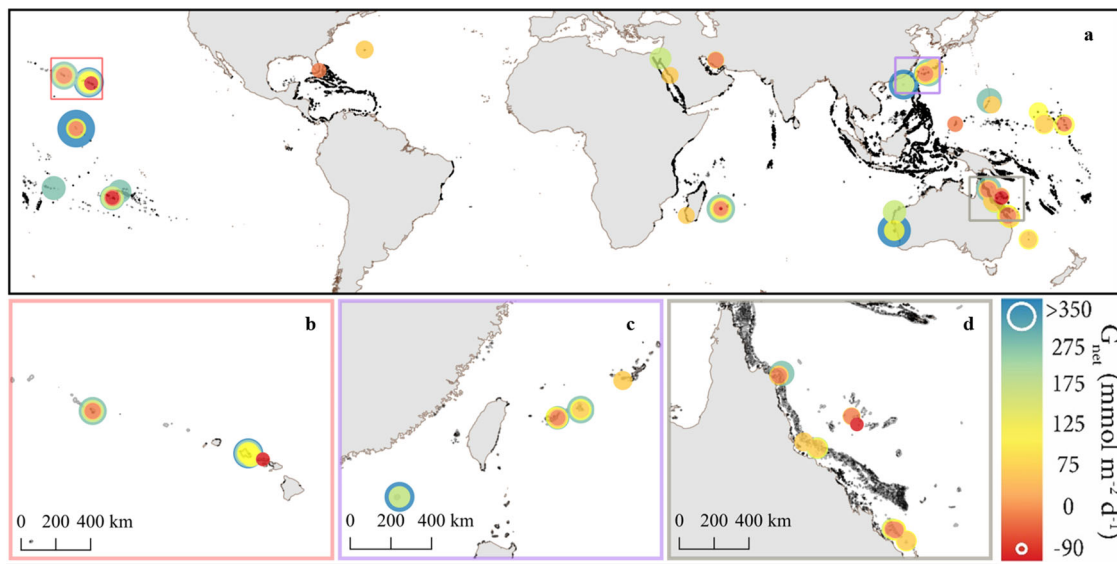


Fig. 1 Global distribution of coral reef ecosystem calcification from our literature review. **a** G_{net} among 36 coral reefs representing 116 diel, in situ hydrochemical-based metabolism investigations. Symbols vary in colour and size to represent varying G_{net} for each study. Black points represent the locations of all reported coral reefs globally⁴⁷. **b-d** Most-studied regions magnified from colour-associated boxes on global map to demonstrate detail in (b) Hawaii, (c) Japan, and (d) Australia. Citations are shown in Supplementary Data 1.

Table 1 Reported and calculated values of available quantitative auxiliary and metabolic data for 116 in situ hydrochemical coral reef metabolism studies.

Variable	Range	\bar{x}	SD	<i>n</i>	<i>n</i> *	Reporting	Error reporting
Ω_{ar}	2.1-4.5	3.44	0.5	65	20	17.4%	55.0%
Coral cover (%)	0.0-100	26	22	93	83	72.2%	24.1%
Depth (m)	0.2-10	1.94	1.7	98	70	60.9%	-
NO ₃ (μM)	0.0-1.2	0.47	0.4	13	9	7.8%	88.9%
PO ₄ (μM)	0.0-0.6	0.22	0.2	16	10	8.7%	80.0%
Temperature (°C)	18-32	26	2.9	83	44	38.3%	52.3%
G_{net} (mmol m ⁻² d ⁻¹)	-90-670	124	109	116	73	63.5%	49.3%
P_{net} (mmol m ⁻² d ⁻¹)	-870-1240	65	254	105	66	57.4%	59.1%

Qualitative data were also included in the GLMM, see ‘Methods’ for details. *n* Denotes the total number of studies which information was reported or calculated. *n** Denotes the number of studies which actively report the data for each parameter. Error reporting indicates the percentage of studies in each category which state the parameter’s uncertainty. Ω_{ar} data not reported were calculated using available data or sourced from other compilation tables^{24,41}.

dissolving ($G_{net} \leq 0$) during the night. Studies reporting nighttime dissolution have a significantly lower rate of diel-integrated G_{net} ($\chi^2 = 31.066, p < 0.001, n = 84$). Hence, reefs that are only net calcifying during the day are not calcifying at a rate to offset nighttime dissolution (Fig. 2). The difference in nighttime production is not an effect of diel-averaged Ω_{ar} and there appears to be no latitudinal, seasonal or decadal trends driving nighttime dissolution status.

