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Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations

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Experiments have shown that ocean acidification due to rising atmospheric carbon dioxide concentrations has deleterious effects on the performance of many marine organisms[1–4]. However, few empirical or modelling studies have addressed the long-term consequences of ocean acidification for marine ecosystems[5–7]. Here we show that as pH declines from 8.1 to 7.8 (the change expected if atmospheric carbon dioxide concentrations increase from 390 to 750 ppm, consistent with some scenarios for the end of this century) some organisms benefit, but many more lose out. We investigated coral reefs, seagrasses and sediments that are acclimatized to low pH at three cool and shallow volcanic carbon dioxide seeps in Papua New Guinea. At reduced pH, we observed reductions in coral diversity, recruitment and abundances of structurally complex framework builders, and shifts in competitive interactions between taxa. However, coral cover remained constant between pH 8.1 and ∼7.8, because massive *Porites* corals established dominance over structural corals, despite low rates of calcification. Reef development ceased below pH 7.7. Our empirical data from this unique field setting confirm model predictions that ocean acidification, together with temperature stress, will probably lead to severely reduced diversity, structural complexity and resilience of Indo-Pacific coral reefs within this century.

Rising atmospheric CO_2 from the burning of fossil fuels and deforestation affects marine systems in several ways. Through its effect on the global climate, it increases sea surface temperatures (now 0.7 °C higher than in pre-industrial times) and intensifies storm and rainfall variability, altering salinity and the terrestrial runoff of nutrients and sediments[8]. It also causes profound changes in sea water chemistry. Atmospheric CO_2 concentrations of ∼390 ppm already exceed by 50–100% the historic envelope of 200–300 ppm in the past >2 million years[9]. The resulting increased partial pressure of carbon dioxide (pCO_2) in sea water has already reduced mean surface seawater pH by 0.1, thus lowering carbonate ion concentrations by 30 μmol kg^{-1}, and the saturation state of sea water for calcium carbonate minerals (Ω) by ∼15%, although the magnitude of these effects varies regionally and with latitude[1,5,10,11].

The declining pH, termed 'ocean acidification', is predicted to have profound implications for marine ecosystems because carbonate ions are an essential substrate for biotic calcification. Coral reefs are of particular concern because their many tens of thousands of species ultimately depend on the structural complexity derived from the corals' carbonate skeletons[5,6]. However, specific knowledge about the capacity of reef ecosystems to acclimatize and/or adapt to long-term exposure to lowered pH (increased pCO_2 and reduced Ω) remains inadequate. Much of our understanding stems from short-term laboratory perturbation experiments of individual organisms or from deterministic models. Perturbation experiments report variable and sometimes severe responses in many marine plants, invertebrates and vertebrates at lowered pH, such as declining calcification, altered physiologies and some effects on survival[2–4]. Although laboratory experiments are indispensable, most are too brief for full organism acclimatization to occur, and co-limiting factors (for example nutrients, currents and irradiance) are difficult to simulate *ex situ*[12,13]. Experiments also provide little information about processes leading to ecosystem adaptation, such as altered reproduction, competition, food webs and disease susceptibility, or genetic adaptation. There is therefore a great need for empirical data documenting the long-term effects of ocean acidification on marine ecosystems acclimatized to high pCO_2, as found around submarine CO_2 vents. Recently, changes in shallow-water marine rocky shore ecosystems have been investigated at volcanic CO_2 vents in the Mediterranean, documenting major declines in many calcifying and non-calcifying organisms and increases in macroalgae and seagrasses at reduced seawater pH (refs 7,14).

Here we report the effects of natural *in situ* exposure to elevated seawater pCO_2 on tropical coral reef communities, coral growth, recruitment, seagrasses and sedimentary properties. The study is based on field investigations of clear-water coral reefs and seagrass communities around three cool volcanic seeps of ∼99% CO_2 gas, and at three adjacent control sites with similar geomorphology, seawater temperature and salinity, that fringe the D'Entrecastraux Islands, Milne Bay Province, Papua New Guinea (Supplementary Figs S1, S2, Table S1).

