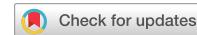


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Crustose coralline algae can contribute more than corals to coral reef carbonate production

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Understanding the drivers of net coral reef calcium carbonate production is increasingly important as ocean warming, acidification, and other anthropogenic stressors threaten the maintenance of coral reef structures and the services these ecosystems provide. Despite intense research effort on coral reef calcium carbonate production, the inclusion of a key reef forming/accreting calcifying group, the crustose coralline algae, remains challenging both from a theoretical and practical standpoint. While corals are typically the primary reef builders of contemporary reefs, crustose coralline algae can contribute equally. Here, we combine several sets of data with numerical and theoretical modelling to demonstrate that crustose coralline algae carbonate production can match or even exceed the contribution of corals to reef carbonate production. Despite their importance, crustose coralline algae are often inaccurately recorded in benthic surveys or even entirely missing from coral reef carbonate budgets. We outline several recommendations to improve the inclusion of crustose coralline algae into such carbonate budgets under the ongoing climate crisis.

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Coral reefs host an incredible array of diversity and are formed via the production and accretion of calcium carbonate (CaCO_3) by resident calcifying species. The existence of reefs requires the maintenance of calcium carbonate structures that depends upon the balance of processes that produce and remove calcium carbonate^{1,2}. These processes have been the subject of intense scientific effort to determine the carbonate 'budgets' of reefs^{3,4}. Calcium carbonate (CaCO_3) on coral reefs is predominantly produced by corals, which build three-dimensional frameworks that allow for rapid accretion, with additional contributions to the framework from other calcifying organisms such as crustose coralline algae (CCA), and sedimentary contributions from the breakdown of corals, CCA, and from the skeletal remains of other calcifying taxa including *Halimeda* spp., foraminifera, and molluscs⁵. Calcium carbonate is removed from the reef framework via chemical dissolution, physical erosion, and bioerosion from parrotfishes, sea urchins, sponges, cyanobacteria, and many other taxa that live within the calcium carbonate structure of the reef^{6,7}. Determining these rates of net calcium carbonate production is also termed the carbonate budget when referring to estimates at a reef level. The magnitude of the contribution of each production and erosion process is driven by numerous environmental and biogeographic factors, and varies highly across spatiotemporal scales³. Understanding how these rates of net calcium carbonate production vary is important for predicting the provisioning of ecosystem services by coral reefs in the future under ongoing environmental change and sea level rise⁸, similar to what occurred in past oceans when atmospheric CO_2 concentrations were elevated and calcareous algae more numerous⁹.

Numerous calcifiers contribute to coral reef carbonate budgets (Fig. 1a), but the contribution of these groups is not equivalent for

the maintenance of the reef structure⁵. Some calcifying taxa predominantly add to integral reef framework structures, whereas others produce particulate skeletal carbonate that contributes primarily to reef sediments^{10,11}. The two main contributors to the most commonly occurring framework structures are corals, which are typically the principal producers of calcium carbonate in coral reef ecosystems, and CCA, an often important but often overlooked framework carbonate producer¹². However, determining how CCA contribute to coral reef net calcium carbonate production and structural stability will be increasingly important as the effects of climate change manifest to reduce coral cover¹³. In this scenario, CCA-driven gross carbonate production will become increasingly important in coral reef net calcium carbonate production^{14–16}.

Rates of calcium carbonate production vary greatly across different sections of the same reef, between reefs, within regions, and between larger geographic regions^{8,17–19}. This is due to variation in the balance between gross calcium carbonate production and erosion that together comprises net carbonate production. Both gross calcium carbonate production and erosion are largely determined by the environmental controls on community composition and the rates of calcification and/or bioerosion of individual substrates within the community (e.g. light, water motion, water quality, temperature, and carbonate chemistry)^{20–25}. Spatial variation in these environmental conditions across coral reef ecosystems can lead to CCA-dominated habitats or even entire regions built by CCA, such as algal reef flats, reef crests and algal ridges (Fig. 1b, Fig. 2)^{26–28}. Temporal shifts in environmental conditions or major disturbances to the coral community (e.g. bleaching or storm damage) can also allow previously coral-dominated reefs to become CCA-dominated^{1,14} (Fig. 1d). Entire reef structures can be dominated by CCA, for

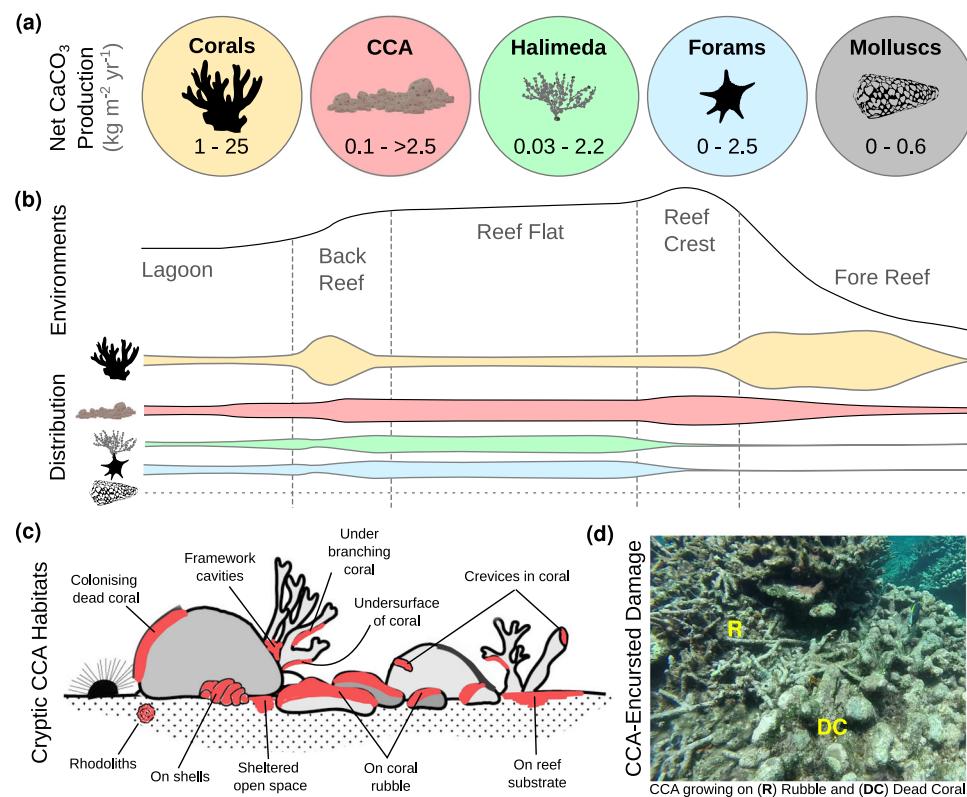


Fig. 1 Coral reef carbonate production and crustose coralline algae (CCA). **a** The contribution of the main groups of reef calcifiers to carbonate budgets (corals, CCA, *Halimeda* spp., foraminifera (forams), and molluscs⁵), along with **b** their approximate distribution across a range of reef environments based on observations by the authors of this study (molluscs are not straightforward because they can be mobile). **c** CCA may be found in numerous cryptic environments within reef habitats, and **d** commonly encrust dead coral and reef rubble after bleaching or storm damage.



Fig. 2 Examples of crustose coralline algal dominated habitats. **a** Jalan (or Tallon) Island, the waterfall reef built of coralline algae in northern Western Australia. **b** Crustose coralline algal community at Starbuck Island, Kiribati. **c** Settlement of crustose coralline algae over dead coral at Millennium Atoll, Kiribati. **d** Montgomery Reef, Australia's largest inshore reef, formed entirely by crustose coralline algae covered by brown algae.

example in the Kimberley region of Australia (380 km^2)²⁹, smaller reefs in Taiwan³⁰, Atol das Rocas in Brazil³¹, or the unique Cup reefs of Bermuda³², and maintain positive net carbonate production rates despite very low coral cover. The existence of CCA reefs further implies that they represent an alternative stable state for reef systems, although the exact conditions that give rise to them, and the threshold and mechanisms at which transitions may occur are unknown. Collectively, these lines of evidence indicate that CCA carbonate production is potentially important in the context of coral reef carbonate production, particularly following disturbances such as coral bleaching events, and in the context of a changing climate that may drive regime-shifts in reef systems (ocean acidification aside).

Here, we: (i) present a meta-analysis of CCA and coral calcification rates to develop a conceptual model for CCA contribution to coral reef net carbonate production; (ii) explore the temporal dynamics of coral vs. CCA net carbonate production through disturbance events using an example from Mo'orea; and (iii) present several suggestions to improve the inclusion of CCA within existing and future estimates of net carbonate production. We focus specifically on the role of CCA in coral reef net carbonate production; and there are extensive resources available for understanding carbonate budgets in general^{1,3,33}. We aim to offer suggestions for both generalists and specialists working within the coral reef sciences to improve our understanding of CCA contribution to carbonate budgets. We consider that there are large uncertainties in many present-day estimates of net carbonate production. Recording accurate net production of a vital group of calcifying taxa will be even more important under the ongoing climate crisis.