Global drivers of coral reef ecosystem calcification. A series of linear mixed effects regression models (LMER, see Methods) were used to gain insight into the drivers of ecosystem calcification using year, study methodology and duration, latitude, seasonal heat type, reef state, P_{net} , Ω_{ar} , temperature, calcifier cover, wave action and depth as potential control variables. Results of the LMER indicated that water depth and calcifier cover significantly influence G_{net} , with wave action and seasonality showing some evidence for affecting G_{net} (Fig. 2 and Supplementary Table 1). Wave action was not significant at $\alpha = 0.05$ ($\chi^2 = 5.597, p = 0.061, n = 84$) though it was retained in the LMER, indicating potential to affect G_{net} . The removal of five outliers made seasonality a significant influence over G_{net} ($\chi^2 = 6.737, p = 0.035,$

$n = 79$). Depth was a significant driver of calcification ($\chi^2 = 4.788, p = 0.029, n = 84$), with the model predicting that for every metre increase in depth, G_{net} significantly decreased by 14.8 ± 6.8 mmol m⁻² d⁻¹, assuming other parameters remain constant. Calcifier cover also significantly influenced G_{net} ($\chi^2 = 15.723, p < 0.001, n = 84$), with a 10% increase in the relative percentage of calcifier cover increasing G_{net} by 4.1 ± 1.0 mmol m⁻² d⁻¹ (Fig. 2, Supplementary Table 1). Calcification is most impacted by changes in benthic communities in reefs with <20% calcifier cover due to the non-linear relationship between calcifier cover and G_{net} ($G_{net} = 42.5 \log(\text{calcifier cover}) + 120.2$).

Seasonal differences in the same coral reef ecosystem were investigated by 30% of studies included here. At locations where ecosystem calcification was estimated over different seasons, G_{net} increased with elevated temperatures ($\chi^2 = 22.232, p < 0.001, n = 26$, Fig. 3, Supplementary Table 1). We note that none of the reefs included in Fig. 3 were located in equatorial waters. The lowest latitude reef included was Lizard Island, GBR at 14.68 °S. Data on sunlight were unavailable for the majority of these studies, but the change in G_{net} did not reflect seasonal variability in the number of daylight hours, indicating that temperature could be the main driver of seasonality influencing G_{net} . ‘Season’ was significant in

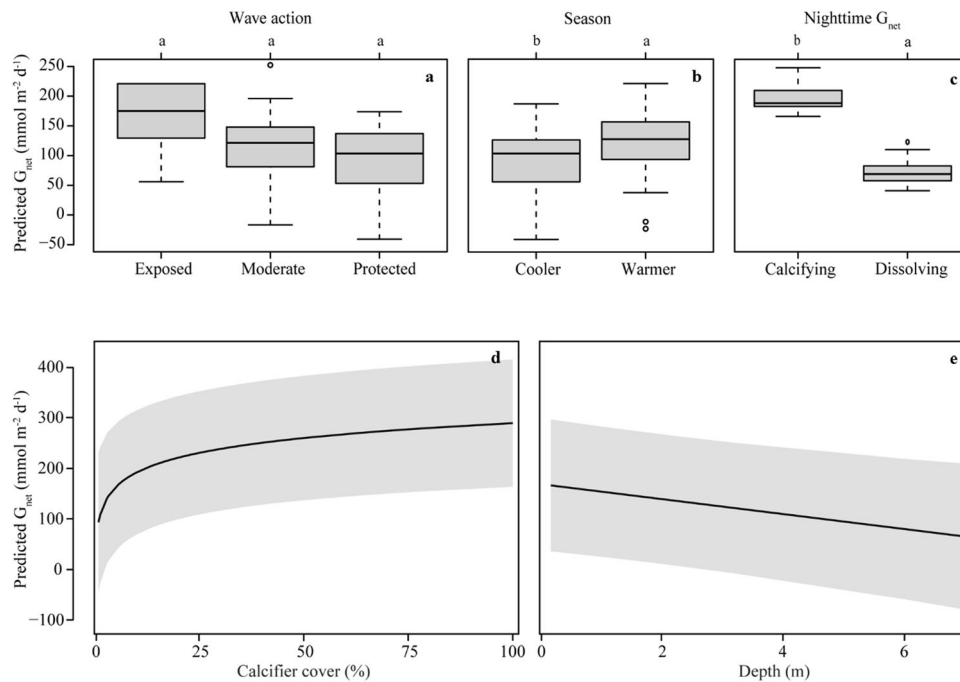


Fig. 2 Predictors of coral reef ecosystem calcification. **a–c** Box and whisker plots indicating the predicted G_{net} for reefs with categorical wave action, seasonality, and nighttime productivity status. The grey boxes show interquartile range as well as the median. Lines outside of boxes indicate minimum and maximum predicted values. Different letters represent statistical significance. **d, e** The predicted G_{net} increase associated with increasing calcifier cover (left) and depth (right) from the LMER, with shading representing 95% confidence intervals. All plots are based on the final LMER models (including any outliers, denoted by circles).

