

# Loss of coral reef growth capacity to track future increases in sea level

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**Sea-level rise (SLR) is predicted to elevate water depths above coral reefs and to increase coastal wave exposure as ecological degradation limits vertical reef growth, but projections lack data on interactions between local rates of reef growth and sea level rise. Here we calculate the vertical growth potential of more than 200 tropical western Atlantic and Indian Ocean reefs, and compare these against recent and projected rates of SLR under different Representative Concentration Pathway (RCP) scenarios. Although many reefs retain accretion rates close to recent SLR trends, few will have the capacity to track SLR projections under RCP4.5 scenarios without sustained ecological recovery, and under RCP8.5 scenarios most reefs are predicted to experience mean water depth increases of more than 0.5 m by 2100. Coral cover strongly predicts reef capacity to track SLR, but threshold cover levels that will be necessary to prevent submergence are well above those observed on most reefs. Urgent action is thus needed to mitigate climate, sea-level and future ecological changes in order to limit the magnitude of future reef submergence.**

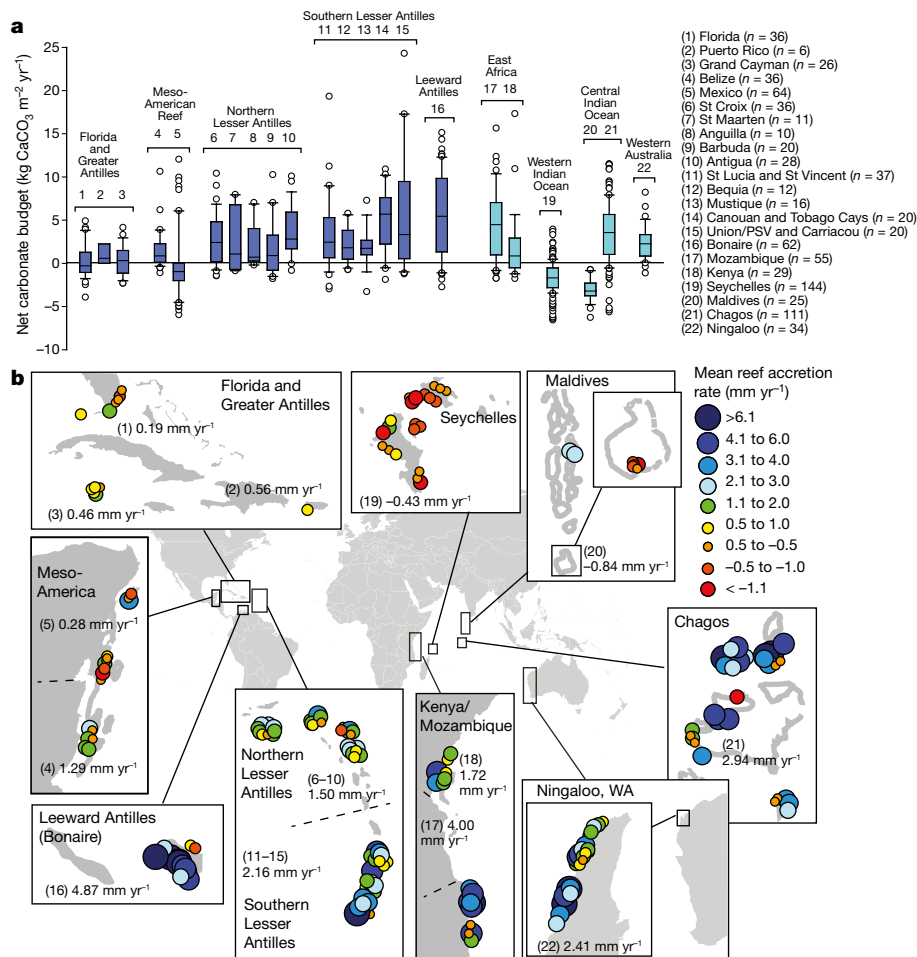
SLR will directly impact coastal communities through shoreline inundation and erosion<sup>1,2</sup>. Along coral-reef-fronted coastlines, the maintenance of reef surface elevation relative to sea level will critically influence magnitudes of future shoreline change and flooding risk<sup>3,4</sup>. This is because reef structure and water depth modulate across-reef and near-shore wave energy regimes<sup>5–7</sup>. Mean water depth increases will occur in areas where vertical growth rates lag behind actual or relative (for example, from glacial isostatic adjustment or land subsidence) increases in sea level<sup>4,8</sup>. This is a widely discussed scenario as the abundance of reef-building species declines globally, limiting reef growth potential<sup>9–14</sup>, while at the same time significant sea-level increases are projected (global mean 0.44 m under RCP2.6 by 2100, 0.74 m under RCP8.5<sup>15,16</sup>). Even modest depth increases of approximately 0.5 m above reefs are projected to increase coastal flooding risk, and change near-shore sediment dynamics<sup>3,5,17,18</sup>. However, datasets to support predictions of magnitudes of above-reef submergence and how these may vary geographically under different RCP scenarios are sparse<sup>19</sup>. This is a major knowledge gap with important socio-economic and policy implications for urbanized tropical coastlines and reef islands given projected costs of adaptation and mitigation planning<sup>4</sup>.

To estimate reef growth capacity under future SLR, we calculated mean increases in water depth above reefs using a large dataset of reef

carbonate budget data collected from more than 200 reefs around two major reef-building regions, the tropical western Atlantic and the Indian Ocean. These data, based on in situ ecological metrics (see Methods), were collected between 2009 and 2017, allowing us to explore intra-regional variations in contemporary carbonate budget states and site-specific temporal dynamics in budget states. Using these data, we derived first-order estimates of maximum vertical reef accretion potential ( $RAP_{max}$ , in mm per year ( $yr^{-1}$ ); see Methods) to explore four key issues. First, we assess inter- and intra-regional variations in site-specific  $RAP_{max}$  rates in the context of recent disturbance histories. Second, we use datasets obtained before and after the 2016 bleaching event for impacted Indian Ocean sites to quantify changes in  $RAP_{max}$  rates and consider the implications for reef growth given the increasingly important control bleaching has on reef health<sup>14,20,21</sup>. Third, we derive best-estimate predictions of reef capacity to track projected rates of SLR, and project total minimum water depth increases at each site by 2100, by comparing site-specific  $RAP_{max}$  rates against recent (1993–2010) altimetry-derived regional SLR rates and those projected under RCP4.5 and RCP8.5 scenarios<sup>22</sup>. Fourth, we quantify the relationship between mean coral cover (as the most widely used reef ‘health’ metric<sup>9,10</sup>) and reef submergence under these same SLR scenarios over the next few decades to identify regional coral cover thresholds that are necessary to limit reef submergence.

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**Fig. 1 | Reef carbonate budgets and accretion rates for the tropical western Atlantic and Indian Ocean. a**, Plots showing site-level carbonate budget data ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) grouped by country or territory within ecoregions. Box plots depict the median (horizontal line), box height depicts first and third quartiles, whiskers represent the 95th percentile, and outliers outside the 95th percentile are shown as circles. Bold numbers

above the plots indicate the country or territory. Numbers in italics adjacent to the countries indicate the number of transects per country/territory. **b**, Calculated maximum reef accretion potential ( $\text{RAP}_{\text{max}}$ ) rates ( $\text{mm yr}^{-1}$ ) for each reef within ecoregions. Numbers in parentheses in each area box denote the country or territory followed by the mean reef accretion rate ( $\text{mm yr}^{-1}$ ).