Results

How important are CCA for reef budgets? How fast do CCA calcify? To compare the rates of CCA and coral calcification we combine data from two different sources. We combined the data

collected by Cornwall et al.³⁴ with additional studies identified using Web of Science with the search term “coralline algae” AND “calcification” OR “growth” OR “carbonate production”, which identified a total of 89 studies from 1979 to 2022. All studies representing calcification rate as a percentage change over time were discarded, resulting in a total of 61 studies. Each study was labelled with the climate zone (Tropical, Warm Temperate, Cool Temperate, and Polar)³⁵ and the method used to measure the calcification rate (Isotopes, Buoyant-Weight (BW) or Relative Growth Rate (RGR), Total Alkalinity Anomaly, X-Ray, CT-scan, and Staining). The dataset was then split into three subsets based on the type of calcification rate measurement, which were either standardised by biomass or by surface area. To compare each study, we converted calcification rates into the most common unit in each subset (e.g. $\mu\text{mol g}^{-1} \text{ h}^{-1}$, $\text{mg cm}^{-2} \text{ d}^{-1}$, and mm yr^{-1}).

To compare the calcification rates of CCA to corals we used data taken from Kornder et al.³⁶, which includes 288 estimates of coral calcification rates from studies published prior to 2016. Within this dataset, we selected only those rates measured by techniques overlapping with the CCA data highlighted above (i.e. buoyant weight and total alkalinity anomaly methods), resulting in 66 records of calcification rate measurements over ten coral genera. Comparison of rates for corals and CCA shows that group-specific, surface area-normalised calcification rates for corals and CCA are highly variable but span similar ranges (Fig. 3). This contrasts with the prevailing opinion in the coral reef community that CCA produce orders of magnitude less gross calcium carbonate than corals and therefore play a minor role in reef building (Fig. 1a). However, corals tend to grow more complex three-dimensional structures than CCA, complicating the comparison between group-specific calcification rates and reef accretion rates. To explore the implications of these group-specific rates for reef carbonate budgets, we construct a conceptual model of the relative contributions of CCA and corals accounting for colony and reef-scale structural complexity.

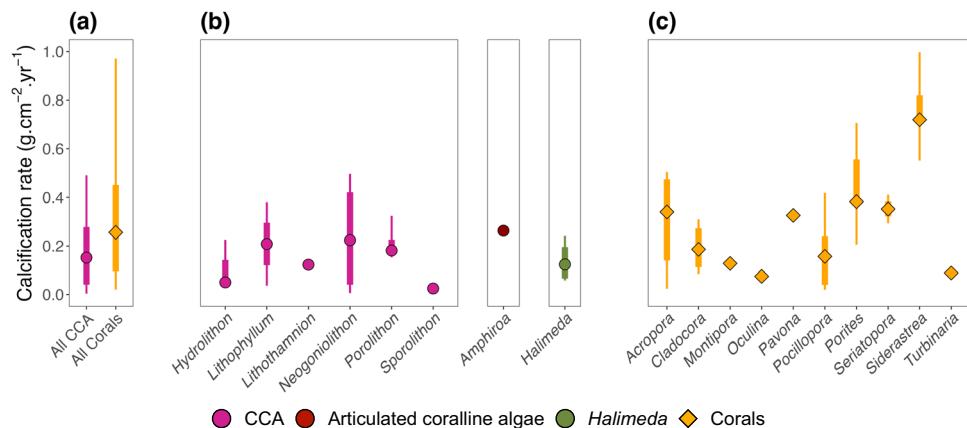


Fig. 3 Crustose coralline algae (CCA), articulate coralline algae, *Halimeda* spp., and coral calcification rates from laboratory measurements. Genus-specific, area-normalised calcification rates for a range of common CCA and coral species compiled from 55 and 66 studies, respectively. Note these are normalised to organism surface area, rather than reef horizontal area. Points show the median, thick error bars show the interquartile range, and thin error bars show the 99% quantile. Aggregate CCA and coral statistics in (a) are calculated from all underlying data for corals, and for CCA only for CCA. Smaller panels in (b) denote articulate taxa and *Halimeda* spp., with both b and c highlight the important variability across different coral and CCA genera.

Conceptual model of CCA contributions to coral reef carbonate production. The surface area-normalised calcification rates ($\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) for CCA and corals (median \pm IQR) from our meta-analysis (Fig. 3) were used to create a conceptual model of the relative contribution of CCA and corals to overall carbonate production (G ; $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$). This is affected by their relative cover and ratios of coral rugosity (R_{coral}) to CCA rugosity (R_{CCA}) within a given reef (i.e. $R_{\text{coral}}: R_{\text{CCA}}$, see Fig. methods for further details on the conceptual model). The morphology of a coral will influence its surface area and, consequently, carbonate production within a given planar reef area. More structurally complex branching corals have a greater colony surface area ($R_{\text{coral}} = 2.97$) compared to massive corals ($R_{\text{coral}} = 1.54$) or flat encrusting corals ($R = 1.00$;³⁷ Fig. 4a). The threshold (% cover) at which the relative contribution of CCA exceeds the relative contribution of coral to the carbonate production ($G_{\text{CCA}} > G_{\text{Coral}}$) increases logarithmically with $R_{\text{coral}}: R_{\text{CCA}}$ from 0 to 4 (Fig. 4b). We find that reefs comprised of branching corals and flat CCA ($R_{\text{coral}}: R_{\text{CCA}} = 2.97$) will require CCA cover to exceed 87% for $G_{\text{CCA}} > G_{\text{Coral}}$ (Fig. 4c), and with massive corals ($R_{\text{coral}}: R_{\text{CCA}} = 1.54$) this reduces to 78% (Fig. 4d). When the rugosity of CCA is equal to that of the corals ($R_{\text{coral}}: R_{\text{CCA}} = 1$), such as with encrusting corals/CCA or when CCA covers structurally complex dead coral skeleton following a disturbance event thereby inheriting the complex morphology, the CCA cover threshold is reduced to 78% (Fig. 4e). Therefore, as reef flattening progresses under ongoing environmental change³⁸, lower % CCA cover is required to exceed the relative contribution of coral to net reef carbonate production, albeit with CCA-dominated reef sites likely producing less CaCO_3 than coral-dominated reef sites (i.e. on the basis of lower surface area-normalised calcification rates; Fig. 4a). Moreover, it is important to note that this conceptual model only accounts for shifts from coral to CCA-dominated reef-states and that declining overall calcifier cover (e.g. shifts to turf, upright fleshy macroalgae, or bare substrate) would nonetheless lead to reduced carbonate production and more complicated net coral reef carbonate production scenarios than those explored here (see ternary diagram and discussion in Perry et al.¹).

Case Study: Mo’orea (French Polynesia). To compare our conceptual model to a real-world example, we use a case study of disturbance-driven coral community decline and subsequent recovery from Mo’orea, French Polynesia, which demonstrates

the increasing contribution of CCA to coral reef carbonate production following a disturbance. Coral cover rapidly declined from $\sim 35\%$ in 2005 to 5% in 2011 due to a combination of crown-of-thorns starfish (COTS) outbreak from 2006–2010, a coral bleaching event in 2007, and Cyclone Oli in 2010^{39–44} with a subsequent recovery of coral cover to $31 (\pm 15\%)$ by 2016 (Fig. 5a). Over the same period, CCA cover increased from 10% in 2005 to 25% in 2010 and subsequently declined to 15% in 2015 (Fig. 5a). Coral carbonate production (% cover coral \times coral calcification rate \times structural complexity) declined sharply from $3.47 \pm 0.58 \text{ kg m}^{-2} \text{ yr}^{-1}$ in 2005 to $0.2 \pm 0.15 \text{ kg m}^{-2} \text{ yr}^{-1}$ in 2011 with a subsequent recovery to pre-disturbance levels by 2016 (Fig. 5b). In comparison, CCA carbonate production (% cover CCA \times CCA calcification rate [mean of Fig. 3]) increased slightly from $0.13 \pm 0.03 \text{ kg m}^{-2} \text{ yr}^{-1}$ in 2005 to $0.31 \pm 0.09 \text{ kg m}^{-2} \text{ yr}^{-1}$ in 2010, returning to around $0.21 \pm 0.07 \text{ kg m}^{-2} \text{ yr}^{-1}$ by 2015 (Fig. 5b). As a result of these shifts in coral and CCA carbonate production, the relative contribution of CCA to the CaCO_3 budget (% CCA contribution = CCA carbonate production / (coral + CCA carbonate production) $\times 100$) increased from $3.57 \pm 0.96\%$ in 2005 to $56 \pm 26.4\%$ in 2010 and subsequently declined to $6.67 \pm 4.37\%$ by 2016 (Fig. 5c). These results are consistent with the outputs of our conceptual model (Fig. 4) as well as previous studies highlighting the increasing contribution of CCA to coral reef carbonate production following coral bleaching disturbance events^{13,15,25}.

Discussion

How do we better include CCA in coral reef carbonate budgets? Census-based carbonate budgets assign gross calcium carbonate production and loss terms (erosion usually) to benthic and fish survey data to estimate the net calcium carbonate production or net loss of calcium carbonate (net erosion)³. Therefore, we must accurately determine both the total cover of CCA and their rugosity with benthic surveys and the net calcium carbonate production rates by measuring CCA net calcification and subsequent bioerosion. For each of these steps, we provide a brief overview of the methods with general recommendations to better include CCA in coral reef carbonate budgets derived from census-based methods. Figure 6 highlights the variety of methods to measure CCA contributions to carbonate budgets, and we also discuss recommended best practices to these methods below.