the LMER (after the removal of five outliers), indicating that summer–autumn seasons (S–A) have a higher average G_{net} than winter–spring seasons (W–S) (Fig. 2). When reefs are grouped into the most-studied geographical regions and latitudinal bins, warmer seasons (S–A) appeared to have higher G_{net} for Australian, USA and Japanese reefs, but calcification rates in French Polynesia are nearly identical regardless of the seasonal bin (Supplementary Fig. 1). Regional differences in G_{net} seasonality do not appear to be a result of latitude (Supplementary Fig. 1). Therefore, the importance of seasonality may vary among regions. Similarly, our model did not determine temperature to be a driver of G_{net} when all study sites were combined.

Temporal trends in ecosystem metabolism. Temporal observations at specific sites provide insight into how coral reefs globally respond to changing environmental conditions. Repeat surveys of G_{net} and P_{net} have, however, only been carried out at seven sites (Fig. 4, $n = 29$ and 26 surveys, respectively). We compiled data from locations with multiple studies undertaken in the same season. This showed that organic productivity increased over time by 3.0 ± 0.8 mmol m⁻² d⁻¹ yr⁻¹ since the 1970s ($p < 0.001$, Fig. 4). Calcification rates for repeat studies were lower than the original studies regardless of year, although half of the reefs were considered healthy (i.e. no recent major stressors or were reported to be ‘recovered’ during the most recent sampling). Out of the four sites with at least three repeat surveys, three sites showed a decrease in calcification ($\Delta G_{net} = -5.5 \pm 3.9\%$ yr⁻¹), and one showed an overall increase ($\Delta G_{net} = +0.4\%$ yr⁻¹). Using the slope of the regression line combining all repeatedly-surveyed sites over time, we estimate that G_{net} is currently dropping at a rate of 1.8 ± 0.7 mmol m⁻² d⁻¹ yr⁻¹ since the 1970s ($p < 0.001$, Fig. 4). If future change continues at the current rate of decline, we can expect average global net-zero calcification around 2054.

Discussion

Long-term trends in coral reef ecosystem calcification. Predicting how metabolic rates of global coral communities will change after stress events is difficult, but past and ongoing trends may give insight into future G_{net} . Projecting the declining trend in ecosystem calcification observed from this dataset obtained between 1971 and 2019 into the future implies that global G_{net} may reach 0 around 2054 at the current rate of decline (Fig. 4).

Our analysis, based on seawater chemistry overlying coral reefs builds on observations from sediment incubations. CO₂ enrichment experiments in sediment chambers imply that coral reef sediments may become net-dissolving between 2031 and 2082⁵⁰. Furthermore, persistent, long-term declines in calcification have been observed in most coral reef regions worldwide^{51–54} using multiple lines of evidence. Skeletal records from the Great Barrier Reef indicate the rate of decline has accelerated in the past two decades, with calcification falling by up to 1.5% year⁻¹ relative to baseline values, as of the late 2000s^{55,56}. Declines in Red Sea coral calcification of 30% in just one decade were associated with increasing sea surface temperatures and extrapolating this dataset to future warming scenarios resulted in the prediction of net-zero coral growth by 2070⁵⁴.

The change in the calcification potential of reefs may be associated with: (1) changes in the benthic calcifier abundance and community structure^{57,58} and (2) the declining ability of corals to calcify under stress⁵⁹. As demonstrated by our model (Figs. 2, 4) and census-based studies⁵³, the loss of coral cover due to stress events such as heat waves will decrease the calcification potential of global reefs. Here, reef calcification is declining at an average rate of $4.3 \pm 1.9\%$ yr⁻¹ (Fig. 4) with a concurrent reduction in mean calcifier cover of 1.8% yr⁻¹, suggesting that loss of coral cover may not be the sole contributor of declining calcification. Stress events can impact metabolic processes, even without a net loss of benthic calcifiers. Corals tend to maximise their chances of survival during stress events by temporarily

