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All methods, additional figures, and source data are available in the supplementary materials. K.W.M., T.P.G., and M.D.M. conceived the project. K.W.M. prepared samples, performed bulk and compound-specific  $\delta^{13}\text{C}$  analyses, and wrote the manuscript.

O.A.S. and T.L. assisted in data analysis and commented on the manuscript. T.P.G. and M.D.M. supervised this project, discussed the results, and commented on the manuscript. We thank M. Hanson, S. Fauqué, and J. Liu for assistance in the laboratory. This work would not have been possible without the captain and crew of the research vessel *Ka'imikai-o-Kanaloa* and the pilots and engineers of the Hawaii Undersea Research Laboratory's Pisces IV and V submersibles. We also thank three anonymous reviewers for valuable feedback on the manuscript. Funding for sample collection was provided by the National Oceanic and Atmospheric Administration's National Undersea Research Program and the National Geographic Society (grant 7717-04). A portion of this work was performed under the auspices of the U.S. Department of Energy (grant DE-AC52-07NA27344). The

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## SUPPLEMENTARY MATERIALS

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 Tables S1 and S2  
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## MARINE CALCIFERS

# Multidecadal increase in North Atlantic coccolithophores and the potential role of rising $\text{CO}_2$

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As anthropogenic carbon dioxide ( $\text{CO}_2$ ) emissions acidify the oceans, calcifiers generally are expected to be negatively affected. However, using data from the Continuous Plankton Recorder, we show that coccolithophore occurrence in the North Atlantic increased from ~2 to more than 20% from 1965 through 2010. We used random forest models to examine more than 20 possible environmental drivers of this change, finding that  $\text{CO}_2$  and the Atlantic Multidecadal Oscillation were the best predictors, leading us to hypothesize that higher  $\text{CO}_2$  levels might be encouraging growth. A compilation of 41 independent laboratory studies supports our hypothesis. Our study shows a long-term basin-scale increase in coccolithophores and suggests that increasing  $\text{CO}_2$  and temperature have accelerated the growth of a phytoplankton group that is important for carbon cycling.

**M**arine organisms that produce external features made of calcium carbonate are susceptible to harmful consequences from ocean acidification (1). Coccolithophores, the main calcifying phytoplankton, are unicellular algae surrounded by calcite plates called coccoliths, whose photosynthesis is strongly carbon-limited (2). Coccoliths are a major source of oceanic particulate inorganic carbon (PIC) and serve as ballast for sinking aggregates (3), thus accelerating carbon export (4). Given increasing partial pressures of atmospheric  $\text{CO}_2$  ( $p\text{CO}_2$ ), global warming, and ocean acidification, it is expected that coccolithophores will be affected, producing concomitant effects on ocean carbon fluxes, dimethyl sulfide fluxes (5), carbonate geochemistry (6), and phytoplankton community structure (6). Current evidence regarding how increased  $p\text{CO}_2$

will affect coccolithophores is contradictory (7–10). Most laboratory manipulations study how coccolithophores respond to the increased  $p\text{CO}_2$  levels predicted for the end of the century rather than to the  $\text{CO}_2$  changes observed in the past five decades.

Here, we report changes in the occurrence of coccolithophores in the North Atlantic during the past 45 years and use random forest (RF) statistical models to evaluate the importance of various environmental drivers for these changes.

The in situ Continuous Plankton Recorder (CPR) surveys were developed to sample plankton in the North Atlantic using ships of opportunity. The surveys have followed the same methodology since 1946 (11). Sample preservation methods (using Borax-buffered formalin) and analysis have remained unchanged since 1958 (12), producing a unique, consistent, multidecadal data set. Although the CPR filtering system was designed to sample larger microplankton, coccolithophores are trapped, particularly in the intersection of the silk fibers (12). It is not possible to accurately quantify organisms that are smaller than the mesh size, but we can use the data set to estimate the probability of coccolithophore occurrence. Although our sampling underestimates natural abundances, this probability is a proxy for changes in coccolithophore abundance (fig. S1).