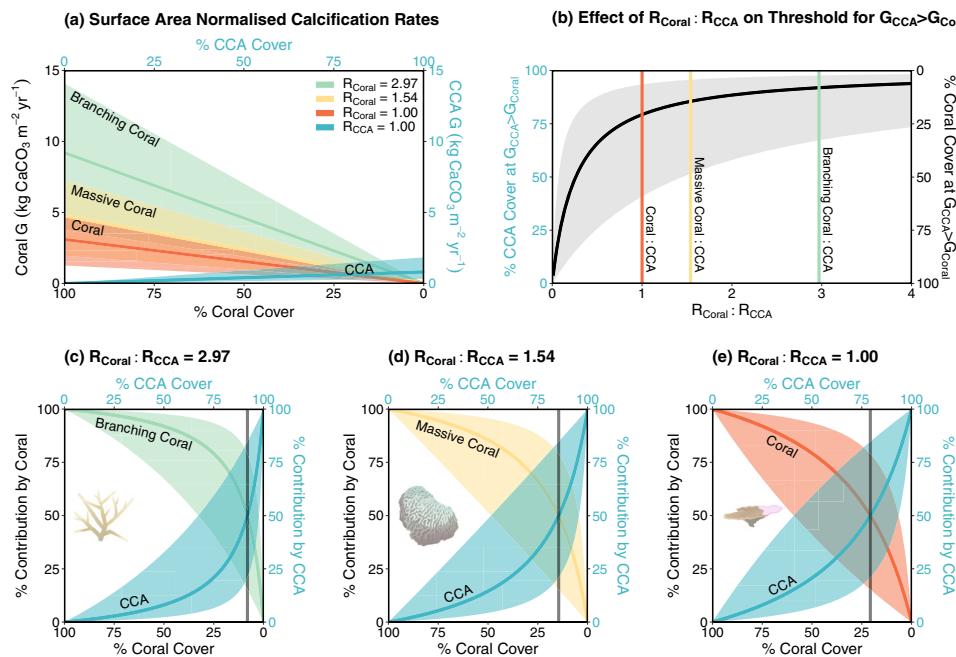


Fig. 4 Simulated tradeoffs between CCA and coral carbonate production. (G , kg $\text{CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$) for reefs dominated by scleractinian corals vs CCA (i.e., $\%_{\text{Coral}} + \%_{\text{CCA}} = 100\%$). **a** Surface area-normalised calcification rates (median \pm interquartile range) from a literature search of CCA and coral calcification rates normalised to surface area of growing tissue scaled to reefs ranging from 100% coral cover to 100% CCA cover (blue) with additional lines considering structural complexity multiplier factors for branching corals (green), massive corals (yellow), and encrusting corals (red). **b** Simulates the % cover of CCA (median \pm interquartile range, left axis) required to contribute more CaCO_3 than the remaining % cover of scleractinian corals (median \pm interquartile range, right axis) for a range of structural complexities ($0 \leq R_{\text{Coral}} : R_{\text{CCA}} \leq 4$). Vertical lines represent scenarios for branching (green), massive (yellow), encrusting corals (red), or any scenario where $R_{\text{Coral}} = R_{\text{CCA}}$ (red). **c–e** Show the % contribution by CCA and **c** branching corals growing over planar CCA, **d** massive corals growing over planar CCA, and **e** encrusting corals growing over planar CCA or any scenario where corals have the same rugosity as CCA for a simulated benthic community ranging from 100% coral cover to 100% CCA cover. Vertical grey lines indicate the threshold where CCA carbonate production is equal to coral carbonate production. See methods for further details on the conceptual model. Coral icons are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

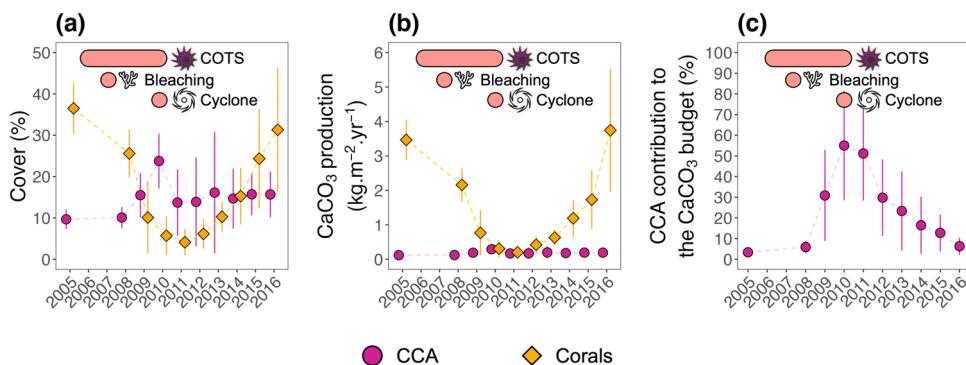


Fig. 5 Case study of CCA contribution to the Mo'orea reef carbonate budget. **a** Annual mean \pm SD% cover of CCA (pink circles) and coral (orange diamonds) are reported for the fore reef of Mo'orea, French Polynesia¹⁸ before, during, and after a series of disturbance events including a crown-of-thorns starfish outbreak from 2006–2010, a coral bleaching event in 2007, and Cyclone Oli in 2010²⁵. **b** The respective % cover from panel **a** were multiplied by CCA calcification rate for CCA and by coral calcification rate from Fig. 2 x reef-scale rugosity for corals¹⁹ to determine mean \pm SD community-level, area-normalised CCA and coral calcification rates. **c** The mean \pm SD% contribution of CCA to the total CaCO_3 budget (i.e., total $G = \text{CCA } G + \text{coral } G$) are reported for each year.

Surveys for census-based carbonate budgets. The first step in creating a census-based carbonate budget is to survey the reef to determine the relative cover of each carbonate producing taxa and the rugosity of each contributing taxa. While non-coral benthic components can be difficult to accurately identify, it is nonetheless important to explicitly differentiate live CCA from bare rock, dead pavement, turf, or other non-calcareous macroalgae categories—each of which would limit the inclusion of CCA in carbonate budgets. Moreover, distinguishing between

visually similar types of encrusting algae is also important since morphologically similar red encrusting Peyssonneliales (e.g. *Peyssonnelia* spp. and *Ramicrusta* spp.) contain much lower proportions of calcium carbonate than CCA^{28,45} and therefore substantially lower contributions to carbonate budgets. CCA coverage may also be underreported in census-based surveys due to what the observer is able to visibly detect and measure^{3,46}. For example, cryptic habitats (i.e. crevices, holes, the undersides of coral colonies, underneath overhangs, and other hidden reef

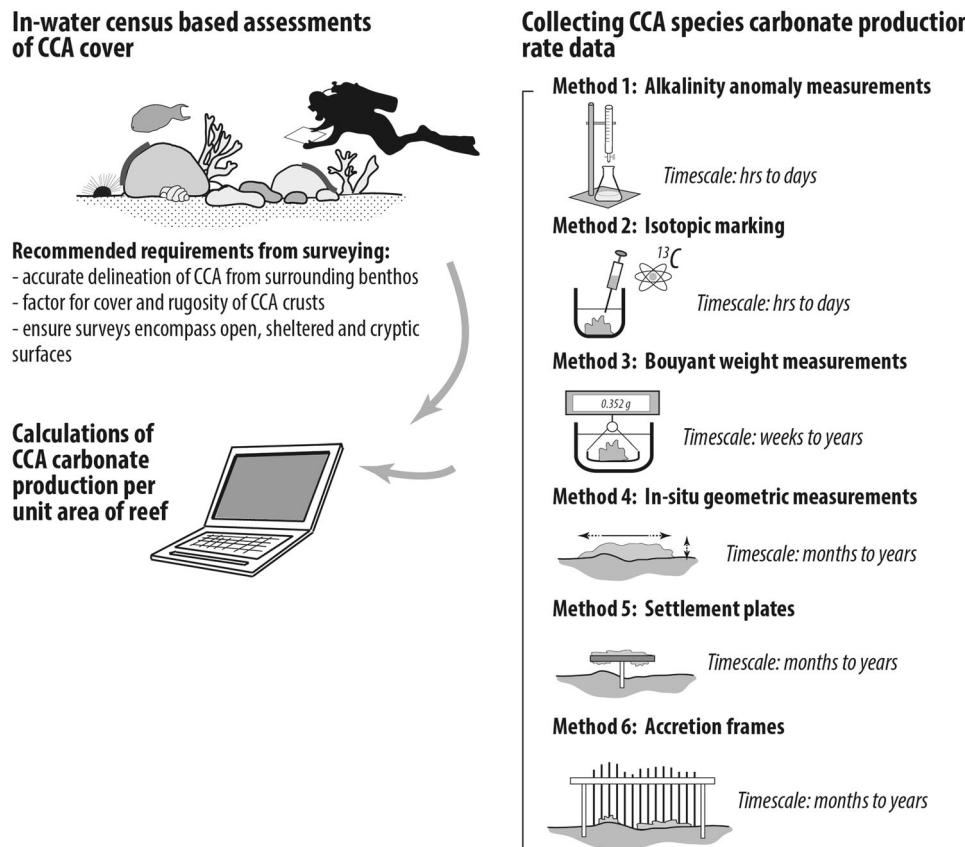


Fig. 6 Methods to measure CCA contribution to carbonate budgets. This includes two steps: (1) in-water census-based assessments of CCA cover and rugosity; (2) measurements of species-specific calcification or carbonate production through total alkalinity anomaly technique, isotope labelling, buoyant weight measurements over time, in situ geometric measurements, settlement plates, or accretion frames.

recesses *sensu*⁴⁷ Fig. 1c) can account for 30–75% of total reef substrate^{47–50}. Existing census-based budget protocols such as ReefBudget have thus been designed to support data collection in a way that factors for each of these issues. Visual surveys in the most cryptic and enclosed habitats are clearly more challenging to include in census approaches, but specific assessments of these habitats can be undertaken using endoscopic reef surveying approaches that can provide even more insight to the communities that dwell inside reef frameworks⁵¹. From the limited data that exist, calcified algae comprise an important proportion of many coral reef cryptic assemblages^{48,52}. While individual calcification rates may be lower than, or on par with, or more than their exposed calcifying algal communities^{53–55}, cryptic calcifying algae undoubtedly play a role in reef carbonate budgets and need to be fully resolved and accounted for. Quantifying CCA coverage alone would allow first-order estimates of CCA contributions to carbonate budgets using average calcification rates (e.g. Fig. 3). However, CCA community structure and calcification rates can be highly variable between sites, making it more appropriate to determine site-specific calcification using the methods outlined below. Ideally, CCA should be identified at species or genus level in the field and in measurements of calcification rates in estimates of gross calcium carbonate production. This might be difficult *in situ*, but sampling in the field paired with molecular identification of sub samples and individuals used in estimates of calcification rates would improve estimates in the most accurate of carbonate budgets^{56,57}. This could be paired with environmental DNA to determine whether the coralline algal sub samples match those of the community at each reef.