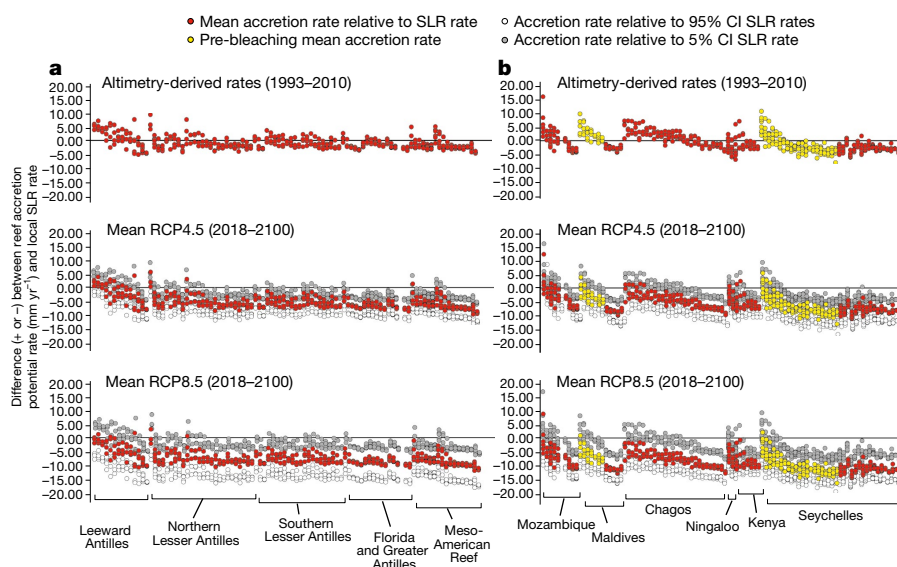
### Carbonate budgets and reef accretion potential

Our data show that contemporary carbonate budgets ( $G$ , where  $G = \text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) of most shallow water (less than 10 m depth) reefs across the tropical western Atlantic ( $2.55 \pm 3.83 G$  (mean  $\pm$  s.d.)) and Indian Ocean ( $1.41 \pm 3.02 G$ ) are currently low (Fig. 1a), and are substantially below the optimal rates (approximately 5–10 G) that have been reported under high coral cover states for both regions<sup>23</sup>. Mean carbonate budgets do not differ significantly between the two ocean regions (generalized linear mixed model (GLMM),  $P = 0.485$ ), but there were significant differences among regions within ocean basins (GLMM,  $P = 0.046$ ). In the tropical western Atlantic, the highest carbonate budgets were calculated on Leeward Antilles reefs ( $5.75 \pm 4.87 G$ ; Fig. 1a), a rate that is closer to historical optimal rates<sup>23</sup>. The lowest rates were along the Mesoamerican Reef (Mexico,  $0.14 \pm 3.81 G$ ; Belize,  $1.52 \pm 2.19 G$ ), in Florida ( $0.16 \pm 1.96 G$ ) and Grand Cayman ( $0.28 \pm 1.74 G$ ; Fig. 1a and Supplementary Table 1). These trends mirror those in coral cover reported in recent basin-wide analyses<sup>24</sup>, and provide compelling evidence that both coral carbonate production ( $4.22 \pm 4.06 G$ ) and bioerosion rates ( $1.74 \pm 1.46 G$ ) are low across many tropical western Atlantic reefs. As with net  $G$ , rates of both coral carbonate production and bioerosion exhibit marked intra-ocean variability (Extended Data Fig. 1) and we note that only sites in the southeast, such as Bonaire (Fig. 1b), are characterized by both high carbonate production and bioerosion rates ( $8.12 \pm 4.60 G$  and  $2.79 \pm 1.08 G$ , respectively; see Extended Data Fig. 1) that are close to historically estimated regional rates<sup>19,25</sup>. In the Indian Ocean, the highest

contemporary budgets were calculated on reefs in Mozambique ( $4.78 \pm 5.01 G$ ) and Ningaloo, Australia ( $2.46 \pm 2.01 G$ ). The lowest (and net negative) rates were calculated at the Seychelles ( $-1.51 \pm 1.90 G$ ) and Maldives sites ( $-2.98 \pm 1.30 G$ ; Fig. 1a and Supplementary Table 1).

Low-carbonate budget states are reflected in low calculated  $\text{RAP}_{\text{max}}$  rates at many sites across both oceans. In the tropical western Atlantic, the mean  $\text{RAP}_{\text{max}}$  rate across all sites is  $1.87 \pm 2.16 \text{ mm yr}^{-1}$  but there is significant intra-ocean variability (GLMM,  $P = 0.032$ ). The highest  $\text{RAP}_{\text{max}}$  rates were calculated at sites in the southern Lesser Antilles ( $2.16 \pm 1.93 \text{ mm yr}^{-1}$ ) and Leeward Antilles ( $4.87 \pm 2.71 \text{ mm yr}^{-1}$ ; Fig. 1b). Low  $\text{RAP}_{\text{max}}$  rates characterize all reefs examined in Florida and the Greater Antilles (Grand Cayman,  $0.46 \pm 0.66 \text{ mm yr}^{-1}$ ; Florida,  $0.19 \pm 0.93 \text{ mm yr}^{-1}$ ; Fig. 1b) and along the Mesoamerican Reef (Belize,  $1.29 \pm 0.89 \text{ mm yr}^{-1}$ ; Mexico,  $0.28 \pm 1.52 \text{ mm yr}^{-1}$ ; Fig. 1b). These low  $\text{RAP}_{\text{max}}$  rates are likely to result from a prolonged period (at least multi-decadal in duration) of ecological decline driven by various regional-scale factors (fishing pressure, coral disease, bleaching, loss of herbivorous taxa and water quality declines<sup>13,26</sup>) that have substantially changed reef ecology.

In the Indian Ocean, mean calculated regional  $\text{RAP}_{\text{max}}$  rates are only  $2.01 \pm 2.33 \text{ mm yr}^{-1}$ . Sites in East Africa (Mozambique,  $4.00 \pm 2.78 \text{ mm yr}^{-1}$ ; Kenya,  $1.72 \pm 1.32 \text{ mm yr}^{-1}$ ) and Ningaloo, Australia ( $2.41 \pm 2.01 \text{ mm yr}^{-1}$ ) have the highest mean  $\text{RAP}_{\text{max}}$  rates, whereas western and central Indian Ocean sites are on average net negative (Seychelles,  $-0.43 \pm 0.95 \text{ mm yr}^{-1}$ ; Maldives,  $-0.84 \pm 0.47 \text{ mm yr}^{-1}$ ; Fig. 1b). This reflects the fact that these areas



**Fig. 2 | Difference between calculated reef accretion potential ( $\text{mm yr}^{-1}$ ) relative to recent (1993–2010) and projected rates of SLR.** **a, b,** Plots showing difference between reef accretion rate and SLR for tropical western Atlantic (**a**;  $n = 95$ ) and Indian Ocean (**b**;  $n = 107$ ) sites. Recent SLR rates are based on altimetry data for the period 1993–2010

were extensively affected by the 2016 bleaching event<sup>27</sup> (Extended Data Fig. 2), with widespread coral mortality to depths of at least 6–7 m. Chagos corals also suffered high mortality during 2016<sup>22</sup> and although post-event budget assessments have yet to be undertaken it is likely that the relatively high mean  $\text{RAP}_{\text{max}}$  rates that we report ( $2.94 \pm 2.06 \text{ mm yr}^{-1}$ ; Fig. 1) for Chagos far exceed contemporary rates. At sites with both pre- and post-2016 data, bleaching significantly reduced both net  $G$  (GLMM,  $P < 0.001$ ) and  $\text{RAP}_{\text{max}}$  (GLMM,  $P < 0.001$ ). Declines were greatest in the Maldives and on ‘recovering reefs’<sup>28</sup> in the Seychelles (Extended Data Fig. 2). There were negligible differences on ‘regime-shifted’ Seychelles reefs as coral cover, net  $G$  and accretion were already low. The major consequence of the 2016 event is that most reefs in the impacted areas are presently in net erosional or non-net accretionary states. Furthermore, given: (1) that not all Seychelles reefs recovered successfully from past (1998) bleaching<sup>28</sup>; and (2) that models predict the rapid onset of annual bleaching for the central Indian Ocean, under both RCP4.5 and RCP8.5 scenarios<sup>21</sup> (that is, well inside the timescales necessary for reef recovery<sup>29,30</sup>) the capacity for Indian Ocean reefs to regain high accretion states is increasingly questionable.