We calculated the annual probability of coccolithophore occurrence as the fraction of samples per year containing coccolithophores. The CPR data show an increase in occurrence of coccolithophores across the North Atlantic from ~2% of samples in the 1960s to more than 20% of samples with coccolithophores in the 2000s (Fig. 1, A to F, and fig. S2). Regional abundances of coccolithophores in the 2000s are at least 10 times higher than those observed at the beginning of the data record. Our observations are supported by a shift in the opal:carbonate ratio in sediment traps in the Atlantic from the 1990s (13), satellite evidence of global poleward expansion of *Emiliania huxleyi* (14), and recurring blooms in areas where coccolithophores were previously absent or sparse (14–17).

To evaluate possible top-down and bottom-up drivers for the increase in coccolithophore occurrence in the North Atlantic, we investigated factors that could affect coccolithophore growth rates and biogeography. Temperature, nutrient availability, light levels, competition, and predation are critical on a local scale. In turn, these may be affected by large-scale processes such as climate modes, global warming, and increases in  $\text{CO}_2$ . The CPR sampling survey is irregular in time and space, making classic time series analysis inappropriate for this data set. Additionally, the effects of different environmental forcings on phytoplankton groups are nonlinear and interdependent. After evaluating a suite of statistical methods (see the supplementary materials), we selected RF models (18), an increasingly popular method in ecology that characterizes structure in high dimensional data while making no distributional assumptions about the response variable or predictors. RF has the advantage of allowing for nonlinearities, geographically and temporally discontinuous data, and the ability to model complex interactions among predictor variables without overfitting the data.

Our RF model predicted the probability of coccolithophore occurrence, defined as the percentage of samples containing coccolithophores in a  $1^\circ$ -by- $1^\circ$  area each month, as a function of more than 20 biological and physical predictors. Because the CPR data set is already complex and discontinuous, we only used in situ measurements of biological and physical parameters without interpolating data. The complete data set included 81,340 observations from 1965 to 2010. The importance of each variable in predicting coccolithophore

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occurrence is ranked in a variable importance plot. Importance is measured as the percentage increase of mean squared error (MSE) in the prediction due to that variable. Partial dependence plots graphically represent the marginal effect of each variable on the response variable. Here, we discuss the top predictors and how these could have driven the observed increase in coccolithophore occurrence.