Special adaptations also need to be made when surveying sites impacted by recent disturbance (e.g. storm damage, bleaching), which can alter the location, rugosity, and community composition of CCA as well as their carbonate production rates^{58,59}. For example, CCA tends to rapidly colonise dead corals following disturbance events (Fig. 1d), allowing them to inherit the three-dimensional structure and thus the rugosity of the former reef for some time^{60,61}. This would potentially represent a situation where the rugosity of CCA could exceed the rugosity of surviving coral (Fig. 4b, where $R_{\text{coral}}: R_{\text{CCA}} < 1$). Subsequently, dead corals that are covered with CCA (Fig. 1d) should be recorded as CCA during any survey, rather than classifying them as coral rubble. While this often occurs, it should be noted that at other times turf rapidly colonises and the coral rubble can break into segments that are not colonised by CCA. Additionally, such turf assemblages could also contain CCA, which should be quantified in the most accurate carbonate budgets.

Measuring carbonate production. Measurements of individual CCA calcification rates are critical for understanding their contribution to the reef framework and carbonate budgets, and their role in binding together substrates on reef habitats^{55,62}. Selecting the ideal technique and timeframe for CCA calcification rate measurements largely depends on the research question, purpose of the study, and the morphology and physiology of the CCA at the site. Here, we group these methods into three general classes: (1) Direct measurements of CCA calcification rates; (2) Accretion substrates for net calcification measurements; and (3) Other methods for quantifying CCA accretion.

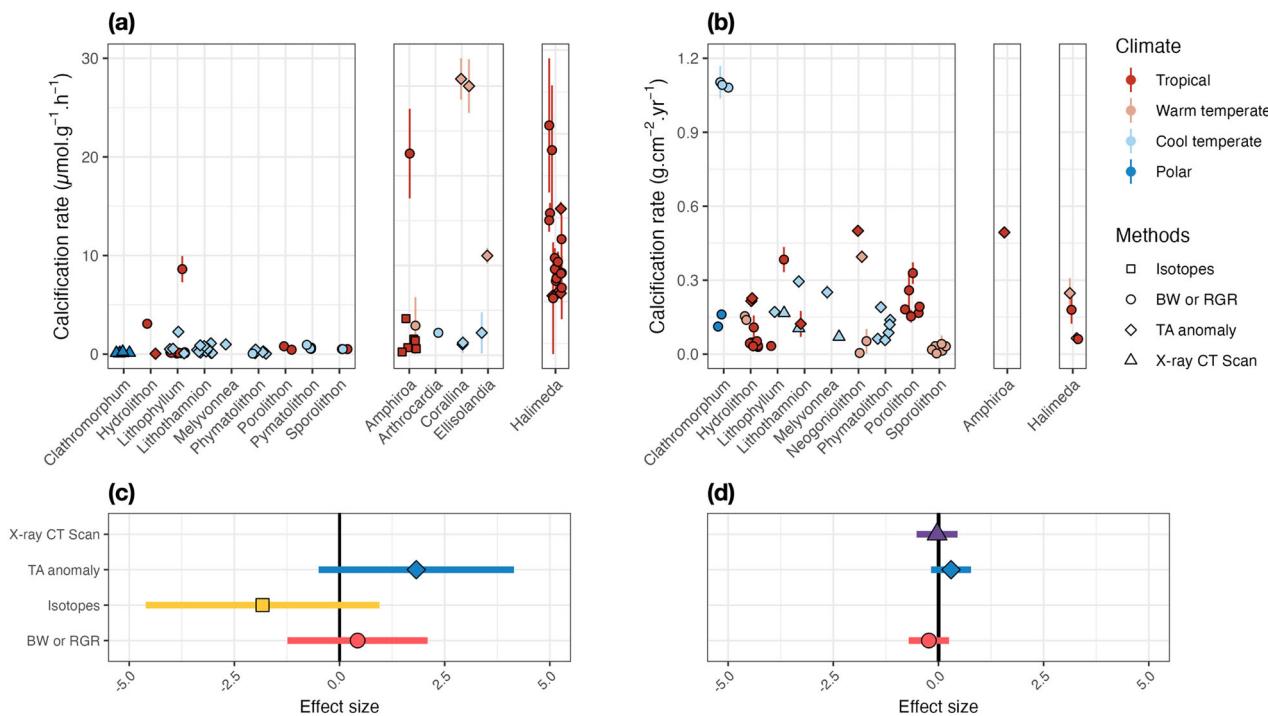


Fig. 7 Comparison of methods to measure calcification rate in individual CCA. We apply a general linear mixed model (GLMM) to our meta-analysis data to examine the influence of measurement method on calcification rate measurements, while accounting for the influence of genus and climate zone (Calcification rate | Methods ~ Genus + Climate zone). **a, b** Calcification rates from all genera of CCA in our meta-analysis with measurement methods and climate zone shown. Smaller panels denote articulate coralline algae and *Halimeda* spp. **c** [biomass normalised rates] and **d** [surface area-normalised rates] demonstrate the influence of the measurement method on the reported calcification rate determined from the GLMM model. In the key, BW refers to Buoyant Weight, RGR to Relative Growth Rate, and CT to Computed Tomography.

Direct measurements of CCA calcification rates. Three main techniques exist to directly measure the net calcification rates of CCA: total alkalinity anomaly, buoyant weighing, and use of isotopes. A calcification rate measurement for use in carbonate budget calculations must be standardised by time and by mass or by surface area, and we therefore exclude vertical accretion measurements such as linear extension from our consideration here. We compare these rates measured previously in Fig. 7 and discuss these methods in this section in greater detail.

The total alkalinity anomaly technique has been widely used for estimating net calcification rates of reef organisms since total alkalinity changes by a factor of two for every mole of CaCO_3 precipitated or dissolved⁶³. A known volume of CCA can be placed in sealed vessels with a known volume of seawater to determine the rate of calcification from the change in seawater total alkalinity over time. Calcification rates measured using the total alkalinity anomaly technique is typically integrated over short time frames (e.g. hours) and are therefore best suited for quantifying short-term calcification rates in response to changes in environmental conditions. Ideally, incubations over a broad range of light, temperature, pH, nutrient, and/or flow conditions are important to encapsulate the range of conditions organisms are exposed to in the natural environment (although some parameters are more important than others)²³. Moreover, light and dark incubations are required to approximate net diel calcification. Adequate water velocity should be simulated within any incubators, as the diffusive boundary layer limits movement of dissolved substance exchange around coralline algae⁶⁴. It could lead to artefactual accumulation or depletion of gases and nutrients, due to the combined effect of photosynthesis, respiration, and calcification, within the diffusive boundary layer. This altered boundary layer chemistry would expose the organism

to an unnatural chemical environment and alter calcification rates⁶⁵.

While the alkalinity anomaly method is effective, depending on the environment, the experimental duration, design, and subject, there are potential sources of error that can lead to over- or underestimates of calcification rates that need to be considered. For example, the presence and titration of particulate CaCO_3 during alkalinity measurements can bias the results, but can be avoided by filtering seawater samples prior to analysis. Furthermore, changes in dissolved organic acids or bases⁶⁶ and/or nutrient uptake or release⁶⁷ during incubations can in certain cases contribute greatly to the total change in alkalinity. Dissolved nutrients can be accounted for by the change in nutrient concentration during the incubation and contribution from organic alkalinity can be estimated by modified titration methods⁶⁶. However, in most oligotrophic coral reef settings, contributions from organic alkalinity and/or inorganic nutrients to changes in total alkalinity are likely small compared to the contribution from calcification, but could become important in enclosure experiments or in areas of elevated dissolved organic material and/or nutrients.

The buoyant weight technique consists of attaching CCA to a substrate and quantifying the changes in buoyant weight over longer timescales of weeks to months to provide an integrated measure of day and night calcification^{68–71}. The buoyant weight technique reflects the net sum of primary net calcification (i.e. active and controlled construction of skeletal material), secondary infilling of the skeleton (i.e. non-active infilling after diagenesis or skeletal breakdown by internal eroders), and skeletal dissolution in addition to any erosion (physical, biological, and chemical) when conducted *in situ*.

Isotopes can be artificially embedded into the calcium carbonate that is taken up during calcification, with the benefit

of the ability to detect growth at much finer scales than stains and weighing techniques, which is useful in slow growing species or during very short growth experiments (i.e. hours). The use of stable isotopes of carbon and oxygen present fewer logistical hurdles than the use of radioisotopes and follow the same general concepts^{72–74}. The most commonly employed stable isotope tracer is ^{13}C , which is added to seawater as a bicarbonate salt ($\text{H}^{13}\text{CO}_3^-$) and incubated with specimens for several hours with the incubation duration dependent on the concentration of added ^{13}C . Large and consistent uptake have been noted within four hours at high tracer concentrations, with variable signals after one hour even at very high doses⁷⁵. The mass of calcium carbonate deposited during the incubation period (i.e. calcification rates) is calculated using the known concentration of the stable isotope label following mass spectrometric carbonate analysis.