### Reef accretion and projected SLR

To assess reef capacity to track local SLR, we compared our calculated  $\text{RAP}_{\text{max}}$  rates against recent altimetry-measured SLR rates for the period 1993–2010 (see Methods) and rates projected under RCP4.5 and RCP8.5<sup>22</sup> (see Methods and Supplementary Table 2). In both regions only around 45% of reefs have calculated mean  $\text{RAP}_{\text{max}}$  rates close to (within  $\pm 1 \text{ mm yr}^{-1}$ ) or above local recent (altimetry-derived) SLR rates. Therefore, for many reefs there is already a divergence between reef growth potential and the local recent rate of SLR (Fig. 2). However, these values fall to only 6.2% and 3.1%, respectively, in the tropical western Atlantic, when we compare calculated  $\text{RAP}_{\text{max}}$  rates for each site to projected mean local RCP4.5 and RCP8.5 rates for the twenty-first century<sup>31</sup>. In the Indian Ocean, only 2.7% of reefs have mean  $\text{RAP}_{\text{max}}$  rates close to (within  $\pm 1 \text{ mm yr}^{-1}$ ) RCP4.5 projections and 1.3% close to mean RCP8.5 projections (Fig. 2). Although a more positive prognosis would be implied in the Indian Ocean on the basis of pre-bleaching states (59% of the reefs had  $\text{RAP}_{\text{max}}$  rates close to (within  $\pm 1 \text{ mm yr}^{-1}$ ) recent measured SLR rates; Fig. 2), our data suggest that few reefs in either region will be able to match average twenty-first

(see Methods). Mean RCP4.5 and RCP8.5 SLR rates (and 5% and 95% confidence intervals (CI)) are based on projections for the period 2018–2100<sup>31</sup> (see Supplementary Table 2). Dots show individual transect data within each site.

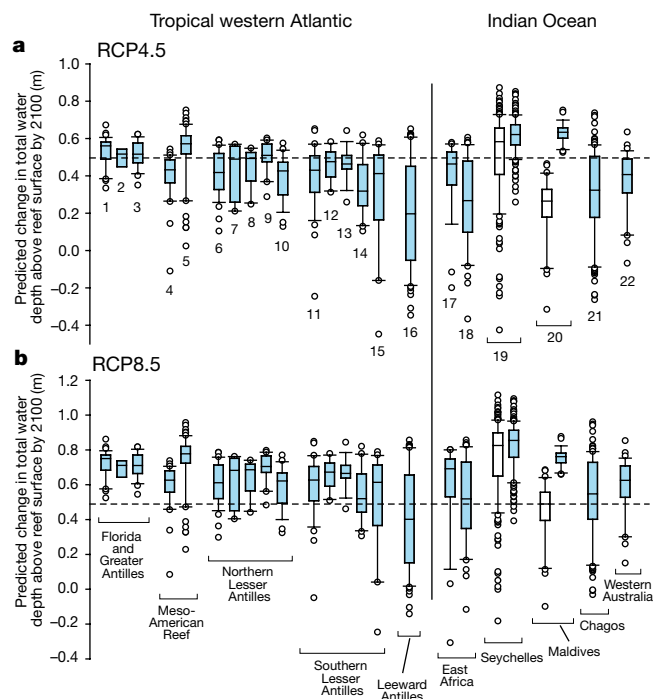
century projected SLR rates (see Supplementary Table 2) if current ecological conditions persist.

### Projections of reef submergence

To assess magnitudes of future reef submergence, we used our calculated  $\text{RAP}_{\text{max}}$  rates to predict total minimum water depth increases above each reef by the end of this century (Fig. 3), and in the Indian Ocean for selected sites based on pre- and post-2016 bleaching data. However, these predictions are probably at the more optimistic end of the spectrum in terms of reef keep-up capacity, both for methodological reasons (see Methods) and because of the lag time between climate warming and SLR. Thus, calculated magnitudes of water depth increase should be considered as best-case scenarios and the minimums for which regions should prepare. Allowing for these caveats, our current projections are that if strong climate mitigation actions can be rapidly implemented (for example, an RCP2.6-type scenario) that restrict SLR rates to close to those measured across our study areas over the last few decades (that is,  $< 3 \text{ mm yr}^{-1}$ ; see Supplementary Table 2), then the difference between reef accretion and SLR rate will on average be low in both regions, assuming that ecological conditions do not deteriorate further (mean  $< 10 \text{ cm}$  increases by 2100; see Supplementary Table 3).

By contrast, significant water depth increases are projected above these reefs by 2100 under both RCP4.5 and RCP8.5 scenarios. Under RCP4.5 projections water depths on the tropical western Atlantic reefs are predicted to increase by 14–66 cm (5–95% confidence interval range) (mean,  $\sim 40 \text{ cm}$  or  $4.8 \text{ mm yr}^{-1}$ ), and between 16 and 104 cm (mean,  $\sim 60 \text{ cm}$  or  $7.2 \text{ mm yr}^{-1}$ ) under RCP8.5 (Fig. 3). In the Indian Ocean mean water depth is estimated to increase by 14–72 cm (mean,  $47 \text{ cm}$  or  $5.6 \text{ mm yr}^{-1}$ ) under RCP4.5 and between 22 and 112 cm (mean,  $71 \text{ cm}$  or  $8.5 \text{ mm yr}^{-1}$ ) under RCP8.5 (Fig. 3 and Supplementary Table 3). Larger average increases of around 63 cm under RCP4.5 (34–92 cm (5–95% confidence interval range)) and 87 cm (41–132 cm) under RCP8.5 (Fig. 3 and Supplementary Table 3) are predicted for bleaching-affected central Indian Ocean reefs in the absence of sustained ecological recovery. The major implications are that while 32% of tropical western Atlantic and 45% of Indian Ocean reefs are predicted to experience increases of over 0.5 m by 2100 under mean local RCP4.5 scenarios, under RCP8.5 projections, 80% of our tropical western Atlantic and 78% of Indian Ocean reefs are predicted to experience minimum mean water depth increases above this level. This is an



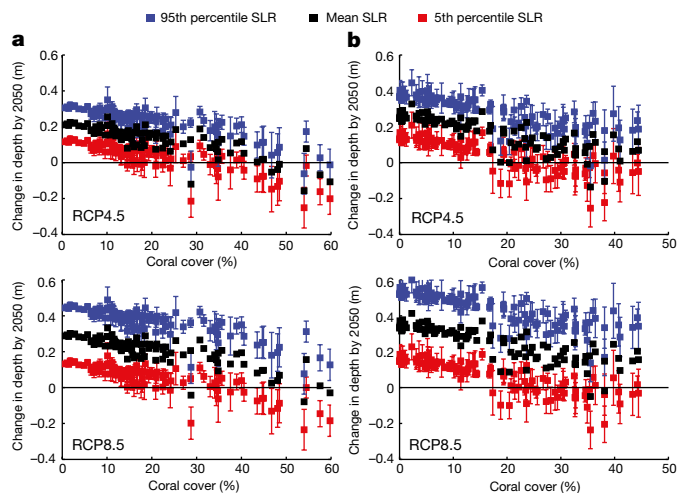


**Fig. 3 | Total predicted increases in water depth above reefs by 2100.** **a, b,** Plots for site-level data showing predicted water depth increases against mean RCP4.5 (**a**) and RCP8.5 (**b**) SLR projections for the period 2018–2100. Box plots depict median (horizontal line), box height depicts first and third quartiles, whiskers represent the 95th percentile, and outliers outside the 95th percentile are shown as circles. White bars denote pre-bleaching data. The dashed line shows the 0.5-m threshold above which significantly increased wave energy regimes are predicted. Site numbers as in Fig. 1.