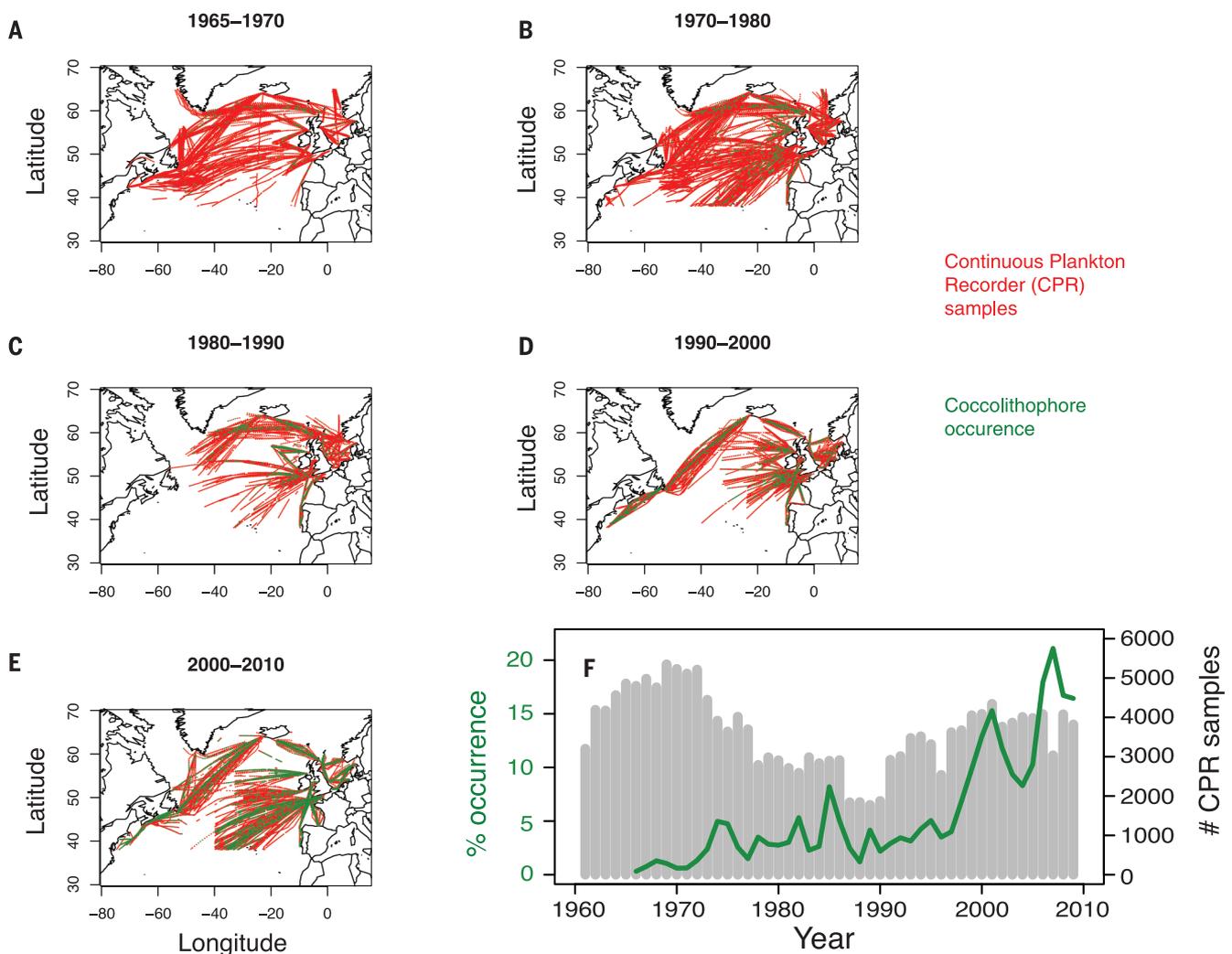
The evaluation of CO<sub>2</sub> as a driver for observed increases in coccolithophore occurrence required special attention. Although *p*CO<sub>2</sub> and CPR data were not collected simultaneously, there is information about spatial and long-term CO<sub>2</sub> variability. We created three random forest models, each with a different predictor for *p*CO<sub>2</sub>: (i) global *p*CO<sub>2</sub>, estimated from Mauna Loa, which varies only in time (“Global\_*p*CO<sub>2</sub>” variable in the RF\_GLOBAL model); (ii) climatological Δ*p*CO<sub>2</sub>, from Takahashi *et al.* (19), which has no interannual variability (“delta\_*p*CO<sub>2</sub>” variable in the RF\_CLIM model); and (iii) local *p*CO<sub>2</sub>, estimated as the sum of the

Mauna Loa and Takahashi data set varying in time and space (“Local\_*p*CO<sub>2</sub>” variable in the RF\_LOCAL model). Local *p*CO<sub>2</sub> in the North Atlantic can be lower than the global atmospheric *p*CO<sub>2</sub> by 100 parts per million (ppm) in certain months (fig. S3).

Local and global *p*CO<sub>2</sub> were the best predictors of coccolithophore occurrence in our RF models (Fig. 2, A and B). In the RF\_GLOBAL analysis, the partial dependence plot shows low coccolithophore occurrence (3 to 5%) at *p*CO<sub>2</sub> ranges between 320 and 360 ppm. This corresponds to atmospheric CO<sub>2</sub> observed at Mauna Loa from 1960 to ~1996. The increase in coccolithophore probability accelerated at *p*CO<sub>2</sub> > 370 ppm (~1997), reaching 22% at 400 ppm. In the RF\_LOCAL model (Fig. 2, B and E, and fig. S4), the partial dependence plot shows a threefold range, with the largest coccolithophore probabilities corresponding to the highest CO<sub>2</sub> values. Maximum probabilities of finding coccolithophores coincided at global and local CO<sub>2</sub> levels above 360 ppm

(Fig. 2, D and E). As discussed below, such dependence falls within the envelope of laboratory responses of coccolithophore growth rates to increased CO<sub>2</sub>.