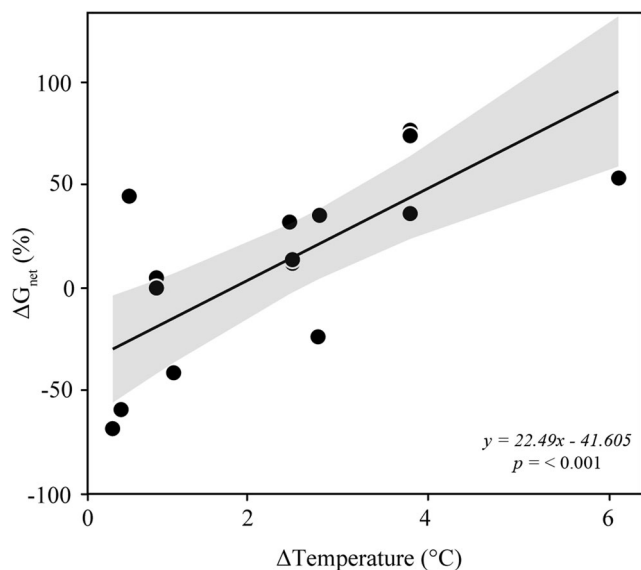


Fig. 3 Change in diel calcification (ΔG_{net}) versus seasonal change in water temperature (ΔT). Data points are included from studies deriving G_{net} from the same site over different seasons ($n = 26$). The black line represents a significant linear regression and grey shading represents the 95% confidence interval. The percent change in G_{net} is calculated as the warmer temperature G_{net} divided by the cooler temperature G_{net} . Because major local stress events or reef degradation can mask the temperature- G_{net} relationship²⁰, data from reefs classified as degraded were not included. This prevents confounding effects of growing local-scale impacts on a global-scale interpretation.

reducing calcification^{59,60}. Recently, a transient coral bleaching event that resulted in no observable coral mortality resulted in ecosystem calcification rates which were 40% lower than post-bleaching rates²⁴. Shifting community structure can also alter metabolic estimates^{10,31}. In times of stress, fast-growing, habitat-forming coral groups are replaced with weedy coral and algal species²⁷.

Our observation of decreasing G_{net} with increasing P_{net} at a global scale supports phase-shift theories. Phase shifting is observed in impacted reefs where lost coral cover is replaced by marine algae⁶¹. Shifting dominance of coral ecosystem functionality to marine algae results in lower reef resilience^{14,62}, biodiversity^{15,63} and provision of ecosystem services⁶⁴. Although high P_{net} is not necessarily the cause for deteriorating reefs and may exist in reefs with high G_{net} ^{9,65}, increasing P_{net} can indicate prior ecological disturbances which trigger the establishment of marine algae. We show increasing P_{net} over time indicating potentially reduced reef state and resilience against future stressors even in reefs with ‘healthy’ G_{net} rates (Fig. 4)^{62,64,65}.

The rate of G_{net} decline presented here is likely to rise as stress events increase in frequency and intensity with climate change^{6,7,66,67}. For example, the most widespread mass-bleaching event so far recorded on the GBR occurred in 2020⁶⁸, suggesting that the rate of G_{net} decline (Fig. 4) may underestimate the magnitude of sudden G_{net} drop related with bleaching events.

Global drivers of ecosystem calcification. Site-specific investigations suggest that G_{net} in coral reefs is driven by a complex combination of factors such as calcifier cover, hydrodynamics (wave action and depth), temperature, light, organic productivity, nutrients and Ω_{ar} ^{34,69–71}. To test whether these local conclusions hold at the global scale, we developed a LMER using our compiled dataset. We found no influence of methodological approach