All these techniques must be accompanied by measurements of organism surface area to provide an area-normalised calcification rate for use in carbonate budget calculations^{70,76,77}. Numerous techniques exist for estimating surface area, spanning a wide range of spatial resolution and precision. The most appropriate technique will depend on the object being measured and the required accuracy of the surface area measurement. Common techniques used for estimating calcifier surface area include the following in approximate order of increasing accuracy (sensu⁷⁸): foiling⁷⁹, photogrammetry^{3,80,81}, wax coating⁸², and CT scanning⁸³.

Accretion substrates for net calcification measurements. Experimental accretion substrates, also known as settlement plates or tiles, are widely used as a non-destructive method to assess the recruitment and growth rates of calcareous reef building organisms including CCA and other encrusting organisms. The deployment of experimental accretion substrates quantifies net calcium carbonate production over a known surface area for a discrete period of time, typically months to years^{84,85}. A variety of accretion substrates, both artificial and natural, have been used to measure *in situ* accretion and the development of CCA communities within different reef habitats. Experimental substrates range in size, shape, and material from dead coral to individually crafted ceramic tiles, glass slides, limestone plates, plastic cattle ear tags, and polyvinyl chloride poles, flat tiles, and cards^{4,84,86}. The substrate type, orientation, microhabitat, and the period of immersion on the reef can greatly impact rates of net carbonate production and CCA species diversity^{85,87}. Recruitment patterns and carbonate production also differ between experimental substrates with CCA communities having rapid initial growth rates until crusts mature^{2,85}.

To quantify net production of calcium carbonate by CCA on accretion tiles, organisms such as sponges, non-calcareous algae, and other encrusting organisms (i.e., serpulids, gastropods, bryozoans) should be removed and accounted for in the budget if they calcify⁵⁵. One benefit of using accretion tiles to estimate CCA carbonate production is that naturally occurring processes of bioerosion (both internal and external) are co-occurring with CCA carbonate production. Accretion tiles therefore represent estimates of net CCA carbonate production and not gross carbonate production when paired with the percent cover of CCA. Also, advice around taxonomic identity should be followed for carbonate budgets to obtain greater details on contribution of different species to the local budgets. However, the duration of deployment and intrinsic material (i.e. ceramic, polyvinyl chloride, and limestone) of the experimental accretion substrates will also influence the bioeroder community composition and their bioerosion rates^{20,24}. Bioerosion has already been implicitly accounted for in the measurements of net carbonate production

by CCA, as opposed to gross calcification inferred from linear extension and skeletal density of corals³, so particular attention should be made to ensure that bioerosion is not accounted for twice for CCA when following census-based carbonate budget methods.

Best practice accretion tile studies for CCA carbonate budget assessment should therefore ground truth results from artificial substrates with naturally occurring reef communities at experimental sites⁸⁸. Substrates should mimic orientation, habitat, and substrate topography as closely as possible. For example, including both upright and downward facing surfaces allows for settlement by both cryptic and non-cryptic CCA⁵⁴ while the sandwiched tiles of Calcification Accretion Units (CAUs)⁸⁹ and complex interstices of Autonomous Reef Monitoring Structures simulate other cryptic spaces⁹⁰. It is also recommended that CCA communities are measured to include seasonal differences, but it is unknown what the ideal duration is, and whether multiple deployments would therefore be needed. Normalisation of carbonate accretion to surface area and time is critical for facilitating meaningful comparisons through space and time and between different sized artificial substrates, individuals, and species.

Recruitment issues and density dependence. Thick encrusting coralline algae can be a dominant feature of shallow high energy tropical reef crest habitats^{26,91}, potentially contributing substantially to reef development^{62,92–94}. CCA are too often treated as a single functional group⁹⁵, but they exhibit variable recruitment, survival, development, and growth rates which can complicate estimates of net community calcification derived from both recruitment tiles and quadrats. Importantly, links between recruitment and adult populations are not well established and density dependence is less well quantified than it is in coral. This increases the complexity for methodological approaches that rely on settlement tiles.

Recruitment patterns depend on supply (e.g. reproduction), which can be related to environmental conditions, where temperature, carbonate chemistry, light, hydrodynamics, and nutrients all could impact reproduction of resident adult CCA and also settlement of juveniles and their post-settlement growth rates^{65,96}. There can also be a seasonal element to reproduction⁹⁷. This means timing and duration of settlement tile deployment might influence CCA cover and calcification estimates of experimental accretion substrates. Once established, post-settlement growth of juveniles on tiles can also vary temporally: following spore settlement and germination, rapid cell division is followed by outward expansion of thalli but this tapers off, with faster calcification in the first 3 months compared to 6 months⁸⁴ and cover peaking between 6 and 11 months⁹⁸. Another consideration is that CCA colonisation can be successional with community shifts on tiles developing over weeks to months⁹⁹.

Finally, adult contributions to net carbonate production may have a density dependent element, with space and competition limiting population size and lateral growth¹⁰⁰, and contribution to carbonate budgets could thus be influenced by continual low-level surface grazing¹⁰¹. Examination of growth rates of adult fragments (2–4 cm in size) showed rapid outward extension of thalli followed by slower upward growth⁹⁶, thus, grazing may even stimulate productivity of crusts and promote community diversity¹⁰², which is further evidenced by wound healing mechanisms in coralline crusts^{100,103}. This means that three different issues could cause the calculation of lower carbonate production rates across tiles deployed for different time periods: (1) increasing bioerosion of older tiles; (2) density dependence in older tiles; or (3) the propensity of CCA to switch from rapid

horizontal calcification to slower vertical calcification when older. For example, CCA carbonate production was ~5 times higher on substrates deployed for less than 1 year compared to greater than one year³. Presently it is difficult to assess CCA production rates in the field in a species-specific manner, owing to difficulties mentioned above. Thus, rates should be expressed with uncertainties to account for some of this inherent variability until more advanced methods become available. Future research should attempt to resolve these issues using multiple experimental approaches and using multi-year deployments with yearly measurements.

Other methods for quantifying CCA accretion. While they are not measurements of carbonate production, radiometrically-dated reef cores, coral reef accretion frames, and structure-from-motion photogrammetry provide direct measurements of CCA accretion. Here we do not discuss linear extension since these measurements typically are not accompanied with estimates of density and surface area that could be used to calculate calcification rates. An exception is perhaps the ‘geometric’ method⁷⁰, where measurements of CCA linear extension (using stains¹⁰⁴) are combined with marginal extension rates and skeletal density of CCA to estimate calcification rates. Reef cores are typically used to measure coral reef framework accretion rates over geological time frames (usually millennia)^{105–108}. Unlike coral cores which target linear extension and calcification rates of individual colonies¹⁰⁹, reef cores sample coral framework, the reef sediment matrix, coralline algae and other framework-contributing components relative to radiometric dates to quantify accretion per unit time.

Coral reef accretion frames can directly quantify accretion rates of contemporary reef flat environments¹¹⁰. This methodology also allows micro-scale interpretation of specific taxa accretion/erosion contributions to overall reef accretion, including direct quantification of areas of the reef flat surface that are dominated by coralline algae. This works by setting a frame with a series of moveable poles that is removed then redeployed over several time periods to determine the vertical accretion of the organisms, also accounting for erosion. In the only location in which this has been deployed to date, reported accretion rates from nodular CCA averaged 19.3 mm y⁻¹ and areas dominated by flat CCA typically accreted at slower rates between 4 and 6 mm y⁻¹¹¹⁰. While this coral reef accretion frame is a useful tool to accurately measure vertical accretion in situ, deployment of the tool is time consuming, requires a relatively flat deployment surface, and low energy sampling (ideally semi-emergent) conditions. Resultant data will need to be corroborated with data from additional time periods (years) and locations to explore inter-annual and inter-site variability in coralline algal growth and reef accretion rates.

Structure-from-Motion photogrammetry, a combination of three-dimensional modelling and imaging, has been used to measure individual coral linear extension rates¹¹¹ and reef accretion rates¹¹². To our knowledge, it has not been used to quantify coralline algal accretion rates. Photogrammetry cannot detect skeletal infilling, and accretion rate measurements using this approach would ultimately need to account for the variation in the skeletal density of different reef calcifiers. This is an interesting avenue for future research given the non-destructive capacity to repeatedly sample reef substrates using this method. Additionally, future work could explore the use of microerosion metres, and laser scanning of tidally-exposed reef upper surfaces, as previously used on rock reefs to measure erosion with sub-mm scale precision^{113,114}. New methods have also been developed using machine learning that can successfully delineate coralline algae in large scale hyperspectral imagery¹¹⁵. These methods all

offer promise. However, there are inherent limitations that would need to be tested and resolved, including those associated with reflectance of surface water.

Bioerosion rates of CCA have been poorly documented, particularly internal bioerosion. However, it can be done by estimating internal skeletal erosion of CCA by endolithic invertebrates using estimates of the area bored by the invertebrates in new skeletal tissue precipitated by the seaweed⁷⁷. Internal bioerosion rates in CCA (total amount of CaCO₃ dissolved) can also be estimated from high-precision buoyant weight methods normalised to surface area and CCA skeletal density¹¹⁶. Future studies are needed to quantify the variability in bioerosion rates in CCA in response to environmental change and across CCA taxa, as well as to understand the relationship between bioerosion and remineralization processes in CCA skeletons (e.g. ref. ¹¹⁷).