Within RF\_CLIM, the climatological “delta\_*p*CO<sub>2</sub>” variable is not a strong predictor (Fig. 2, C and F). Instead, the Atlantic Multidecadal Oscillation (AMO) becomes the top predictor in this model, and other climate modes [Arctic Oscillation (AO) and Multivariate ENSO Index (MEI)] rise in their ranking relative to RF\_LOCAL and RF\_GLOBAL, reflecting the importance of interannual variability. Recent studies have linked the AMO with phytoplankton (20) and coccolithophore variability (15). The AMO index tracks temperature anomalies in the North Atlantic, and its positive trend in recent decades could mask global warming or enhance CO<sub>2</sub> effects (Fig. 3). AMO ranked 13th in the RF\_GLOBAL model, second in RF\_LOCAL, and first in the RF\_CLIM analyses (Fig. 2, A to C, respectively). We propose two explanations: Either AMO has a true effect on coccolithophore



**Fig. 1.** Distribution of CPR samples (red) and coccolithophore observations (green) per decade. (A) 1960s, (B) 1970s, (C) 1980s, (D) 1990s, (E) 2000s, and (F) comparison of annual sampling effort (total number of samples per year in the North Atlantic) versus average probability of coccolithophore occurrence in raw data (sum of samples with coccolithophore records per year/total number of samples per year × 100). Each sample corresponds to observations found in 10 cm of CPR silk (or ~3 m<sup>3</sup> of water).

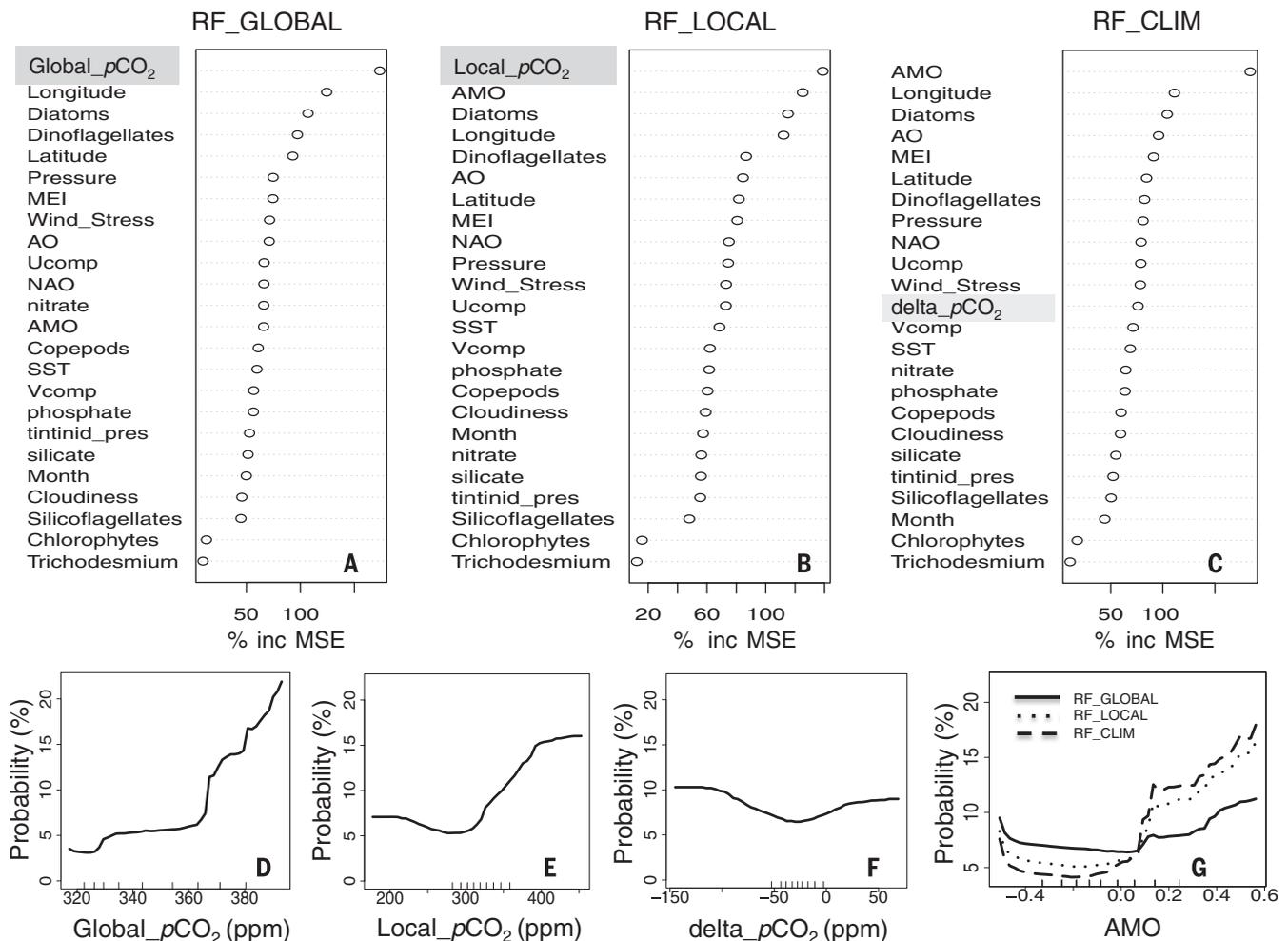
abundance or, in the absence of “global  $\text{CO}_2$ ” or “local  $\text{CO}_2$ ,” AMO is the only other variable with a similar long-term trend in the past two decades (Fig. 3). The highest coccolithophore probabilities are found during the recent positive AMO phases (Fig. 2G). If the coccolithophore increase were due to positive AMO, their occurrence should have been high during previous positive phases—i.e., the 1960s (Fig. 3). Unfortunately, the scarce information before 1965 limits our ability to draw strong conclusions, but, based on the variability explained and the ranking in partial dependence plots (Fig. 2, A to G), we propose that AMO could be an important secondary driver. AMO has been related to changes in the Meridional Overturning Circulation that would alter nutrient supply (27). Positive AMO periods are associated with greater upward transport of nutrients in convective regions but lower upward transport elsewhere. If AMO were the only mechanism responsible for the coccolithophore increase, it would be expected to produce opposite effects in the northwestern