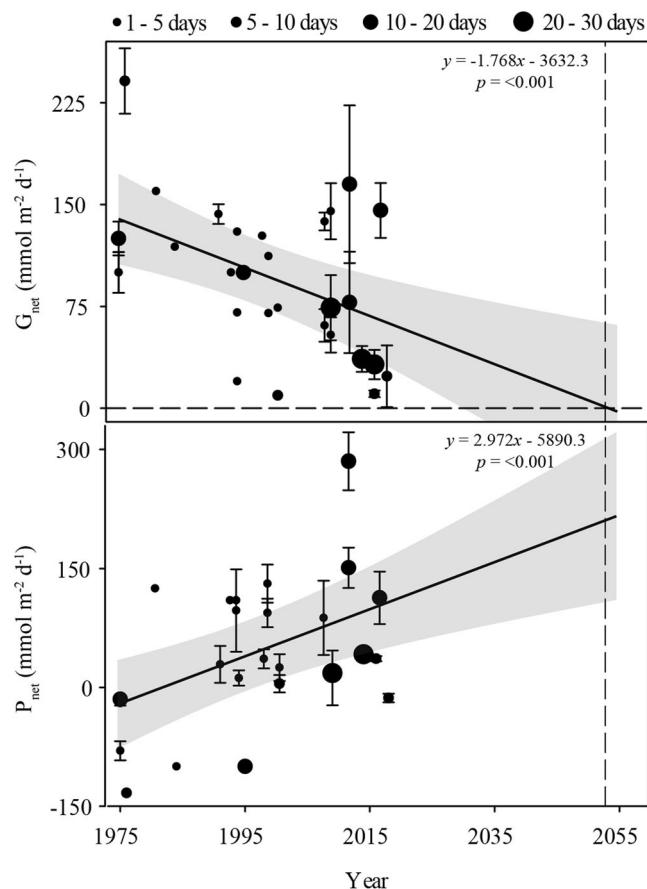


Fig. 4 Long-term changes in coral reef ecosystem calcification (G_{net}) and productivity (P_{net}) for well-studied reefs. Data were compiled from observations which occurred using the same site and seasonal bin over different years (Supplementary Data 1). Black lines represent significant linear regressions and grey shading represents 95% confidence intervals. Symbol size reflects the duration of the study in the number of days. Horizontal dashed line represents net-zero calcification and vertical dashed line represents the when G_{net} will approach net-zero. Sites affected by groundwater discharge are excluded. P_{net} excludes McMahon et al.¹⁶ because it was sampled during a major bleaching event and was considered an outlier ($P_{\text{net}} = -868 \text{ mmol m}^{-2} \text{ d}^{-1}$). $n = 29$ for G_{net} and $n = 26$ for P_{net} . Error bars are included when standard errors were reported or could be calculated from information presented in the paper.

on calcification estimates such as sampling strategy or study duration. We found no significant influence of latitude, reef state, P_{net} , or Ω_{ar} on G_{net} (Supplementary Note 1). However, calcifier cover and depth were significant drivers of G_{net} , and seasonality, temperature and wave action were influential (Figs. 2, 3, Supplementary Table 1).

Calcifier cover. The amount of coral and other calcifying organisms within an ecosystem is a key driver of its calcification rates⁷². Indeed, calcifier cover was the most significant predictor of G_{net} in our model compiling all studies (Fig. 2, Supplementary Table 1). As the structural complexity and planar area of calcifiers reacting with the surrounding water increases, so does the calcification potential⁷³. However, site-specific disparities between G_{net} and coral cover have been observed^{9,21,74–76}. One hypothesis for local calcifier- G_{net} non-linearity includes the introduction of unaccounted-for, external carbon that affects metabolic activity and calculations. Localised inputs of CO_2 -enriched groundwater

may explain some of the low G_{net} in high calcifier cover reefs⁹, where acidified reef waters potentially drive skeletal or sediment dissolution⁷⁷. However, due to the complexity of coral reef ecosystems, it can be difficult to ascertain specific disparities between G_{net} and calcifier cover^{74,78,79}. Our result that increased calcifier cover enhanced G_{net} on a global scale indicates that current and future declines in coral cover due to stress events^{2,58,80} will affect ecosystem calcification rates.

Reef hydrodynamics. Wave action and depth can drive ecosystem calcification (Fig. 2, Supplementary Table 1) through their relationship with residence times, nutrient delivery and the indirect effects on the equations used to calculate G_{net} ⁷⁸. Wave action influences G_{net} from its associations with seawater chemistry and coral ecology, with higher coral diversity at wave-exposed reefs³⁰. In wave-exposed reefs, increasing wave heights promote water circulation and calcification^{69,81,82}. The modelled relationship between wave action and G_{net} (Fig. 2) might have been stronger if wave action was in the form of a continuous numerical variable (such as average or maximum wave heights or energy flux) rather than broad classifications based on reef type ('exposed', 'moderate' and 'protected') that can be retrieved from the literature. However, wave heights or energy are challenging to measure and are rarely reported. Residence time could have a significant influence on G_{net} at a local scale^{37,78,83}, but is not a relevant factor in all methodologies³², is associated with large errors^{16,20,84}, and is rarely reported in a unit pertinent to our study. Therefore, residence times were not included in our meta-analysis. Residence times also depend on water depth, which was found to be a significant predictor of G_{net} (Fig. 2) and pH variability within a reef⁸⁵. Potential explanations for how depth influences G_{net} include depth-driven light attenuation, benthic ecology or thermal stratification of the water column.

Due to light attenuation, the benthos receives progressively less light at increasing depths with corals at 6.5 m receiving only 5% of the light as those at 0.5 m⁸⁶. However, corals growing in deeper water may be better adapted to utilise light⁸⁷ or require less light for calcification⁸⁸. Vertical stratification of the water column can result in colder temperatures, decreased boundary layer flow (and therefore less nutrient delivery to corals), or biased interpretation if water samples for deeper sites are taken at the sea surface⁸⁹. In census-based studies, a recent meta-analysis determined that water depth did not have a significant influence on carbonate budgets³¹. However, census-based studies rely on calculating G_{net} from skeletal linear extension and density change rates obtained from the literature. Skeletal observations may have been determined in multiple locations from mesocosms or at various depths in situ, reducing the perceived influence of depth on G_{net} ⁹⁰.