Coral communities at 3 m depth were compared between control sites ('low pCO_2': bubble streams >5 m from the transect lines, medians per site 7.97–8.14 pH at total scale, 296–494 ppm pCO_2) and reef sections with moderate seep activity ('high pCO_2': bubble streams <5 m from the transect lines, pH 7.73–8.00, 444–953 ppm pCO_2; Fig. 1a,b, Supplementary Fig. S3, Table S2). The median saturation state of sea water for the calcium carbonate mineral aragonite (Ω_{arag}) was 3.5 at the control sites and 2.9 at the seeps. The zones of most vigorous venting were covered by sand or rocks with individual coral colonies, macroalgae or dense seagrass (Fig. 1c, Supplementary Fig. S4). No reef development was found at a pH less than 7.70 (>1,000 ppm CO_2), and hence the most intensely venting zones were excluded from the reef assessment.

The field surveys showed that at high compared with low pCO_2 sites, hard coral cover was similar (33% versus 31%; Fig. 2a, Supplementary Table S3). However, the cover of massive *Porites*

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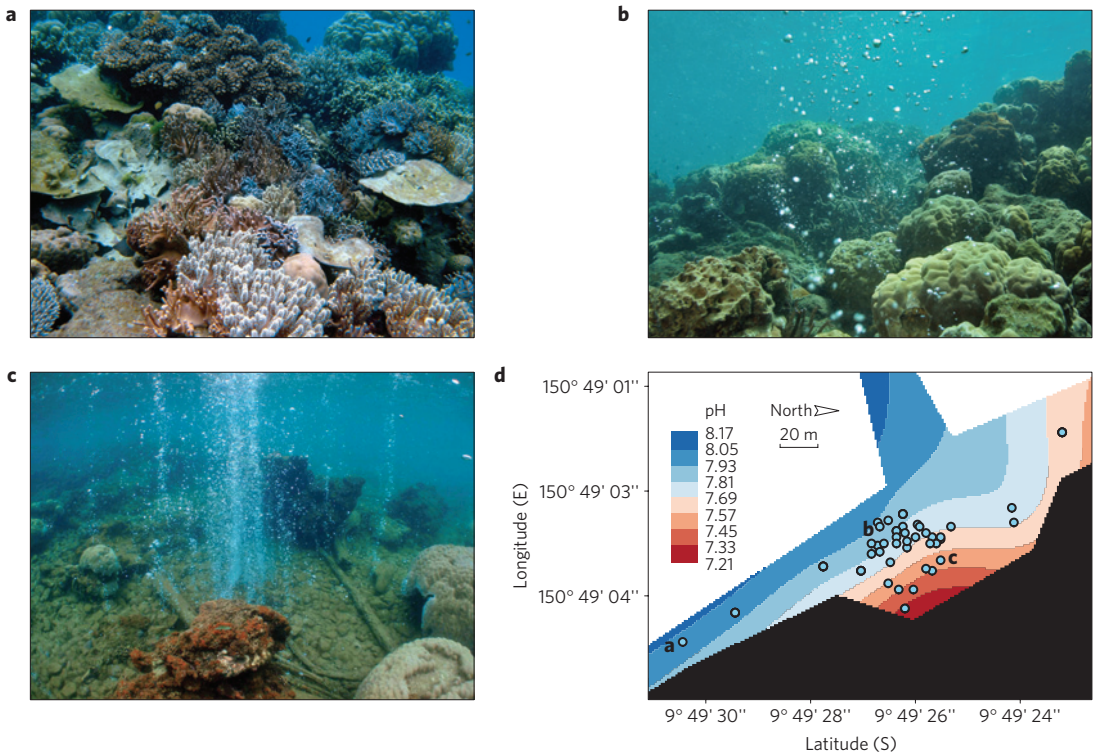

Figure 1 | Volcanic CO_2 seeps of Milne Bay. Seascapes at **a**, control site ('low pCO_2': pH ~ 8.1), **b**, moderate seeps ('high pCO_2': pH 7.8–8.0), and **c**, the most intense vents (pH < 7.7), showing progressive loss of diversity and structural complexity with increasing pCO_2. **d**, Map of the main seep site along the western shore of Upa-Upasina (marked as grey; map: Supplementary Fig. S1). Colour contours indicate seawater pH, and the letters indicate the approximate locations of seascapes as shown in **a**–**c**.

corals doubled, whereas the cover of structurally complex corals (with branching, foliose, and tabulate growth forms, that is, excluding massive, submassive and encrusting growth forms) was reduced three fold. The taxonomic richness of hard corals was reduced by 39%. The cover of fleshy non-calcareous macroalgae doubled and seagrass increased eight fold, whereas the cover of crustose coralline algae (important calcareous substrata for coral settlement) and of other red calcareous algae was reduced seven fold. Cover and richness of soft corals and sponge cover were also significantly reduced. The density and taxonomic richness of hard coral juveniles were reduced 2.8- and 2-fold, respectively, and of soft coral juveniles 18- and 12-fold, at the high pCO_2 sites (Fig. 2b). Even juvenile densities of massive *Porites* declined >fourfold at high pCO_2, despite the high representation of this taxon in the adult community.