Conclusions

We highlight that CCA carbonate production can be spatially and temporally high. Presently, it is difficult to assess the global contribution of CCA to carbonate production of coral reefs, given the underestimates of CCA cover and area-normalised calcification rates outlined here. However, through conceptual models and the Mo’orea case study presented here, we have shown that CCA can account for large proportions of coral reef carbonate production, especially following disturbances such as coral mass mortality events. Additional emphasis on CCA, and other non-scleractinian calcifiers, and the inclusion of the methods discussed above will be important for the coral reef research community to improve estimates of coral reef carbonate production and the relative contribution of CCA to this important process. Thus, we recommend improvement of these methods that include accurate measurements of specific-specific carbonate production rates and covers where possible, using molecular identification and photogrammetry in the most complex and accurate surveys. Increasing frequency and intensity of coral bleaching events under the ongoing climate crisis will continue to drive further declines in coral cover suggesting that CCA are likely to emerge as increasingly important contributors to the construction and maintenance of coral reef carbonate structures in the Anthropocene.

Methods

We simulated tradeoffs between CCA and coral carbonate production (G, kg CaCO₃ m⁻² y⁻¹) for reefs dominated by scleractinian corals vs CCA (i.e. %Coral + %CCA = 100%) using the calcification rates (median ± interquartile range) from our meta-analysis (Fig. 3). First, the surface area-normalised calcification rates (median ± interquartile range) from the literature search of CCA and coral calcification rates normalised to surface area of growing tissue (Fig. 3) were scaled to reefs ranging from 100% coral cover to 100% CCA cover. Given that corals typically build more complex structures than CCA, the relative rugosity of corals will typically be greater than the rugosity of CCA (i.e. R_{Coral}:R_{CCA} > 1). We therefore multiplied the area-normalised coral calcification rates by a rugosity factor of R_{Coral}:R_{CCA} = 2.97 (branching *Acropora prolifera* rugosity³⁷) to represent branching corals, a factor of R_{Coral}:R_{CCA} = 1.54 (*Porites astreoides* rugosity³⁷) to represent massive corals, and a factor of R_{Coral}:R_{CCA} = 1.00 (*Undaria humilis* rugosity³⁷) to represent encrusting corals compared to the planar surface area-normalised calcification rates (R_{Coral}:R_{CCA} = 1.00) for CCA. We then simulated the % cover of CCA (median ± interquartile range) required to contribute more CaCO₃ than the remaining % cover of scleractinian corals (median ± interquartile range) for a range of structural complexities wherein R_{Coral}:R_{CCA} ranged from 0 to 4. We explicitly explored scenarios for branching (R_{Coral}:R_{CCA} = 2.97), massive (R_{Coral}:R_{CCA} = 1.54), and encrusting corals (R_{Coral}:R_{CCA} = 1.00). Note, however, that R_{Coral}:R_{CCA} = 1.00 represents any scenario where corals have the same rugosity as CCA, which could, for example, represent either encrusting corals and encrusting CCA (R_{Coral}=R_{CCA} = 1), branching corals overgrown by encrusting CCA (R_{Coral}=R_{CCA} = 2.97), or any scenario where R_{Coral} = R_{CCA}. Values of R_{Coral}:R_{CCA} < 1 might represent situations where the rugosity of CCA exceeds the rugosity of coral, for example colonisation of structurally complex dead corals or coral rubble (Fig. 1). We then evaluated the % contribution to total calcification by CCA relative to branching corals growing over planar CCA (R_{Coral}:R_{CCA} = 2.97), massive corals growing over planar CCA (R_{Coral}:R_{CCA} = 1.54), and encrusting corals growing over planar CCA or

any scenario where corals have the same rugosity as CCA ($R_{\text{Coral}}:R_{\text{CCA}} = 1.00$) for a simulated benthic community ranging from 100% coral cover to 100% CCA cover. These analyses allowed us to quantify the threshold where CCA carbonate production is equal to coral carbonate production for the simulated benthic communities composed of CCA and corals. We note that all traditional surveying methods, including this analysis, are likely underestimating CCA contribution due to cryptic CCA being missed. See the discussion for more details.

Case study: Mo'orea (French Polynesia). To compare our conceptual model to a real-world example, we use a case study of disturbance-driven coral community decline and subsequent recovery from Mo'orea, French Polynesia, which demonstrates the increasing contribution of CCA to coral reef carbonate production following a disturbance. We estimate shifts in CCA and coral carbonate production by combining the area-normalised CCA and coral calcification rates from this study (Fig. 3) with measurements of coral reef benthic community composition from Carpenter et al.¹¹⁸ and structural complexity from Carlot et al.¹¹⁹ assuming a planar reef with structurally complex corals such that $R_{\text{CCA}} = 1$ and $R_{\text{Coral}} = R_{\text{survey}}$.

Reporting summary. Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data are available at https://github.com/JayCrlt/CCA_Methods

Code availability

Codes are available at https://github.com/JayCrlt/CCA_Methods

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References

- Perry, C. T., Spencer, T. & Kench, P. S. Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. *Coral Reefs* **27**, 853–866 (2008).
- Stearn, C. W., Scoffin, T. P. & Martindale, W. Calcium carbonate budget of a fringing reef on the West Coast of Barbados Part I—zonation and productivity. *Bull Marine Sci* **27**, 479–510 (1977).
- Lange, I. D., Perry, C. T. & Alvarez-Filip, L. Carbonate budgets as indicators of functional reef “health”: a critical review of data underpinning census-based methods and current knowledge gaps. *Ecol. Indicat.* **110**, 105857 (2020).
- Perry, C. T. et al. Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral Reefs* **31**, 853–868 (2012).
- Montaggioni, L. F. & Braithwaite, C. J. R. in *Developments in Marine Geology* (Elsevier, 2009).
- Scoffin, T. & Hawkins, C. M. Calcium carbonate budget of a fringing reef on the west coast of Barbados. II. Erosion, sediments and internal structure. *Bulletin of Marine Science* **30**, 475–508, (1980).
- Eyre, B. D., Andersson, A. J. & Cyronak, T. Benthic coral reef calcium carbonate dissolution in an acidifying ocean. *Nat. Clim. Change* **4**, 969 (2014).
- Perry, C. T. et al. Loss of coral reef growth capacity to track future increases in sea level. *Nature* **558**, 396–400 (2018).
- Pomar, L., Baceta, J. I., Hallock, P., Mateu-Vicens, G. & Bassó, D. Reef building and carbonate production modes in the west-central Tethys during the Cenozoic. *Marine Petrol. Geol.* **83**, 261–304 (2017).
- Scoffin, T. P., Tudhope, A. W., Brown, B. E., Chansang, H. & Cheeney, R. F. Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. *Coral Reefs* **11**, 1–11 (1992).
- Dawson, J. L., Smithers, S. G. & Hua, Q. The importance of large benthic foraminifera to reef island sediment budget and dynamics at Raine Island, northern Great Barrier Reef. *Geomorphology* **222**, 68–81 (2014).
- Wolfe, K. et al. in *Oceanography and Marine Biology* (Taylor & Francis, 2020).
- Kayanne, H. et al. Seasonal and bleaching-induced changes in coral reef metabolism and CO₂ flux. *Glob. Biogeochem. Cycles* **19**, 1–11 (2005).
- Courtney, T. A. et al. Rapid assessments of Pacific Ocean net coral reef carbonate budgets and net calcification following the 2014–2017 global coral bleaching event. *Limnol. Oceanogr.* **67**, 1687–1700 (2022).
- Courtney, T. A. et al. Recovery of reef-scale calcification following a bleaching event in Kāne'ohe Bay, Hawai'i. *Limnol. Oceanogr. Lett.* **3**, 1–9 (2018).
- Cornwall, C. E. et al. Global declines in coral reef calcium carbonate production under ocean acidification and warming. *Proc. Natl Acad. Sci. USA* **118**, e2015265118 (2021).
- Smith, S. V. & Kinsey, D. W. Calcium carbonate production, coral reef growth, and sea level change. *Science* **194**, 937–939 (1976).
- Shaw, E. C., Hamylton, S. M. & Phinn, S. R. Incorporating benthic community changes into hydrochemical-based projections of coral reef calcium carbonate production under ocean acidification. *Coral Reefs* **35**, 739–750 (2016).
- Perry, C. T. et al. Caribbean-wide decline in carbonate production threatens coral reef growth. *Nat. Commun.* **4**, 1402 (2013).
- Tribollet, A. & Golubic, S. in *Coral reefs: An ecosystem in transition*. (Springer, 2011).
- Pratchett, M. S., Anderson, K. D., Hoogenboom, M. O., Widman, E. & Baird, A. H. Spatial, temporal and taxonomic variation in coral growth—implications for the structure and function of coral reef ecosystems. *Oceanogr Marine Biol. Annu. Rev.* **53**, 215–295 (2015).
- Perry, C. T., Kench, P. S., O'Leary, M. J., Morgan, K. M. & Januchowski-Hartley, F. Linking reef ecology to island building: Parrotfish identified as major producers of island-building sediment in the Maldives. *Geology* **43**, 503–506 (2015).
- Courtney, T. A. et al. Environmental controls on modern scleractinian coral and reef-scale calcification. *Sci. Adv.* **3**, e1701356 (2017).
- Schönberg, C. H. L., Fang, J. K. H., Carreiro-Silva, M., Tribollet, A. & Wissak, M. Bioerosion: the other ocean acidification problem. *ICES J. Marine Sci.* **74**, 895–925 (2017).
- Courtney, T. A., Kindeberg, T. & Andersson, A. J. Coral calcification responses to the North Atlantic Oscillation and coral bleaching in Bermuda. *PLoS ONE* **15**, e0241854 (2020).
- Adey, W. H. Algal ridges of the Caribbean sea and West Indies. *Phycologia* **17**, 361–367 (1978).
- Adey, W. H. The algal ridges and coral reefs of St. Croix: their structure and Holocene development. *Atoll Res. Bull.* **187**, 1–67 (1975).
- Littler, M. M. & Littler, D. S. Models of tropical reef biogenesis: the contribution of algae. *Prog. Phycol. Res.* **3**, 323–364 (1984).
- Le Nohaïc, M. et al. Marine heatwave causes unprecedented regional mass bleaching of thermally resistant corals in northwestern Australia. *Sci. Rep.* **7**, 1–11 (2017).
- Liou, C.-Y., Yang, S.-Y. & Chen, C. A. Unprecedented calcareous algal reefs in northern Taiwan merit high conservation priority. *Coral Reefs* **36**, 1253–1253 (2017).
- Gherardi, D. & Bosence, D. Composition and community structure of the coralline algal reefs from Atol das Rocas, South Atlantic, Brazil. *Coral Reefs* **19**, 205–219 (2001).
- Coates, K. A. et al. in *Coral Reefs of the United Kingdom Overseas Territories* (ed. Sheppard CRC). (Springer Netherlands, 2013).
- Browne, N. K. et al. Predicting responses of geo-ecological carbonate reef systems to climate change: a conceptual model and review. *Oceanogr. Marine Biol. Annu. Rev.* **59**, 229–370 (2021).
- Cornwall, C. E. et al. Understanding coralline algal responses to ocean acidification: Meta-analysis and synthesis. *Glob. Change Biol.* **28**, 362–374 (2022).
- Nybäkken, J. W. *Marine biology: An ecological approach*, 5th edn. (Benjamin Cummings, 2001).
- Kornder, N. A., Riegl, B. M. & Figueiredo, J. Thresholds and drivers of coral calcification responses to climate change. *Glob. Change Biol.* **24**, 5084–5095 (2018).
- González-Barrios, F. J. & Álvarez-Filip, L. A framework for measuring coral species-specific contribution to reef functioning in the Caribbean. *Ecol. Indicat.* **95**, 877–886 (2018).
- Álvarez-Filip, L. et al. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc. R. Soc. B Biol. Sci.* **276**, 3019–3025 (2009).
- Adam, T. C. et al. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS ONE* **6**, e23717 (2011).
- Pratchett, M. S., Trapon, M., Berumen, M. L. & Chong-Seng, K. Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. *Coral Reefs* **30**, 183–193 (2011).
- Han, X., Adam, T. C., Schmitt, R. J., Brooks, A. J. & Holbrook, S. J. Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia. *Coral Reefs* **35**, 999–1009 (2016).
- Adjoudra, M. et al. Recovery of coral assemblages despite acute and recurrent disturbances on a South Central Pacific reef. *Sci. Rep.* **8**, 9680 (2018).
- Cyronak, T. et al. Diel temperature and pH variability scale with depth across diverse coral reef habitats. *Limnol. Oceanogr. Lett.* **5**, 193–203 (2020).
- Carlot, J. et al. Juvenile corals underpin coral reef carbonate production after disturbance. *Glob. Change Biol.* **27**, 2623–2632 (2021).
- Bassó, D. Carbonate production by calcareous red algae and global change. *Geodiversitas* **34**, 13–33 (2012). 21.