Temperature and seasonality. The temperature effect on G_{net} was scale-dependent. Although our model indicated no overarching influence of temperature on global G_{net} rates, individual reefs had greater G_{net} with higher water temperatures and in warmer seasons^{20,71} (Figs. 2, 3). Similarly, when all previous site-specific models that use physicochemical parameters to predict G_{net} were compiled, the only model to significantly correlate with global G_{net} observations relied on temperature alone^{42,67}. In general, increasing temperatures increase coral growth until a thermal threshold is reached²⁹. The magnitude of this effect can be dependent on species, location or latitude^{56,91}. High-latitude reefs may initially benefit from increasing ocean temperatures with some having rising calcification rates^{4,91}, supporting our observation of increasing G_{net} with warming on seasonal time scales (Fig. 3, Supplementary Fig. 1). However, the benefit of increased G_{net} on reefs from rising temperatures will be negated

when bleaching events occur, which can decrease ecosystem calcification >100%^{16–18} due to coral mortality and sub-lethal stress⁵⁹. Declining calcification on lower-latitude reefs is likely due to rising temperatures rather than ocean acidification⁹¹, indicating that ocean warming will have latitude- and magnitude-specific impacts on coral reefs.

Research needs. Our meta-analysis reveals several knowledge gaps with regard to monitoring and reporting of environmental parameters (Table 1). Reporting essential auxiliary variables would increase our understanding of the drivers of coral ecosystem metabolism and the ability to build predictive models. The LMER initiated with 46 out of 116 studies due to unavailable data (see Methods). Less than 10% ($n = 10$) of studies reported all key numerical variables used in the model (G_{net} , P_{net} , depth, calcifier cover, temperature, and Ω_{ar}). More consistent reporting of uncertainties would likely minimise model prediction uncertainties. Clearer explanations of approaches and metabolic calculations would also improve comparability among studies and contribute to a global understanding. Specifically, daytime and nighttime productivity rates, hours of sunlight, PAR, temperature and seawater carbon chemistry metrics would be useful to disentangle how ocean warming and acidification are affecting coral ecosystems.

Due to the logistical difficulties of nighttime sampling, many studies report calcification rates for the daytime only. Nighttime G_{net} rates vary widely from positive to negative and, therefore, have a variable effect on diel-integrated calcification rates. Information relating to nighttime calcification was only reported for 72% of studies. Since dissolution is more sensitive to ocean acidification than calcification^{50,92,93}, studies focusing exclusively on daytime G_{net} may not capture the full story about how ocean acidification may be affecting the ecosystem's metabolism. Additionally, the relative contribution of calcification and dissolution in a reef can indicate changes in long-term ecosystem health and future persistence⁹⁴. Our result that reefs which dissolve at night have significantly lower diel G_{net} rates (Fig. 2) highlights the need for overnight observations.

Certain locations and latitudes are underrepresented in efforts to estimate G_{net} . Equatorial coral reefs (<10° latitude) comprise 26% of global coral reefs, though only <10% of ecosystem metabolism studies occurred here (Fig. 1). With underrepresentation of equatorial reefs, there have been no ecosystem-scale metabolic estimates at some of the most biodiverse coral ecosystems in the world such as reefs in the coral triangle^{95,96}. Quantifying metabolic rates of coral ecosystems in warmer climates could help to provide insight into how other reefs may respond to increasing temperatures.

Conclusions

Overall, our compiled global dataset and analyses provide insight into the long-term drivers of coral ecosystem calcification (Figs. 2, 3). We reveal a significant decline in coral ecosystem calcification ($4.3 \pm 1.9\% \text{ yr}^{-1}$) and increase in organic productivity within the last 50 years. Our results also support recent arguments that Ω_{ar} is not a main driver of global coral reef calcification and may not be useful to predict long-term G_{net} . Depth and benthic calcifier cover were the most important predictors of global G_{net} . Seasonal changes in water temperature also influence G_{net} , with warmer temperatures facilitating higher calcification rates. However, the overall effect of ocean warming and heat waves will likely counteract any benefits of elevated G_{net} when temperatures rise above thermal bleaching thresholds. The rate of G_{net} decline presented here is likely to increase non-linearly as mass-stress events become more frequent and severe. At the current rate of

decline, we can expect to observe net-zero calcification in coral reefs around 2054.

Methods

Study selection from the literature. We conducted a systematic review on peer-reviewed coral reef ecosystem calcification studies to investigate trends in experimental designs and drivers of G_{net} . The data collected to support a quantitative meta-analysis were compiled from studies estimating G_{net} via in situ hydrochemical methods where observations occurred during the day and at night. Literature was searched for on Google Scholar. Because the focus was to obtain relevant papers pertaining to our meta-analysis criteria, we did not limit literature searches according to predetermined Boolean structured statements. Searches used combinations of the terms ‘coral reef’, ‘metabolism’, ‘carbonate budgets’, ‘carbon budgets’, ‘calcification’, ‘ecosystem’ and ‘productivity’, as well as searching references within relevant papers. Studies were excluded if diel-integrated G_{net} rates, or the information necessary to calculate these, were not available, or if major external carbon sources such as river or groundwater inputs were documented at the time of sampling. Calculation of metabolic rates and auxiliary information occurred where sufficient information was given in the text, supporting information, or where original data was provided by the corresponding author (Supplementary Data 1). Studies were collected for analysis until April 2020. Seven studies were not included due to lack of data, with no response to our request for information from the corresponding author. Four studies were not included due to the invalidation of sampling methodology assumptions (i.e. the introduction of unaccounted for carbon into the system).