The pH for each 10-m section along the study transects at the largest seep site (Upa-Upasina) was spatially predicted from the observed pH data (Supplementary Fig. S3). As seawater pH declined from 8.1 to 7.8, reef communities gradually changed, without a clear threshold (Fig. 3, Supplementary Table S4). In particular, hard coral richness, coral juveniles, and crustose coralline algae progressively declined with declining pH.

Differences in rates of calcification and tissue thickness in massive *Porites* between the high and low pCO_2 sites were small (Fig. 2c, Supplementary Table S3). However, massive *Porites* colonies were paler at high pCO_2, and had almost twice the density of externally visible macrobioeroders in their living surfaces compared to low pCO_2 sites. Similarly, *in situ* growth measurements found small differences in linear extension in the ubiquitous coral *Pocillopora damicornis*. Clades of endosymbiotic dinoflagellate algae did not change in response to high pCO_2 in *P. damicornis* (90% with clade D1, 10% with C1 at both seeps and controls) and *Acropora millepora* (100% with clade C3).

At both the high and low pCO_2 sites in Milne Bay, mean calcification rates of massive *Porites* over the past 12 years were 30% lower than expected given their latitude[15] (Fig. 4). This finding is in agreement with an increasing body of data that show that rates of calcification in massive *Porites*, *P. damicornis* and other corals have declined by 14–30% over the past ~2 decades in large geographic regions around the world, with the two global factors, temperature stress and/or ocean acidification, considered the most likely cause(s)[16,17]. Milne Bay summer maximum sea surface temperatures have exceeded the long-term averages in 9 of these last 12 years[18]. Severe coral bleaching occurred in the region in 1996, followed by minor bleaching in 1998 and 2000–2001 (Supplementary Information). The similar and low calcification rates at the high and low pCO_2 sites suggest that calcification in massive *Porites* is relatively insensitive to a reduction to pH 7.8, and that another factor (possibly temperature stress) has had a stronger effect on calcification. Nevertheless, even massive *Porites* were infrequent near the most intense vents where seawater pH was <7.7, in agreement with experiments showing a 55–75% reduction in *Porites* calcification at pH 7.49 and 7.19 compared to that at ambient pH (ref. 19).

Seagrass communities at the intense seeps (>500 ppm pCO_2) had three to four times higher shoot densities and below-ground biomass compared with those at the control site, but reduced diversity (Fig. 2d). On seagrass blades, calcareous epiphyte cover and densities of the large foraminifera *Marginopora vertebralis* were both nearly zero near the seeps. The increases in seagrass and macroalgal cover and reductions in epiphytes and carbonate organisms are similar to the findings reported from volcanic CO_2 vents in the Mediterranean[7].

Surface sediments at high pCO_2 sites were almost free of inorganic carbon, calcareous biota and their remains (foraminifera, small gastropods and calcareous spicules; Fig. 2e), whereas