46. Courtney, T. A. et al. Comparing chemistry and census-based estimates of net ecosystem calcification on a rim reef in Bermuda. *Front. Marine Sci.* **3**, 1–15 (2016).
47. Buss, L. W. & Jackson, J. B. C. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am. Natural.* **113**, 223–234 (1979).
48. Kornder, N. A. et al. Implications of 2D versus 3D surveys to measure the abundance and composition of benthic coral reef communities. *Coral Reefs* **40**, 1137–1153 (2021).
49. Gischler, E. & Ginsburg, R. N. Cavity dwellers (coelobites) under coral rubble in Southern Belize barrier and atoll reefs. *Bull. Marine Sci.* **58**, 570–589 (1996).
50. Scheffers, S. R., Van Soest, R. W., Nieuwland, G. & Bak, R. P. Coral reef framework cavities: is functional similarity reflected in composition of the cryptic macrofaunal community? *Atoll Res. Bull.* **583**, 1–24 (2010).
51. Richter, C., Wunsch, M., Rasheed, M., Kötter, I. & Badran, M. I. Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. *Nature* **413**, 726–730 (2001).
52. Caragnano, A., Colombo, F., Rodondi, G. & Basso, D. 3-D distribution of nongeneculate corallinales: a case study from a reef crest of South Sinai (Red Sea, Egypt). *Coral Reefs* **28**, 881–891 (2009).
53. Hepburn, L. J., Blanchon, P., Murphy, G., Cousins, L. & Perry, C. T. Community structure and palaeoecological implications of calcareous encrusters on artificial substrates across a Mexican Caribbean reef. *Coral Reefs* **34**, 189–200 (2015).
54. Mallela, J. Coral reef encruster communities and carbonate production in cryptic and exposed coral reef habitats along a gradient of terrestrial disturbance. *Coral Reefs* **26**, 775–785 (2007).
55. Mallela, J. Calcification by Reef-Building Sclerobionts. *PLoS ONE* **8**, e60010 (2013).
56. Twist, B. A. et al. The need to employ reliable and reproducible species identifications in coralline algal research. *Marine Ecol. Prog. Ser.* **654**, 225–231 (2020).
57. Gabrielson, P. W., Hughey, J. R. & Diaz-Pulido, G. Genomics reveals abundant speciation in the coral reef building alga *Porolithon onkodes* (Corallinales, Rhodophyta). *J. Phycol.* **54**, 429–434 (2018).
58. Anton, A. et al. Differential thermal tolerance between algae and corals may trigger the proliferation of algae in coral reefs. *Glob. Change Biol.* **26**, 4316–4327 (2020).
59. Cornwall, C. E., Diaz-Pulido, G. & Comeau, S. Impacts of ocean warming on coralline algal calcification: Meta-analysis, knowledge gaps, and key recommendations for future research. *Front. Marine Sci.* **6**, 1–10 (2019).
60. Birkeland, C. et al. Different resiliencies in coral communities over ecological and geological time scales in American Samoa. *Marine Ecol. Prog. Ser.* **673**, 55–68 (2021).
61. McClanahan, T. R., Muthiga, N. A., Maina, J., Kamukuru, A. T. & Yahya, S. A. Changes in northern Tanzania coral reefs during a period of increased fisheries management and climatic disturbance. *Aquatic Conserv. Marine Freshwater Ecosyst.* **19**, 758–771 (2009).
62. Bak, R. P. M. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Netherlands J. Sea Res.* **10**, 285–337 (1976).
63. Smith, S. V. & Kinsey, D. W. in: *Coral reefs: research methods* (eds. Stoddart D, Johannes R.) (UNESCO, 1978).
64. Cornwall, C. E., Pilditch, C. A., Hepburn, C. D. & Hurd, C. L. Canopy macroalgae influence understorey corallines' metabolic control of near-surface pH and oxygen concentration. *Marine Ecol. Prog. Ser.* **525**, 81–95 (2015).
65. Comeau, S. et al. Flow-driven micro-scale pH variability affects the physiology of corals and coralline algae under ocean acidification. *Sci. Rep.* **9**, 12829 (2019).
66. Kerr, D. E., Brown, P. J., Grey, A. & Kelleher, B. P. The influence of organic alkalinity on the carbonate system in coastal waters. *Marine Chem.* **237**, 104050 (2021).
67. Gazeau, F., Urbini, L., Cox, T. E., Alliouane, S. &Gattuso, J. P. Comparison of the alkalinity and calcium anomaly techniques to estimate rates of net calcification. *Marine Ecol. Prog. Ser.* **527**, 1–12 (2015).
68. Davies, S. P. Short-term growth measurements of corals using an accurate buoyant weighing technique. *Marine Biol.* **101**, 389–395 (1989).
69. Jokiel, P. L., Maragos, J. E. & Franzisket, L. Coral growth: buoyant weight technique. *Coral Reefs: Research Methods* 529–541 (UNESCO, 1978).
70. Lewis, B., Kennedy, E. V. & Diaz-Pulido, G. Seasonal growth and calcification of a reef-building crustose coralline alga on the Great Barrier Reef. *Marine Ecol. Prog. Ser.* **568**, 73–86 (2017).
71. Roik, A., Roder, C., Röthig, T. & Voolstra, C. R. Spatial and seasonal reef calcification in corals and calcareous crusts in the central Red Sea. *Coral Reefs* **35**, 681–693 (2016).
72. Pearse, V. B. Radioisotopic study of calcification in the articulated Coralline Alca Bossiella Orbigniana 1. *J. Phycol.* **8**, 88–97 (1972).
73. Pentecost, A. Calcification and photosynthesis in *Corallina officinalis* L. using the $^{14}\text{CO}_2$ method. *Br Phycol. J.* **13**, 383–390 (1978).
74. Borowitzka, M. A. & Veski, M. Ultrastructure of the Corallinaceae. II. The vegetative cells of *Lithothrix aspergillum*. *J. Phycol.* **15**, 146–153 (1979).
75. McCoy, S. J., Pfister, C. A., Olack, G. & Colman, A. S. Diurnal and tidal patterns of carbon uptake and calcification in geniculate inter-tidal coralline algae. *Marine Ecol.* **37**, 553–564 (2016).
76. Lewis, B., Lough, J. M., Nash, M. C. & Diaz-Pulido, G. Presence of skeletal banding in a reef-building tropical crustose coralline alga. *PLoS ONE* **12**, e0185124 (2017).
77. Ramírez-Viaña, A., Diaz-Pulido, G. & García-Urueña, R. Bioerosion of reef-building crustose coralline algae by endolithic invertebrates in an upwelling-influenced reef. *Coral Reefs* **40**, 651–662 (2021).
78. Veal, C. J., Holmes, G., Nunez, M., Hoegh-Guldberg, O. & Osborn, J. A comparative study of methods for surface area and three-dimensional shape measurement of coral skeletons. *Limnol. Oceanogr. Methods* **8**, 241–253 (2010).
79. Marsh, J. A. Primary productivity of reef-building calcareous red algae. *Ecology* **51**, 255–263 (1970).
80. Ferrari, R. et al. 3D photogrammetry quantifies growth and external erosion of individual coral colonies and skeletons. *Sci. Rep.* **7**, 16737 (2017).
81. Conley, D. D. & Hollander, E. N. R. A non-destructive method to create a time series of surface area for coral using 3D photogrammetry. *Front. Marine Sci.* **8**, 1–12 (2021).
82. Stimson, J. & Kinzie, R. A. The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. *J. Exp. Marine Biol. Ecol.* **153**, 63–74 (1991).
83. Naumann, M. S., Niggli, W., Laforsch, C., Glaser, C. & Wild, C. Coral surface area quantification—evaluation of established techniques by comparison with computer tomography. *Coral Reefs* **28**, 109–117 (2009).
84. Kennedy, E. V., Ordoñez, A., Lewis, B. E. & Diaz-Pulido, G. Comparison of recruitment tile materials for monitoring coralline algal responses to a changing climate. *Marine Ecol. Prog. Ser.* **569**, 129–144 (2017).
85. Mallela, J. The influence of micro-topography and external bioerosion on coral-reef-building organisms: recruitment, community composition and carbonate production over time. *Coral Reefs* **37**, 227–237 (2018).
86. Kuffner, I. B., Hickey, T. D. & Morrison, J. M. Calcification rates of the massive coral *Siderastrea siderea* and crustose coralline algae along the Florida Keys (USA) outer-reef tract. *Coral Reefs* **32**, 987–997 (2013).
87. Adey, W. H. & Vassar, J. M. Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). *Phycologia* **14**, 55–69 (1975).
88. Mallela, J., Milne, B. C. & Martinez-Escobar, D. A comparison of epibenthic reef communities settling on commonly used experimental substrates: PVC versus ceramic tiles. *J. Exp. Marine Biol. Ecol.* **486**, 290–295 (2017).
89. Johnson, M. D., Price, N. N. & Smith, J. E. Calcification accretion units (CAUs): A standardized approach for quantifying recruitment and calcium carbonate accretion in marine habitats. *Methods Ecol. Evol.* **13**, 1436–1446 (2022).
90. Plaisance, L., Caley, M. J., Brainard, R. E. & Knowlton, N. The diversity of coral reefs: what are we missing? *PLoS ONE* **6**, e25026 (2011).
91. Dean, A. J., Steneck, R. S., Tager, D. & Pandolfi, J. M. Distribution, abundance and diversity of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* **34**, 581–594 (2015).
92. MacIntyre, I. G. Re-evaluating the role of crustose algae in the construction of coral reefs, in *8th International Coral Reef Symposium* (Springer, Berlin, Germany, 1997).
93. Montaggioni, L. F. et al. Continuous record of reef growth over the past 14 k.y. on the mid-Pacific island of Tahiti. *Geology* **25**, 555–558 (1997).
94. Teichert, S., Steinbauer, M. & Kiessling, W. A possible link between coral reef success, crustose coralline algae and the evolution of herbivory. *Sci. Rep.* **10**, 17748 (2020).
95. Deinhart, M., Mills, M. S. & Schils, T. Community assessment of crustose calcifying red algae as coral recruitment substrates. *PLoS ONE* **17**, e0271438 (2022).
96. Cornwall, C. E. et al. A coralline alga gains tolerance to ocean acidification over multiple generations of exposure. *Nat. Clim. Change* **10**, 143–146 (2020).
97. Ordoñez, A. *Effects of ocean acidification on the supply-side ecology of crustose coralline algae in the Great Barrier Reef*. (Griffith University, 2015).
98. Arnold, S. N. & Steneck, R. S. Settling into an Increasingly Hostile World: The Rapidly Closing “Recruitment Window” for Corals. *PLoS ONE* **6**, e28681 (2011).
99. Mariath, R., Rodriguez, R. R. & Figueiredo, M. A. O. Succession of crustose coralline red algae (Rhodophyta) on coral reefs exposed to physical disturbance in the southwest Atlantic. *Helgoland Marine Res.* **67**, 687–696 (2013).
100. Dethier, M. N. & Steneck, R. S. Growth and persistence of diverse intertidal crusts: survival of the slow in a fast-paced world. *Marine. Ecol. Prog. Ser.* **223**, 89–100 (2001).