We compiled qualitative information from each publication on the study year, location, data collection duration (in days), wave action based on reef type (exposed, moderate or protected), season (placed into bins based on heat type: ‘H’ for summer–autumn and ‘C’ for winter–spring), methodology (slack water, flowing water, chamber, offshore TA anomaly and benthic gradient flux), nighttime production status (net calcifying or dissolving) and coral reef state (degraded or healthy/unspecified). The ‘degraded’ category includes reefs originally described to experience major local impacts or to recover from pulse (e.g. cyclone or bleaching mortality) or press stressors (e.g. eutrophication, acidification). Study sites without a clear description about the level of degradation were classified as ‘healthy/unspecified’.

Exposed reef types included those described directly in the literature as being exposed to wave action, or were described as on the ‘seaward edge’ of reef flats or reef crest sites. ‘Moderate’ wave action was denoted for those sites which were described as such, as well as mid-reef flat and mid-fringing reef sites. ‘Protected’ reef types from wave exposure included sites in back reef and lagoonal sites, as well as sites described in original manuscripts as being protected from wave action.

The ‘flowing water’ methodology consisted of studies using Eulerian, Lagrangian, or similar variants to collect samples and calculate water residence times. The ‘chamber’ methodology group consisted of field experiments isolating the benthos and overlying water from natural circulation (incubation chamber and control volume studies). To be included, chamber studies were required to use chambers including multiple benthos components (i.e. not encapsulating only a single coral). The offshore TA anomaly methodology group consisted of studies which compared reef water carbonate chemistry with offshore water carbonate chemistry where the residence time was calculated separately. See Supplementary Data 1 for examples.

We also gathered quantitative data including diel-averaged aragonite saturation state (Ω_{ar}), temperature, coral and coralline algal cover (combined to one ‘calcifier cover’ term), depth, seawater nutrient concentrations (nitrate (NO_3^-) and orthophosphate (PO_4^{3-})), diel-integrated net organic and inorganic productivity (P_{net} and G_{net}), and any associated errors for each variable that was reported in the manuscript (standard deviations or standard errors as reported). Non-reported variables were left blank (Table 1). Light/PAR data were collected but was not analysed due to the many different methods of measuring and reporting units, of which many are not possible to convert to a standard unit. For publications where multiple seasons or locations were studied, data were compiled for each sampling campaign and included as separate lines of metadata in Supplementary Data 1. P_{net} rates include those gathered from studies which used either oxygen- or dissolved inorganic carbon-based (DIC) methodologies. These methodologies are similar as they each rely on the assumption that seawater chemistry is altered by primary productivity in the ecosystem, and account for atmospheric exchange of CO_2 and O_2 . Analyses of DIC to estimate P_{net} was not widely used before the 2000s. Therefore, P_{net} derived from both methodologies had to be included to incorporate P_{net} as a variable in this model.

The seawater chemistry investigations summarised here quantify calcification on the ecosystem scale, but cannot resolve the specific taxa driving calcification. In addition to corals, there are several reef organisms such as molluscs and bryozoans that calcify and therefore alter seawater carbon chemistry⁹⁷. However, local scale and census-based calcification investigations indicate that corals and calcifying algae usually dominate G_{net} in coral reef ecosystems^{30,31}.

Statistical analysis. We conducted a series of LMER models with parameter estimates using restricted maximum likelihood on the data of published literature regarding in situ coral reef ecosystem calcification rates, in R ⁹⁸ using the lmer function in the lme4 package (version 1.1-21)⁹⁹. The LMER models included fixed and random effects, and followed a standard and widely accepted statistical

approach to provide a framework for data interpretation that can be replicated from our metadata and updated as more field data become available. By integrating multiple quantitative and qualitative controls, the LMER model provides deeper insight than conventional linear models^{99–101}. Due to the frequent occurrence of missing values for explanatory variables throughout the dataset, we adopted a backward-selection process in the LMER, which increased the number of data points included in each subsequent model following the removal of a parameter. The backward-selection process used Akaike Information Criterion and Bayesian Information Criterion as a guide¹⁰², whereby one variable was removed at a time between each subsequent model sequence until a final model was reached that could not be improved by removing any further variables. After each model sequence and the successive removal of a covariate, the data frame was reassigned so there were effectively more data points in subsequent models as covariates became fewer.