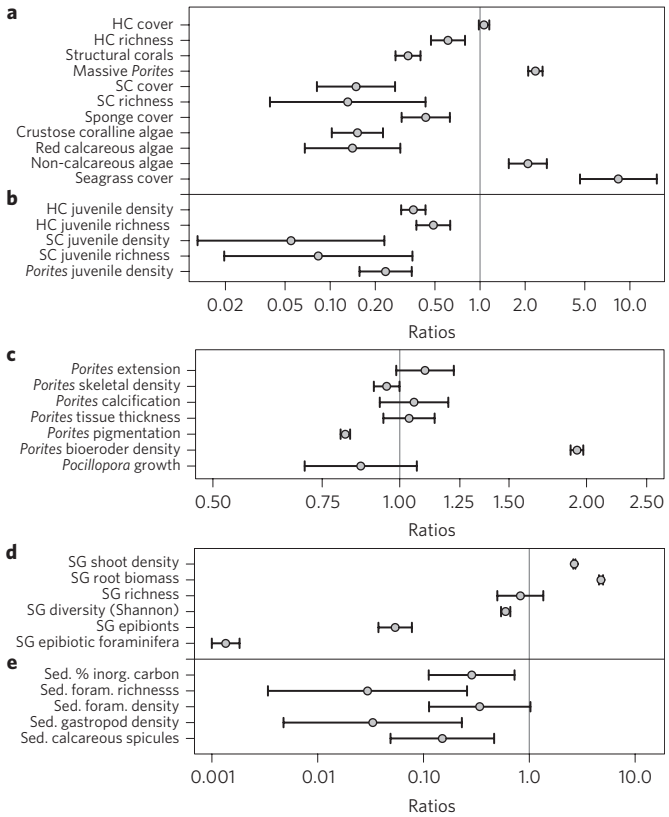

Figure 2 | Response ratios (high pCO_2/low pCO_2, averaged across the three reefs), summarizing the observed biotic changes. Differences are significant at the 5% level if the error bars (upper and lower 2 SE) do not include the value 1.0. The panels include **a**, reef communities including hard and soft corals (HC, SC); **b**, juvenile corals; **c**, skeletal extension, density and calcification, tissue thickness, colony pigmentation and densities of externally visible macrobioeroders in massive *Porites*, and linear extension in *Pocillopora damicornis*; **d**, seagrass (SG) shoot density, below-ground biomass, diversity, epibiont cover, densities of foraminifera; **e**, sediment properties and associated calcifying biota. Foram. is Foraminera, sed. is sedimentary and inorg. is inorganic.

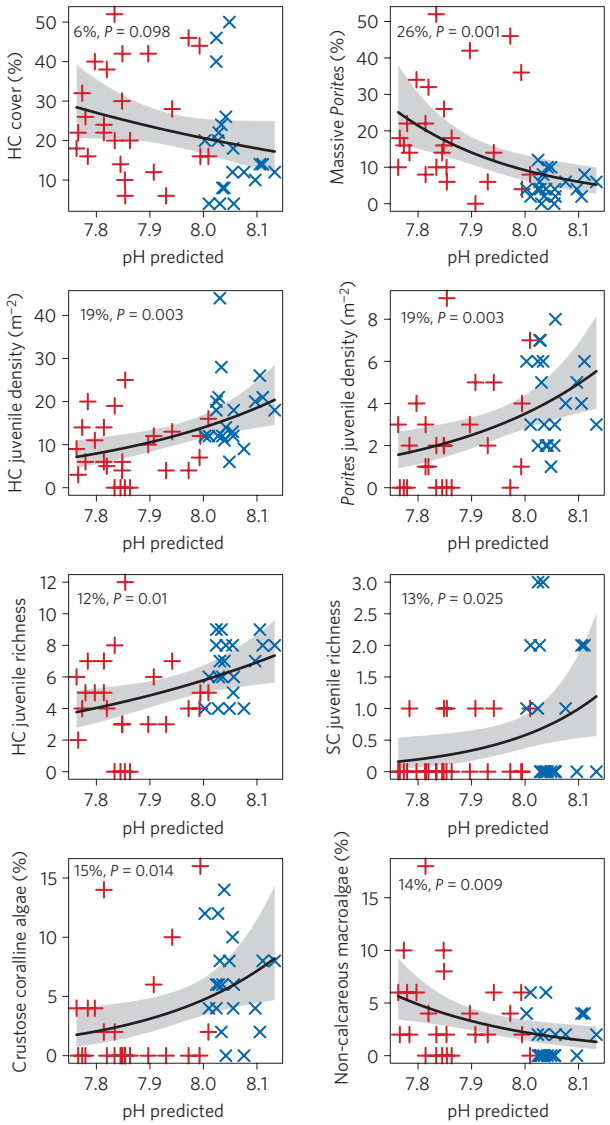

Figure 3 | Progressive changes in reef biota along a pH gradient at Upa-Upasina Reef. Red and blue symbols indicate high and low pCO_2 transect sections respectively, and mean pH was predicted from seawater measurements ($N = 74$; Supplementary Fig. S3A and B). The black lines indicate the log-linear fits and the grey bands indicate upper and lower 2 SE. Also presented are the percentage variance explained by pH, and the significance of the relationships. Abbreviations as in Fig. 2.

organic carbon, nitrogen and siliceous spicules did not change along the pH gradient. Indeed, across the high pCO_2 sites, total seawater alkalinity was elevated by $\sim$50 μEquiv kg^{-1} sea water (Supplementary Table S2), suggesting continued net carbonate dissolution. The more sparsely seeping Esa'Ala high pCO_2 site sediments still contained $\sim$5% inorganic carbon (controls: 6–10%), however many foraminifera tests were corroded or pitted.