and eastern regions. Instead, all regions show increasing trends (fig. S2).

We hypothesize that synergistic effects due to  $\text{CO}_2$ , AMO, and global warming differentially accelerated coccolithophore growth rates, driving recent increases in their occurrence. Compared to other phytoplankton groups, coccolithophore photosynthesis is severely carbon-limited (2), and sedimentary records show a predominance of coccolithophores during warm interglacial (22) and high  $\text{CO}_2$  periods (23). Many studies agree that coccolithophores respond to an increase in  $\text{CO}_2$  by decreasing PIC and increasing particulate organic carbon (POC), but there is disagreement with respect to the effects on growth rates (see the supplementary materials). We assembled a compendium of published growth rates as a function of  $\text{CO}_2$  (41 laboratory experiments from 16 independent publications) (Fig. 4, fig. S5, and supplementary materials). Results show a quasi-hyperbolic increase in coccolithophore growth rates with  $p\text{CO}_2$ , with scatter partly produced by

differences in experimental treatments: temperature, species, strain, nutrients, and irradiance. Our local  $p\text{CO}_2$  estimates between 1965 and 2010 (blue box in Fig. 4) correspond to the ranges in  $p\text{CO}_2$  where, based on Fig. 4, we would expect changes in coccolithophore growth rates. This compilation reconciles previous contradictory conclusions on the effects of  $\text{CO}_2$  on coccolithophore growth rates (supplementary materials), buttressing our hypothesis that  $\text{CO}_2$  enhances coccolithophore growth. Additional RF analyses of other top-down and bottom-up processes (e.g., grazing, nutrients, and temperature) are included in the supplementary materials.