important depth threshold as recent models<sup>32</sup> suggest that, on average, wave energy regimes will increase especially rapidly once water depth increases exceed 0.5 m. Of major future concern is that, because of the delayed response of processes contributing to SLR (deep ocean warming, and ice sheet and glacier mass loss), these submergence trends are projected to increase towards the end of the century<sup>16,31,33</sup>. Therefore, the higher end projections of water depth increases for each scenario may be more realistic (Supplementary Table 3), rapidly exacerbating the threat to coastal communities and to small island developing states<sup>1,4</sup>.

### Reef state and submergence trajectories

An especially pressing issue for reef and coastal managers is the question of which reefs are most likely to experience submergence over the coming decades, and how this relates to reef state. The percentage of live coral cover is the most widely reported metric of reef state and we thus used our data to examine whether a metric as simple as coral cover had predictive capacity for projecting changes in sea level above reefs. Although our datasets span two biogeographical provinces, a range of depths (2–13 m) and a diversity of community structures, coral cover explained up to 62% of the projected increase in net water depth by the year 2050 (Fig. 4 and Extended Data Table 1). Simulations uncover that high coral cover states would experience little water depth increase with some even extending closer to the surface. However, statistical fits to our data suggest that coral cover levels of around 40% in the tropical western Atlantic, and approximately 50% in the Indian Ocean, are needed to avoid the prospect of net reef submergence in the next few decades (by 2050) under mean RCP4.5 SLR projections. However, this threshold increases to nearly 60% in the tropical western Atlantic and nearly 70% in the Indian Ocean under the current emissions trajectory of RCP8.5. Given that coral cover levels across the sites in our dataset average only  $20.6 \pm 13.9\%$  in the tropical western Atlantic, and  $17.8 \pm 12.6\%$  in the Indian Ocean region (Supplementary Table 1),



**Fig. 4 | Relationships between mean coral cover (%) and changes in water depth (m) above reefs by 2050.** **a, b,** Model simulations (100 per site and SLR scenario) showing predicted changes (y axis) in mean water depth (m) above reefs as a function of coral cover (x axis). **a,** Tropical Western Atlantic sites ( $n = 95$  reefs). **b,** Indian Ocean sites ( $n = 104$  reefs). Mean change in depth is shown as the centre point. Error bars are s.d. Simulations show trends under lower (5th percentile), mean and upper (95th percentile) projections of SLR under RCP4.5 and RCP8.5 SLR scenarios.

there is therefore a high probability that mean water depths above reefs will increase by at least a few tens of centimetres in the coming decades.

### Summary

The potential for a high proportion of reefs (over 75% across our sites under RCP8.5) to experience water depth increases greater than 0.5 m by 2100 is of concern, because modelling studies suggest this will be sufficient to open higher wave-energy windows that will increase sediment mobility, shoreline change and island overtopping<sup>1–3,17,18</sup>. We also show that major climate-driven perturbations, specifically coral bleaching, can drive major declines in reef accretion potential. The most worrying end-point scenario is that if predictions of increasing bleaching frequency are realized<sup>21,34</sup> and result in more frequent mortality, reefs may become locked into permanent low accretion rate states, leading to increasing rates of submergence under all SLR scenarios. Ocean acidification and thermal impacts on calcification represent additional threats and may negatively impact reef calcification and increase bioerosion<sup>35,36</sup>. These collective threats will be exacerbated by the low coral cover states that define many reefs, and which our analysis suggests will be insufficient to prevent reef submergence. Our approach represents a first step in improving our predictive capabilities in these areas, but given the societal relevance and economic costs of SLR along populated tropical coastlines<sup>4</sup>, and that coral reefs have the potential to have a key role in nature-based defence strategies, these issues should have a high priority on the research agenda.

### Online content

Any Methods, including any statements of data availability and Nature Research reporting summaries, along with any additional references and Source Data files, are available in the online version of the paper at <https://doi.org/10.1038/s41586-018-0194-z>.

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#### Additional information

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## METHODS

Field data to calculate biological carbonate production and erosion rates, from which net reef carbonate budgets ( $G$ , where  $G = \text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) could be calculated, were collected from reef sites spanning both the tropical western Atlantic (TWA) and Indian Ocean regions. All data were collected between 2009 and 2017 (see Supplementary Table 1). At most TWA sites, these data were collected using the ReefBudget methodology<sup>37</sup>, and for Indian Ocean sites, using a previously reported adapted version of this methodology<sup>12,38</sup> that factors for regional differences in coral assemblages and bioeroding communities. Data were collected through a number of discrete projects, however, in all cases, the aim was to capture data from the main shallow-water reef-building zones within a range of sites within each country. Survey depths and habitat types thus reflected this variability, although were kept as consistent as possible within countries, and replicate transects within sites were always depth-consistent. In the TWA, data were mostly collected within the 8–10-m depth fore-reef zone. However, where field/logistical conditions allowed, data were collected also at shallower (around 5-m depth) sites, although the number of locations for which data from both depths could be collected was limited. In the Indian Ocean region, survey depths and habitat zones are more variable reflecting the more diverse range of reef types and geomorphologies associated with the countries in our dataset. Our data thus provide an overview of the range in budgetary states, and the resultant accretion potential, of reefs within a country, accepting that not every reef or setting can be realistically assessed. No budget data were collected from high-energy reef-crest settings (<2 m depth) due to physical working constraints, but we note that reported long-term accretion rates for such settings (where these systems are usually dominated by coralline algae) are generally less than 1–2 mm per year<sup>39,40</sup>, rates that are not dissimilar to those calculated at many sites in this study. The number of replicate transects (see Supplementary Table 1) varied between sites (ranging from 3 to 8) depending on field logistics and weather constraints.

Following the ReefBudget methodology, benthic data were collected using a 10-m transect as a guide line below which a separate 1-m flexible tape was used to measure the distance within each linear 1 m covered by each category of benthic cover. All overhangs, vertical surfaces and horizontal surfaces below the line were thus surveyed. Scleractinian corals were recorded to species level in the TWA, and to genera and morphological level (for example, *Acropora* branching, *Porites* massive and so on) in the Indian Ocean. Substrate rugosity was calculated as total reef surface divided by linear distance (a completely flat surface would therefore have a rugosity of 1). To calculate rates of coral carbonate production, we integrated the mean percentage of cover of each coral species with species-specific (or nearest equivalent species) measures of skeletal density ( $\text{g cm}^{-3}$ ) and linear growth rate ( $\text{cm yr}^{-1}$ ), as derived from published sources (<http://geography.exeter.ac.uk/reef-budget/>). These data were then combined with rugosity measures to yield a value for coral carbonate production ( $G$ ) relative to actual transect surface area. For several sites in both regions carbonate production rates were calculated slightly differently, because community composition data were based on standard linear intersect methodologies. These were TWA sites in the Windward and Leeward Antilles and, in the Indian Ocean, at Ningaloo and Seychelles. In these cases, individual coral colony cover data were scaled up to derive a three-dimensional measure of cover by using genera or growth form-specific rugosity metrics. For several Indian Ocean sites (Maldives and Seychelles) that were known to be severely affected by the 2016 bleaching event, we also report post-bleaching changes in carbonate production rates, with census data collected using the same methodology as that used pre-bleaching.