The implications of the observed ecological changes for the future of coral reefs are severe. The decline in structurally complex framework-forming corals at lowered pH is likely to reduce habitat availability and quality for juvenile fish and many invertebrates[20]. The low coral juvenile densities (including those of *Porites*) probably slows coral recovery after disturbance, suggesting reduced community resilience. The loss of crustose coralline algae that serve as settlement substratum for coral larvae probably impedes larval recruitment, and the doubling of non-calcareous macroalgae reduces the available space for larvae to settle. Susceptibility to storm breakage would also increase, if internal macrobioeroder densities in massive *Porites* are indicative of borer densities in other coral taxa and reef substrata. Indeed, high bioerosion rates have been reported from reefs where deepwater upwelling reduces Ω_{arag} (ref. 21). However, the causal mechanisms and implications of these and many other of the observed changes, such as increased macroalgal cover and bioeroder densities, and declines in sponges, soft corals and numerous other taxa at lowered pH remain poorly understood.

Natural limitations exist in using the Milne Bay CO_2 seeps as proxies to assess the future of coral reefs. The seeps are surrounded by areas with ambient pH, supplying larvae of sensitive taxa for recolonization, and hence partly offsetting the negative effects of ocean acidification on recruitment. As a result of wave mixing, pCO_2 approaches background values during windy periods, providing respite from low pH, especially during the trade-wind seasons. The Milne Bay seeps are located within the coral triangle at 9° latitude, where conditions for reef development are ideal; reefs at higher latitudes with low Ω_{arag} may be more susceptible to ocean acidification. Reefs around the seeps are also under relatively low anthropogenic pressures (Supplementary Information), and it is likely that ocean acidification may affect reefs more severely if they are already stressed from terrestrial runoff or overfishing.

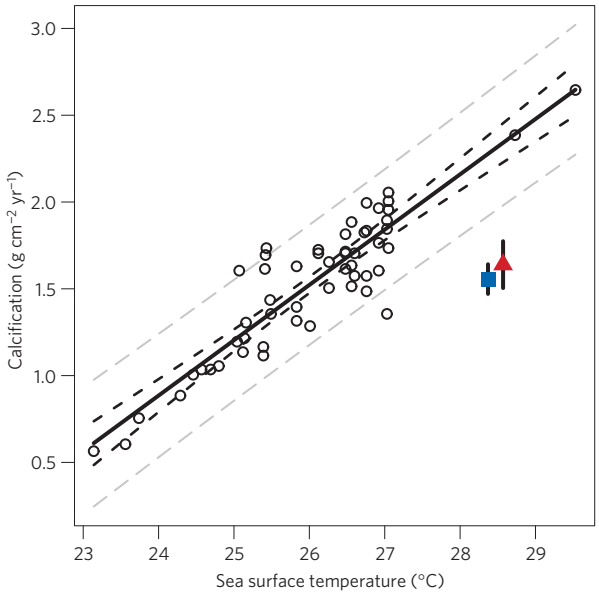

Figure 4 | Mean rates of calcification of massive *Porites* at the Milne Bay seep sites and other Indo-Pacific regions as a function of mean annual sea surface temperature. Circles represent colonies from many Indo-Pacific regions (averaged over 1961–1990; $N = 10$–15 colonies per point; from ref. 15). Solid line: linear regression fit, black and grey dashed lines: upper and lower 95% confidence and prediction intervals, respectively. Red triangle and blue square: calcification of massive *Porites* at high- and low-pCO_2 sites, respectively ($N = 17$ and 12 colonies; vertical bars: upper and lower SE).