We tested whether G_{net} was significantly influenced by any of the explanatory variables, including P_{net} , latitude (degrees), wave action (exposed, moderate or protected), duration of study (days), heat type of season (summer–autumn and winter–spring), study methodology, reef state, Ω_{ar} , temperature, calcifiers (% benthic cover) and depth (m). A random intercept term for location was included in the model to account for site-specific variability. Data on nutrients were collected but not included in the LMER due to low reporting ($n \leq 10$). Additionally, due to the underreporting of variance in sampled G_{net} , we were unable to include a weighting for G_{net} in the model, such as following an inverse-variance method. Latitude (in decimal degrees) was converted to absolute values to represent relative distance from the equator. Reef state was reduced to a categorical factor with two levels (i.e. healthy/unspecified or suffering a level of degradation), as reported in the various publications. The coefficient of calcifiers was log-transformed because this provided a better correlation with G_{net} (-0.95) than without transformation (-0.75). Default parameters were used in the lme4 package, with the full statistical model taking the form:

$$y_{ij} = \beta_0 + \beta_{P_{\text{net}}} \chi_{ij}^{P_{\text{net}}} + \beta_{\text{lat}} \chi_{ij}^{\text{lat}} + \beta_{\text{wave}} \chi_{ij}^{\text{wave}} + \beta_{\text{duration}} \chi_{ij}^{\text{duration}} + \beta_{\text{heat}} \chi_{ij}^{\text{heat}} \\ + \beta_{\text{method}} \chi_{ij}^{\text{method}} + \beta_{\text{health}} \chi_{ij}^{\text{health}} + \beta_{\Omega_{\text{ar}}} \chi_{ij}^{\Omega_{\text{ar}}} + \beta_{\text{temp}} \chi_{ij}^{\text{temp}} \\ + \beta_{\text{calc}} \log(\text{calc}_{ij}) + \beta_{\text{depth}} \chi_{ij}^{\text{depth}} + U_i + \varepsilon_{ij} \\ U_i \sim N(0, \sigma_U^2) \\ \varepsilon_{ij} \sim N(0, \sigma_{\varepsilon}^2)$$

where y_{ij} is the predicted G_{net} for the i th sample within location j . β_0 is a fixed intercept, with β regression coefficients for each of the fixed effects. U_i is the random effect of location j . ε_{ij} is the residual error for the i th sample within location j .

LMER was also used on refined datasets. To predict the change in G_{net} as a function of seasonal change in temperature, the full dataset was reduced to studies estimating ecosystem calcification at a specific location over two or more seasons. Degraded reefs were not included to focus on the effect of temperature changes on ‘baseline’ G_{net} . We also investigated long-term changes in G_{net} and P_{net} by compiling the results of studies undertaken on the same reef over different years. To control for seasonal changes in temperature, only observations during the same seasonal bins were included. The model structure was similar to the initial model in that a random intercept was included in the model to account repeated sampling at the location level. Default model parameters with the lme4 package were also used, with no weightings for either G_{net} or P_{net} , due to an underreporting of sample variance.

For the initial models, parameters were checked for collinearity and prioritised. Prioritisation defined which variables were included in the model until the model fully parameterised without overfitting. All models were assessed for model fit and confirmed assumptions of homoscedasticity and linearity. A sensitivity analysis using Cooks distance was used to assess the influence of individual observations¹⁰³, leading to the removal of outliers when required. The only outliers ($n = 5$) detected occurred in the ‘season’ variable. Model fit was assessed by visual inspection of residual plots using the lattice package¹⁰⁴. Homoscedasticity was also further assessed through a Levene’s test using the car package¹⁰⁵. Analysis of Deviance tables using Type II Wald Chi-square tests, from the ‘car’ package¹⁰⁶ was used to assess the significance of fixed-effect coefficients in the final model. Further pairwise comparisons using Tukey Contrasts in the ‘multcomp’¹⁰⁷ package, using Bonferroni–Holm correction, were also used to examine within-factor groups for variables in the final model.

Data availability

The authors declare that the data supporting the findings of this study and its source data are available within the paper and its Supplementary Information Files. The metadata is also available on the SEANOE database at <https://doi.org/10.17882/80022>.

Code availability

The authors declare that the R code supporting the findings of this study are available within the paper.

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Author contributions

K.D. and I.S. conceived the idea and wrote the paper. K.D. calculated and compiled the metadata and undertook preliminary analyses. K.D., A.C., I.S. and B.K. contributed to the study design and data interpretation. A.C. wrote the R code and performed statistical analyses. A.C. and J.T. assisted with mapping and graphical interpretations with input from K.D. and I.S. All authors were involved in paper editing.

Competing interests

The authors declare no competing interests.

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