101. Steneck, R. S. The ecology of coralline algal crusts: Convergent patterns and adaptive strategies. *Ann. Rev. Ecol. Syst.* **17**, 273–303 (1986).
102. Wai, T.-C. & Williams, G. A. The relative importance of herbivore-induced effects on productivity of crustose coralline algae: Sea urchin grazing and nitrogen excretion. *J. Exp. Marine Biol. Ecol.* **324**, 141–156 (2005).
103. Manning, J. C., Carpenter, R. C. & Miranda, E. A. Ocean acidification reduces net calcification and wound healing in the tropical crustose coralline alga, *Porolithon onkodes* (Corallinales, Rhodophyta). *J. Exp. Marine Biol. Ecol.* **520**, 151225 (2019).
104. Lewis, B. & Diaz-Pulido, G. Suitability of three fluorochrome markers for obtaining in situ growth rates of coralline algae. *J. Exp. Marine Biol. Ecol.* **490**, 64–73 (2017).
105. Dechnik, B. et al. Influence of hydrodynamic energy on Holocene reef flat accretion, Great Barrier Reef. *Quat. Res.* **85**, 44–53 (2016).
106. Perry, C. T. & Smithers, S. Cycles of coral reef ‘turn-on’, rapid growth and ‘turn-off’ over the past 8500 years: a context for understanding modern ecological states and trajectories. *Glob. Change Biol.* **17**, 76–86 (2011).
107. Ryan, E. J., Smithers, S. G., Lewis, S. E., Clark, T. R. & Zhao, J.-X. The variable influences of sea level, sedimentation and exposure on Holocene reef development over a cross-shelf transect, central Great Barrier Reef. *Diversity* **10**, 110 (2018).
108. Smithers, S. & Larcombe, P. Late Holocene initiation and growth of a nearshore turbid-zone coral reef: Paluma Shoals, central Great Barrier Reef, Australia. *Coral Reefs* **22**, 499–505 (2003).
109. Cooper, T. F., O’Leary, R. A. & Lough, J. M. Growth of Western Australian Corals in the Anthropocene. *Science* **335**, 593–596 (2012).
110. Kench, P. S. et al. Sustained coral reef growth in the critical wave dissipation zone of a Maldivian atoll. *Commun. Earth. Environ.* **3**, 9 (2022).
111. Lange, I. D. & Perry, C. T. A quick, easy and non-invasive method to quantify coral growth rates using photogrammetry and 3D model comparisons. *Methods. Ecol. Evol.* **11**, 714–726 (2020).
112. Rossi, P., Castagnetti, C., Capra, A., Brooks, A. J. & Mancini, F. Detecting change in coral reef 3D structure using underwater photogrammetry: critical issues and performance metrics. *Appl. Geom.* **12**, 3–17 (2020).
113. Spencer, T. Marine erosion rates and coastal morphology of reef limestones on Grand Cayman Island, West Indies. *Coral Reefs* **4**, 59–70 (1985).
114. Yuan, R., Kennedy, D. M., Stephenson, W. J. & Finlayson, B. L. The precision and accuracy of measuring micro-scale erosion on shore platforms. *Marine Geol.* **443**, 106691 (2022).
115. Schürholz, D. & Chennu, A. Digitizing the coral reef: Machine learning of underwater spectral images enables dense taxonomic mapping of benthic habitats. *Methods Ecol. Evol.* **14**, 596–613 (2023).
116. Reyes-Nivia, C., Diaz-Pulido, G. & Dove, S. Relative roles of endolithic algae and carbonate chemistry variability in the skeletal dissolution of crustose coralline algae. *Biogeosciences* **11**, 4615–4626 (2014).
117. Diaz-Pulido, G. et al. Greenhouse conditions induce mineralogical changes and dolomite accumulation in coralline algae on tropical reefs. *Nat. Commun.* **5**, 3310 (2014).
118. Carpenter, R. C. MCR LTER: Coral Reef: Long-term Population and Community Dynamics: Benthic Algae and Other Community Components, ongoing since 2005 ver 32. Environmental Data Initiative. <https://doi.org/10.6073/pasta/0bf200e9e0f099de69826f57b18ff3da> (Accessed 2023-04-03) (2020).
119. Carlot, J. et al. Coral reef structural complexity loss exposes coastlines to waves. *Sci. Rep.* **13**, 1683 (2023).

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