To calculate rates of bioerosion, we also undertook census studies to determine abundance and size of parrotfish and bioeroding urchins (both to species level) per unit area of reef following the methods previously reported for TWA and Indian Ocean sites<sup>12,37</sup>. All parrotfish abundance data were collected along replicate  $30 \times 4\text{-m}^2$  belt transects, except in Chagos ( $50 \times 5\text{-m}$  belts), Seychelles ( $7.5\text{-m}$  radial surveys) and Ningaloo ( $100 \times 10\text{-m}$  belts). To calculate bioerosion rates by each individual fish, we used models based on total length and life phase to predict the bite rates (bites per hour) for each species, as reported in Perry et al.<sup>12,37</sup>. To calculate bioerosion rates by urchins, we undertook additional surveys at each site, using either  $10 \times 2\text{-m}$  or  $10 \times 1\text{-m}$  belt transects to determine the species and test sizes of urchins per unit area of reef. Census data were then combined with published species/test class size erosion rate data<sup>12,37</sup> to yield a measure of erosion rate. Rates of endolithic bioerosion were estimated for most TWA sites based on a census of endolithic sponge tissue cover per unit area of reef substrate<sup>37,41</sup>. Exceptions were sites in Bonaire and the Windward Antilles, where surveys were not conducted and literature-derived rates from the TWA were applied. Endolithic bioerosion rates were estimated at all Indian Ocean sites by applying rates from the literature to available benthic substrate<sup>12</sup>.

To calculate maximum reef accretion potential ( $\text{RAP}_{\text{max}}$ ) rates ( $\text{mm yr}^{-1}$ ) at each site, we followed a previously used method<sup>11,12</sup> based on the conversion of measured site-specific net carbonate production rates ( $G$ ) as proposed previously<sup>42</sup>.

In this conversion net carbonate production is taken as the sum of calculated gross carbonate production by corals and coralline algae minus erosion rate. We then also factored for variations in accumulating reef framework porosity as a function of coral community type and for sediment reincorporation<sup>42</sup>. Stacking porosity values ranging from around 80% void space for branching coral assemblages to about 20% for head coral-dominated assemblages, with rates of approximately 50% for mixed assemblages, were proposed previously<sup>43</sup>. However, since coral communities are rarely entirely monospecific, we used the following assumptions in our calculations: that void space estimates of 30% were appropriate for head and massive coral-dominated assemblages, 70% for branched and tabular coral-dominated assemblages and 50% for mixed coral assemblages as determined for each site from benthic coral community data. Sediment reincorporation was factored for by allowing for a proportion of the bioeroded framework (that is converted to sediment) to be reincorporated back into the accumulating reef structure. This proportion was calculated as the sum of 50% of the parrotfish-derived sediment (as a highly mobile bioeroder that defecates randomly over the reef), as well as all sediment produced by urchins and by macrobioerosion. To keep our estimates conservative, we worked on the assumption that only around 50% of this bioerosional sediment yield is actually incorporated back into the reef (see also Hubbard et al.<sup>44</sup>), and excluded any sediment generation by other benthic sediment producers (for example, *Halimeda*).

Owing to the absence of empirical data on rates of physical reef framework removal per unit area of reef surface over time, we did not factor for physical loss rates. For the same reason, we also did not factor for chemical dissolution of the substrate. The accretion rates that we report, which we consider as current best-estimates of accretion potential across the entire upper portion of a reef profile (on the basis that accretion can result from both in situ coral accumulation and the supply of physically derived rubble from shallow fore-reef areas to the crest/flat<sup>45</sup>, are thus defined as a rate of maximum reef accretion potential, or  $\text{RAP}_{\text{max}}$ ). We therefore consider these rates to represent the upper limits of how fast reefs may be accreting at present, and acknowledge that if physical framework loss and chemical dissolution rates<sup>46</sup> could be appropriately factored for at the site level our projected rates would probably be lower. How much lower will depend on spatial variations in physical disturbance regimes and the susceptibility of coral taxa to physical disturbances, and both are likely to vary markedly at intra-regional scales. Testing the validity of our high end ( $\text{RAP}_{\text{max}}$ ) rates is thus not simple.

Evidence from Holocene core records of reef growth, when ecological conditions (in terms of the abundance of high-rate carbonate-producing taxa, for example, *Acropora* spp.) are considered to have been more optimal, suggest that many reefs exhibited an impressive capacity to either 'keep-up' or to 'catch-up' during periods of past rapid SLR. Indeed, calculated vertical accretion rates from the early Holocene, when sea levels were rising rapidly, were as high as 12–15 mm  $\text{yr}^{-1}$  in both the TWA and Indian Ocean regions<sup>47</sup>. Although longer term average accretion rates were lower (for example, approximately 3–4 mm  $\text{yr}^{-1}$  in the TWA<sup>48</sup>; and a little below this in the Indian Ocean region<sup>47</sup>), these still exceed those estimated for many modern reefs in our dataset, and fall well below even mean RCP4.5 SLR scenarios (see Supplementary Table 2). Furthermore, reef core studies that might allow some assessment of very recent accretion histories on a site-by-site basis, that is with a focus on the last couple of hundred years of reef growth, are sparse/absent and would make for inherently problematic comparisons because of the magnitudes of coral community change that have occurred at most sites over the last few decades.

However, one useful (albeit subarea-specific) comparator is the recent work of Yates et al.<sup>49</sup>, which used historical bathymetric data from the 1930s to 1980s and Lidar-derived digital elevation models from the late 1990s to 2000s in Florida to calculate net changes in seafloor elevation. This data integrates for the effects of any physical and chemical losses and suggests net negative accretion rates in the upper Florida Keys of around  $-1.5\text{ mm yr}^{-1}$  (over the past 68 years), of  $-4.5\text{ mm yr}^{-1}$  in the lower Florida Keys (over the past 66 years) and of  $-2.7\text{ mm yr}^{-1}$  in the US Virgin Islands (over the past 33 years). Our data from different sites in this region (southeast Florida, the upper Florida Keys and the Dry Tortugas) and which do not include data from lagoon sands and seagrass beds that were integrated within the previous study<sup>49</sup>, have average contemporary accretion rates of  $-0.4$ ,  $1.7$  and  $0.8\text{ mm yr}^{-1}$ , respectively. Our rates are thus, as expected for the various reasons outlined above, a little but not markedly higher, suggesting they provide a reasonable estimate of high end reef accretion potential.

To test for differences in net  $G$  and calculated accretion rates between sites and countries across our dataset, we fitted GLMMs to assess whether rates showed statistically significant differences between oceans and regions ( $n = 885$  transects), as well as for the effects of bleaching and the interaction with location (Maldives, Seychelles recovering and regime-shifted) ( $n = 338$  transects), while controlling for site depth and the random effect of site. All GLMMs were fitted using a Gaussian distribution via the lmer function of the package lme4<sup>50</sup> in R<sup>51</sup>, with significance assessed using  $F$ -ratio statistics calculated via the ANOVA function in the CAR<sup>52</sup>.



package. Model assumptions of normality and homogeneity of variance were assessed graphically and found to be adequately met. We found a very weak effect of depth on net  $G$  (and thus  $RAP_{max}$  rates) across our dataset, with net  $G$  typically being slightly higher on the deeper reefs ( $P=0.001$ ,  $r=0.160$ ). Although our datasets do not allow a detailed consideration of this issue at the within-region level, the fact that average accretion rates do not noticeably decline with depth across the upper fore-reef depth intervals is consistent with trends inferred from Holocene core records in the TWA region<sup>48</sup>.