Bearing in mind these caveats, our data nevertheless suggest that tropical coral reefs with high coral cover can still exist at seawater pH of 7.8 (750 ppm pCO_2, 150 μmol kg^{-1} carbonate ions, or Ω_{arag} 2.5), albeit with severe losses in biodiversity, structural complexity and resilience. As pH declines from 8.1 to 7.8 units, the loss of the stenotopic fast-growing structurally complex corals progressively shifts reef communities to those dominated by slow-growing, long-lived and structurally simple eurytopic massive *Porites* (Fig. 1a,b). As a result of this shift in species composition, coral cover seems to be unaltered during the transition from 8.1 to ~7.8 pH units. Reef development ceases at 7.7 pH units (980 ppm pCO_2, 125 μmol kg^{-1} carbonate ions, 2.0Ω_{arag}), suggesting these values are terminal thresholds for any form of coral reef development. This threshold is higher than those previously derived from global spatial correlations between aragonite saturation state and reef development[5], possibly because the high latitude reefs and upwelling sites where low aragonite saturation states are naturally found are also exposed to very low or fluctuating temperatures, which is not the case at the Milne Bay seep sites. The threshold is also higher than those derived from deterministic model predictions, possibly because these models assess pH changes and projected increases in temperature stress simultaneously[6] (the seeps are not yet subjected to the projected warming of >2 °C).

The rate of atmospheric CO_2 increase continues to accelerate, with emission scenarios predicting CO_2 concentrations of 540–970 ppm and a decline in seawater pH by 0.14–0.35 units globally (to 7.9–7.7 units, $\Omega_{arag} = 3.0$–2.1) for 2100 (refs 8,22). The range of exposures of the seep sites are therefore comparable to end-of-century pCO_2 projections (however, without the additional stress due to the predicted warming). Our study demonstrates that many ecological properties in coral reefs will gradually change as pH declines to 7.8, and that it would be catastrophic for coral reefs if seawater pH dropped below 7.8 (at 750 ppm pCO_2). We have shown here that large differences in sensitivity between organisms to declining pH result in complex changes in tropical ecosystems, with a few taxa and processes winning, but many more losing prominence. Temperature stress leading to reduced coral calcification (for example in massive *Porites*) has the potential to further accelerate and exacerbate the losses. Our data add to the mounting body of evidence that shows a rapid transition to a low CO_2 emissions future is necessary to minimize the risk of profound losses of coral reef ecosystem functions and services, not only due to climate change, but also due to ocean acidification.

Methods

Chemical analyses. Volcanic gas samples were collected by pooling gas from 10 separate bubble streams in replicate 250 ml glass bottles, and analysed with a micro gas chromatograph (Hewlett Packard M200; Supplementary Table S1). A small boat deployable pCO_2 monitoring system (showerhead equilibrator, LiCOR 820 Infrared Gas Analyser linked to a GPS, and submersible pump) was used to measure $pCO_2 \sim 1$ m above the benthos. Water samples were taken with a Niskin bottle or by divers. One aliquot was immediately analysed for temperature and salinity with a YSI Model 30 Portable Conductivity, Salinity and Temperature Meter. Another aliquot was analysed for pH (within 1 h) using a Mettler Toledo pH probe and meter, and converted to the total pH scale[23]. Two more aliquots were fixed with mercuric chloride and stored in 125 ml PET bottles for later determination of total alkalinity ('open-cell' Gran titration[23]) and dissolved inorganic carbon (UIC Coulometer). Other seawater parameters (Ω_{arag}, pCO_2) were calculated from pH, total alkalinity, salinity and temperature using CO2SYS (ref. 24). Salinity was measured with a Guildline 8410A Portable Salinometer. Seawater elemental composition was analysed with an inductively coupled plasma-optical emission spectrometer (ICP-OES) (Varian).

Biotic responses. Fifty-metre-long transects were laid shore-parallel at 3 m depth (5 and 4 transects at the seep and control sites of Upa-Upasina, respectively, 2 each at the seep and control sites of Esa'Ala and Dobu). Photographs were taken every metre along the transects for later analysis of benthic cover and reef community composition[25], and all scleractinian and octocoral juveniles (<5 cm diameter) were recorded *in situ* within a 0.30 m wide belt. Proximity to seeps (<5 m or >5 m) was used to classify each 10-m transect section as high or low pCO_2.

For retrospective analyses of growth rates in massive *Porites*, short cores (~25 cm long, 3.5 cm diameter) were extracted from the upper surfaces of >0.5 m tall colonies at 3 m depth ($N = 29$; 4–8 cores from each site). Cores were sliced, X-rayed to identify annual density bands, and skeletal density was measured with an americium-241 gamma densitometer[15]. The rate of calcification was defined as the product of annual linear extension (growth between adjacent density minima) and skeletal density, and averaged over the past 12 years for each core (the period common to all but one of the cores). Tissue thickness was determined along the core cross-sections. Macrobioeroder densities (counts of all externally visible orifices), and colony surface pigmentation (colour chart readings[26]) were investigated *in situ* on 20–29 massive *Porites* colonies per site.

In-situ short-term skeletal growth rates of the coral *Pocillopora damicornis* were determined with an optical micrometer (Keyence 7,000 LED/CCD). *P. damicornis* was chosen for this study because, unlike in many other structurally complex corals, sufficient replicates were found even at the high pCO_2 sites. One 40–50 mm branch was collected from each of 15 colonies at the high and low pCO_2 sites of Upa-Upasina (3 m depth). These were glued to base plates, and their height in relation to a reference rod determined before and after a 6-day deployment at the collection sites.

Denaturing gradient gel electrophoresis (DGGE) fingerprinting of the second ribosomal internally transcribed spacer (ITS2), in combination with sequencing[27], was used to identify the endosymbiotic algae associating with *A. millepora* and *P. damicornis* corals from high and low pCO_2 sites at both Dobu and Upa-Upasina (15 replicate colonies per site and species). ITS2 products were separated using 8% poly-acrylamide gels with a 35–65% denaturant gradient (formamide and urea) in an INGENYphorU DGGE unit for 15 h at 75 V. A representative of each band was cut, re-amplified, sequenced (Macrogen Ltd, Korea), and compared with sequences in the public library GenBank (http://www.ncbi.nlm.nih.gov).

Seagrass shoot density and species composition (dominated by *Cymodocea rotunda* and *Cymodocera serrata*) were quantified in fifteen 400 cm^2 quadrats at <1 m depth at the high and low pCO_2 sites of Esa'Ala. Below-ground biomass was harvested, dried at 60 °C and weighed. Calcareous epibiont cover and foraminifera densities (*Marginopora vertebralis*) on seagrass blades were analysed using photography and *in situ* measurements at the high and low pCO_2 sites of Upa-Upasina and Esa'Ala.

Sediment geochemistry and foraminiferal assemblages in the upper 1 cm sediment layer were assessed along the benthic transects and seagrass sites (20 samples in total). Sediments were wet-sieved (63 μm mesh), dried, weighed, sorted (200 foraminifera per sample), and the abundances of siliceous, calcareous and echinoid spicules, *Halimeda* segments and small gastropods were estimated. Total carbon was analysed in dried and ground sediment samples (LECO Truspec CN Analyzer), and organic carbon and nitrogen were analysed after dissolving

inorganic carbon with 1 M HCl (Shimadzu TOC-V Analyzer, calibrated with the certified reference MESS-1, and two in-house standards).

Statistical methods. Generalized additive models[28] were used to predict pH values from the field observations to each 10-m section of the transects (see below) and to spatial grids of the three reefs for the purposes of display. The degree of smoothness of the spatial smoothers was selected by cross-validation. Despite the patchiness in seawater chemistry, the spatial models explained 44%, 74% and 59% of deviance in the pH data of Upa-Upasina, Dobu and Esa'Ala, respectively (Supplementary Fig. S4). Ratios of observed variables for low to high pCO_2 sites (Fig. 2) were estimated using generalized linear models (GLMs). The models used a log link function to constrain estimated ratios to be non-negative, and their variance was taken to be proportional to the mean[29]. The models also included the effects of reefs, and the reported ratios (Fig. 2, Supplementary Table S3) represent weighted averages across the three reefs. GLMs were also used to assess changes in biota along the pH gradient at Upa-Upasina (Fig. 3, Supplementary Table S4). All statistical analyses used the software R (ref. 30).

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Author contributions

All authors were involved with either fieldwork or data analyses. K.E.F. initiated and designed the study and wrote the manuscript, with contributions from all others. C.L. and R.O. analysed the seawater chemistry, C.H., S.N., K.E.F. and J.M.L. collected and analysed the *Porites* data, C.L. the *in situ* coral growth data, K.E.F. and S.N. the reef community data, S.U. the sediments and foraminifera, N.M. and S.U. the seagrass and epibiont data, and G.D. and K.E.F. conducted the statistical analyses.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permissions information is available online at http://www.nature.com/reprints. Correspondence and requests for materials should be addressed to K.E.F.