To assess the capacity of the reefs in our datasets to match recently observed and future projected changes in sea level, and to estimate magnitudes of water depth increases relative to projected reef accretion by 2100 at each site, we compared our calculated  $RAP_{max}$  data against local sea-level change data (Supplementary Table 2). In these comparisons, we assume steady-state ecological conditions persisting. For recent observed rates of change, we compared our  $RAP_{max}$  rates against altimetry data for the period 1993–2010 from combined TOPEX/Poseidon, Jason-1, Jason-2/OSTM and Jason-3 satellite altimetry fields ([http://www.cmar.csiro.au/sealevel/sl\\_data\\_cmar.html](http://www.cmar.csiro.au/sealevel/sl_data_cmar.html); downloaded on 22 January 2018). The fields used are monthly averages on a  $1^\circ \times 1^\circ$  grid with the seasonal (annual and semi-annual) signal removed, and include inverse barometer and GIA corrections. The observed rates were computed by fitting a linear trend to the monthly 1993–2010 time series at the nearest available ocean grid point to the reef location. For the period 2018–2100, we used sea-level projections under the RCP4.5 and RCP8.5 scenarios<sup>31,33</sup>. These regional sea-level projections factor for changes in ocean density and dynamics, changes in atmospheric pressure, and glacier and ice sheet surface mass balance contributions based on output from 21 CMIP5 (Climate Model Intercomparison Phase 5<sup>53</sup>) atmosphere–ocean coupled climate models. In addition, the projections account for model-based contributions from anthropogenic groundwater extraction, for glacial isostatic adjustment and observation-based estimates of ice sheet dynamical processes. The regional sea-level patterns of mass redistribution account for changes in gravitational, deformational and rotational feedbacks. As for the recent observed rates of change, the spatial resolution of the SLR projections is  $1^\circ \times 1^\circ$  and the closest grid point (nearest neighbour) is extracted for comparison to the coral reef data (Supplementary Table 2).

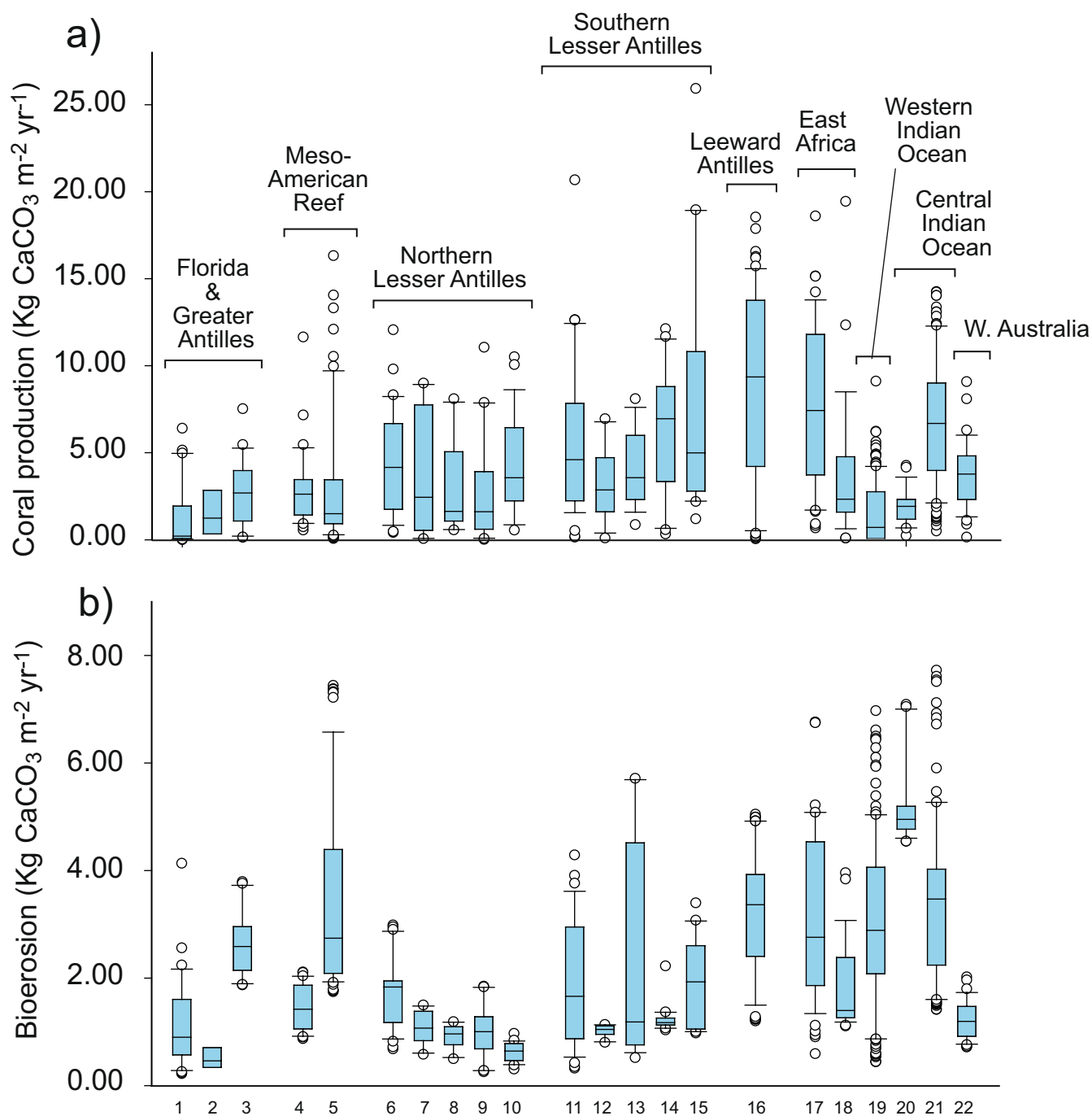
To obtain a greater insight into the importance of coral cover on near-future reef submergence, we undertook Monte Carlo simulations of carbonate budgets, potential accretion rates and projected increases in depth under SLR. One hundred simulations were carried out per site during which community structure was sampled randomly from the site-level statistical distribution of corals, CCAs and sources of bioerosion (that is, sampling from the observed mean and standard deviation of species-specific  $G$  or erosion rate at the site). Each simulation was extended to estimate the change in seawater depth at the year 2050 for six reference rates of SLR (as above): the 5th percentile, mean, and 95th percentile of the rate of SLR for each of two greenhouse gas (GHG) emission scenarios, RCP4.5 and RCP8.5. For each site, we obtained the mean and standard deviation for each of the six SLR references. Analyses of differences in accretion rate, rates of SLR, and increases in depth over reefs were carried out using non-parametric mixed effects models based on Euclidean distance<sup>54</sup>. This technique is analogous to parametric linear mixed effects models but makes no assumptions about the statistical distribution of errors. Fixed effects included biogeographical region (TWA versus Indian Ocean), GHG emissions scenario (RCP4.5 versus RCP8.5) and coral cover. Country was added as a random effect nested within biogeographical region. The only exception to this approach was the use of linear mixed effects models in order to estimate threshold levels of coral cover where the net submergence of reefs was zero. Models were fitted using the same structure as in PERMANOVA<sup>55</sup> but the predict function was used to estimate model fits for  $y=0$ . Analysis showed that a shift towards lower GHG emissions (RCP4.5) reduced the degree of reef submergence (Fig. 4; PERMANOVA,  $P<0.001$ ) and emissions scenario gained in importance when switching from lower to mean to upper (95 percentile) bounds of projected SLR, explaining 2%, 44%, and 54% of the variance in reef submergence, respectively (Extended Data Table 1). Under the upper bounds of SLR, biogeographical region also became significant (PERMANOVA,  $P=0.005$ ) with submergence being slightly greater in the Indian Ocean (Fig. 4b). Under this pessimistic scenario, threshold levels of coral cover required to avoid net reef submergence

were approximately 13% higher in the Indian Ocean than the TWA (73% versus 60%) even under RCP4.5. This relative vulnerability of reefs in the Indian Ocean was associated with higher rates of SLR (0.94 mm yr<sup>-1</sup> greater; PERMANOVA,  $P=0.02$ , Extended Data Tables 2, 3) rather than any biogeographical difference in accretion potential (PERMANOVA,  $P=0.65$ ; Extended Data Table 4). Although Indian Ocean reefs are generally more resilient than those of the TWA<sup>56</sup>, current ecological trajectories suggest that few coral reef locations will be likely to maintain sufficiently high coral cover levels to keep pace with future SLR, resulting in greater incident wave energy exposure, and changing spectrum of wave processes, along reef-fronted shorelines<sup>3,6</sup>.

**Reporting summary.** Further information on experimental design is available in the Nature Research Reporting Summary linked to this paper.

**Data availability.** Net carbonate budget and reef accretion rate data, and measured and projected sea-level data supporting the findings of this study are available within the paper and its Supplementary Information. Site-level coral cover and carbonate production and bioerosion datasets are available from the corresponding author upon request.

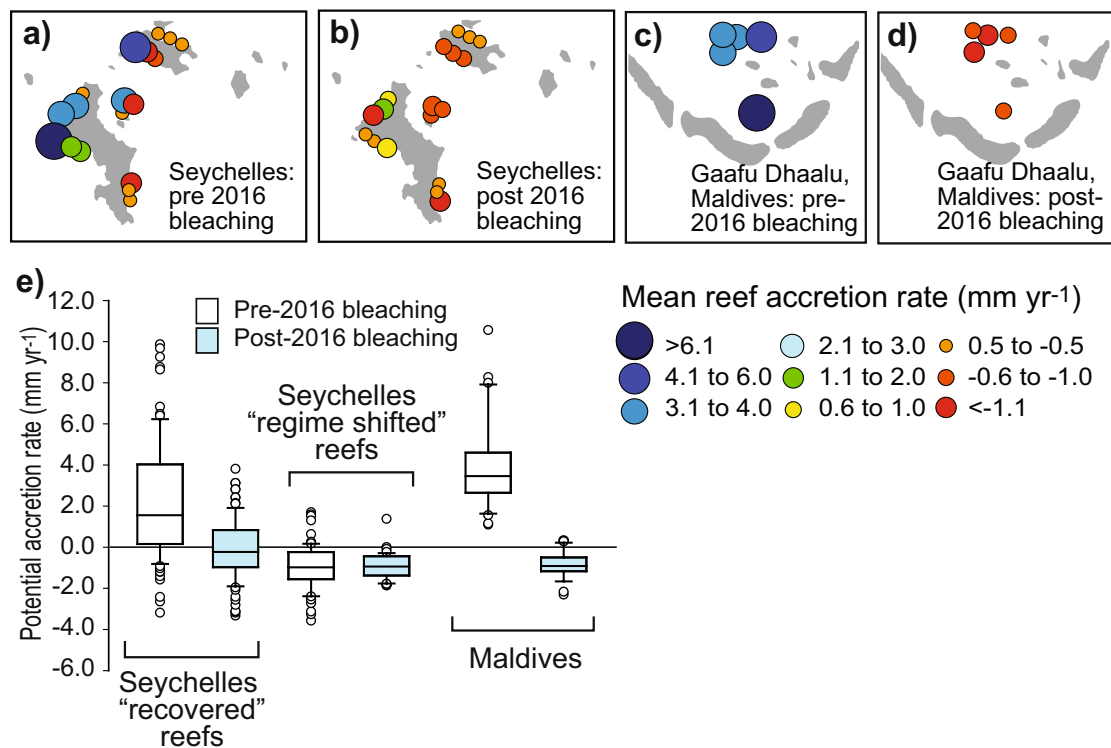
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**Extended Data Fig. 1 | TWA and Indian Ocean coral carbonate production and bioerosion rates.** Plots showing mean site level coral carbonate production rate (**a**) and bioerosion rate (**b**) data ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) grouped by country or territory within ecoregions for TWA and Indian Ocean sites. Box plots depict the median (horizontal line), box height depicts first and third quartiles, whiskers represent the 95th percentile, and outliers outside the 95th percentile are shown as circles. Country/territory codes are as follows: (1) Florida ( $n = 36$ ); (2) Puerto Rico ( $n = 6$ ); (3) Grand Cayman ( $n = 26$ ); (4) Belize ( $n = 36$ ); (5) Mexico

( $n = 64$ ); (6) St. Croix ( $n = 36$ ); (7) St. Maarten ( $n = 11$ ); (8) Anguilla ( $n = 10$ ); (9) Barbuda ( $n = 20$ ); (10) Antigua ( $n = 28$ ); (11) St. Lucia and St. Vincent ( $n = 37$ ); (12) Bequia ( $n = 12$ ); (13) Mustique ( $n = 16$ ); (14) Canouan and Tobago Cays ( $n = 20$ ); (15) Union/PSV and Carriacou ( $n = 20$ ); (16) Bonaire ( $n = 62$ ); (17) Mozambique ( $n = 55$ ); (18) Kenya ( $n = 29$ ); (19) Seychelles ( $n = 144$ ); (20) Maldives ( $n = 25$ ); (21) Chagos ( $n = 111$ ); (22) Ningaloo ( $n = 34$ ).  $n$  indicates the number of transects per country or territory.





**Extended Data Fig. 2 | Reef accretion before and after the central Indian Ocean 2016 bleaching event.** **a–d,** Calculated  $\text{RAP}_{\text{max}}$  rates ( $\text{mm yr}^{-1}$ ) before (**a, c**) and after (**b, d**) the 2016 bleaching event in the Seychelles and the Maldives. **e,** Plot shows changes in  $\text{RAP}_{\text{max}}$  rates at 'recovered' ( $n = 96$ ) and 'regime-shifted' reefs<sup>37</sup> ( $n = 72$  pre-bleaching,  $n = 48$

post-bleaching) in the Seychelles, and Maldives ( $n = 35$  pre-bleaching,  $n = 25$  post bleaching). Box plots depict the median (horizontal line), box height depicts first and third quartiles, whiskers represent the 95th percentile, and outliers outside the 95th percentile are shown as circles.

**Extended Data Table 1 | Effects of biogeography, coral cover, GHG emissions scenario and range of SLR projection on the future submergence of coral reefs by 2050****A) Future submergence (depth change) based on lower (5<sup>th</sup> percentile) SLR projections**

Source	df	SS	MS	Pseudo-F	P (perm)	Variance
						%
coralcover	1	1.9178	1.9178	135.76	0.001	62.1
Region	1	1.1627E-3	1.1627E-3	0.11133	0.725	2.0
RCP	1	2.8203E-2	2.8203E-2	15.608	0.001	1.7
Country (Region)	23	0.31843	1.3845E-2	7.662	0.001	11.3
Res	363	0.65591	1.8069E-3			22.9
Total	389	2.9215				

**B) Future submergence (depth change) based on mean SLR projections**

Source	df	SS	MS	Pseudo-F	P (perm)	Variance
						%
coralcover	1	1.9866	1.9866	140.62	0.001	44.6
Region	1	5.4554E-2	5.4554E-2	1.7012	0.197	1.1
RCP	1	0.65409	0.65409	361.04	0.001	30.5
Country (Region)	23	0.31843	1.3845E-2	7.6419	0.001	7.9
Res	363	0.65764	1.8117E-3			15.9
Total	389	3.6713				

**C) Future submergence (depth change) based on upper (95<sup>th</sup> percentile) SLR projections**

Source	df	SS	MS	Pseudo-F	P (perm)	Variance
						%
coralcover	1	2.0557	2.0557	145.51	0.001	26.5
Region	1	0.24799	0.24799	7.4611	0.005	5.7
RCP	1	2.1014	2.1014	1151.9	0.001	54.2
Country (Region)	23	0.31843	1.3845E-2	7.5891	0.001	4.5
Res	363	0.66222	1.8243E-3			9.1
Total	389	5.3857				

Results of PERMANOVA analyses with coral cover, biogeographic region (TWA versus Indian Ocean) and GHG emissions scenario (RCP4.5 versus RCP8.5) as fixed effects and country nested within (biogeographic) region as random effect.

**Extended Data Table 2 | Effect of biogeographic region on rates of SLR**

Source	df	SS	MS	Pseudo-F	P (perm)	Variance
						%
Region	1	4.0348	4.0348	5.5794	0.02	33.9
Country (Region)	25	20.489	0.81955	835.79	0.001	65.6
Res	168	0.16474	9.8057E-4			0.5
Total	194	39.115				

PERMANOVA analysis testing the effect of biogeographic region on the upper 95% of predicted rates of SLR.



**Extended Data Table 3 | Differences between SLR rates between biogeographic regions (mm yr<sup>-1</sup>)**

	Difference in SLR projection (mm yr <sup>-1</sup> ) (Indian Ocean – Tropical Western Atlantic)		
	Component of SLR Projection		
	Lower bound (5 <sup>th</sup> percentile)	Mean	Upper bound (95 <sup>th</sup> percentile)
RCP4.5	0.03	0.33	0.61
RCP8.5	0.59	0.76	0.94

The difference in SLR rates between biogeographic regions (mm yr<sup>-1</sup>) under two GHG emission scenarios and for all three components of SLR projections. Projections are higher in the Indian Ocean except in RCP4.5 lower percentile (0.03), which was not significant.

**Extended Data Table 4 | Variability in potential accretion rate**

Source	df	SS	MS	Pseudo-F	P (perm)	Variance
						%
coralcover	1	1756.9	1756.9	135.43	0.001	63.2
Region	1	2.4775	2.4775	0.15683	0.653	1.8
Country (Region)	23	292.4	12.713	7.6839	0.001	11.6
Res	364	602.25	1.6545			23.4
Total	389	2654.1				

Results of PERMANOVA analysis showing local (coral cover) versus regional (TWA versus Indian Ocean) effects on the variability in potential accretion rate.

## Reporting Summary

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### Statistical parameters

When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

n/a Confirmed

- ☐ ☒ The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement
- ☐ ☒ An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- ☐ ☒ The statistical test(s) used AND whether they are one- or two-sided  
*Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
- ☐ ☒ A description of all covariates tested
- ☐ ☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- ☐ ☒ A full description of the statistics including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- ☐ ☒ For null hypothesis testing, the test statistic (e.g.  $F$ ,  $t$ ,  $r$ ) with confidence intervals, effect sizes, degrees of freedom and  $P$  value noted  
*Give  $P$  values as exact values whenever suitable.*
- ☒ ☐ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- ☐ ☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- ☒ ☐ Estimates of effect sizes (e.g. Cohen's  $d$ , Pearson's  $r$ ), indicating how they were calculated
- ☐ ☒ Clearly defined error bars  
*State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on [statistics for biologists](#) may be useful.

### Software and code

Policy information about [availability of computer code](#)

Data collection

N/a

Data analysis

R and MatLab

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- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
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Net carbonate budget and reef accretion rate data, and measured and projected sea-level data supporting the findings of this study are available within the paper and its supplementary information files. Site level coral cover and carbonate production and bioerosion datasets are available from the authors on request.



## Field-specific reporting

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## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study describes spatial variations in rates of coral reef accretion in relation to recent and projected rates of sea level rise. Field data to calculate biological carbonate production and erosion rates, and from which net reef carbonate budgets ( $G$ , where $G = \text{kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) and accretion rates ( $\text{mm yr}^{-1}$ ) could be calculated were collected from reef sites spanning both the Tropical Western Atlantic (TWA) and Indian Ocean (IO) regions. All data were collected between 2009 and 2017 (see SI Table 1). At most TWA sites these data were collected using the ReefBudget methodology of Perry et al. 2012 and for IO sites using a previously reported adapted version of this methodology that factors for regional differences in coral assemblages and bioeroding communities. Data were collected through a number of discrete projects, but in all cases the aim was to capture data from the main shallow water reef-building zones within a range of sites within each country. No temporal replication was attempted (except in the southern Maldives and Seychelles which experienced coral bleaching) because the data were based on one-off benthic surveys. However, we sought to survey at multiple sites within each setting/habitat type to provide replication where possible -- with the usual constraints of field surveying work
Research sample	The data are based on benthic reef surveys, to determine coral and other benthic reef cover, substrate available to endolithic bioeroders and the abundance and test size of bioeroding urchins, as well as visual census of parrotfish species abundance and size. Data were collected along replicate, depth-consistent, transects in each site. Coral and CCA calcification rates were then determined based on published rates from the literature and bioerosion rates were based on conversions based on published species size/type relationships.
Sampling strategy	Individual reef sites were selected that were considered to provide a representative selection of the major shallow water settings and environments in each of the countries where we worked. Data were collected from along replicate transects (average 5 transects per site; range 3-15) - see Methods. As is typical of reef based field surveys weather, underwater and field logistical constraints influenced within-site sample size and strategy, and sometimes limited the number of sites where we could work.
Data collection	As noted above data collection was undertaken at different sites between 2009 and 2017. Data were collected following the field procedure as outlined in the Methods but by different groups of the authorship depending on expedition membership.
Timing and spatial scale	Field census data were collected at different times between 2009 and 2017 as indicated in the Methods and as listed in SI Table 1
Data exclusions	No data were excluded
Reproducibility	No experiments per se were conducted - rather, and as stated above, our data are based on one-off surveys conducted on reefs across a wide range of geographic locations.
Randomization	This study does not use experimental groups per se, but rather (as in 1 above) we have sought to capture a representative selection of the major shallow water settings and environments in each of the countries where we worked.
Blinding	Blinding is not relevant to this type of study because the data are based on in-situ underwater surveys (not to clustered data/sample sets). Transects were established at fixed distances away from a randomized start point on each reef, with surveys typically being undertaken by alternative divers on each transect.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

## Field work, collection and transport

Field conditions	Data were collected under a wide range of conditions across sites, but as far as possible under low wind/wave conditions.
Location	Data collection was conducted on reefs across a wide range of geographic locations in the Tropical Western Atlantic and Indian Ocean regions (specific site locations are listed in SI Table 1).
Access and import/export	No collections or import or export of samples was undertaken.
Disturbance	Data were collected using census or benthic surveys with no impact on the benthic habitats

## Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Unique biological materials
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology
<input type="checkbox"/>	<input checked="" type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants

Methods

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging

Animals and other organisms

Policy information about [studies involving animals](#); [ARRIVE guidelines](#) recommended for reporting animal research

Laboratory animals	N/A
Wild animals	The size and species (or genera) of corals were recorded along all benthic transects. Similarly, observations were made of the species and size of bioeroding urchins and of parrotfish. However, no corals, urchins or parrotfish were sampled or manually handled during these surveys and were thus unharmed.
Field-collected samples	N/A