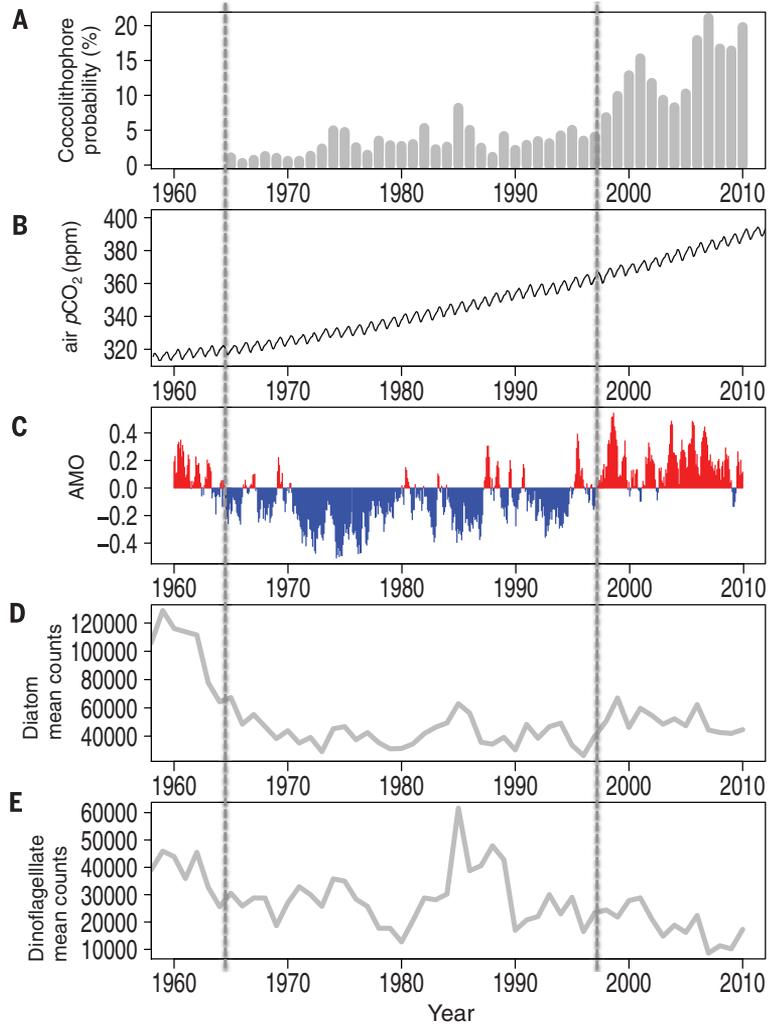
To project future coccolithophore abundances under elevated  $\text{CO}_2$  levels, we need to reassess the baseline. Our results show that today's numbers are an order of magnitude greater than those in the 1960s and will likely continue to increase before growth rates stabilize at  $\sim 500$  ppm. This is critical for understanding changes in the export ratio, biological pump, and alkalinity pump. Our compilation suggests that the changes seen



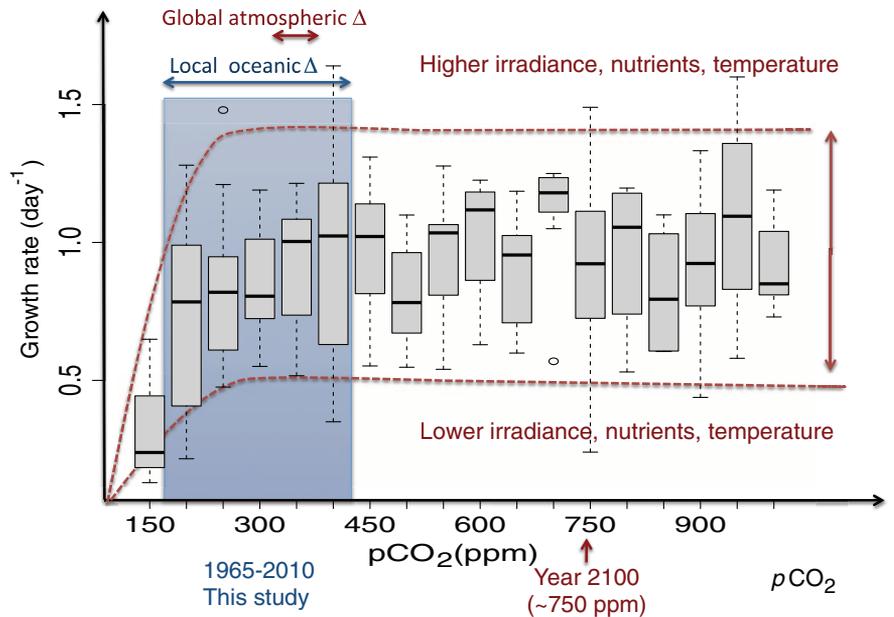
**Fig. 2. RF analyses.** (A to C) Variable importance plots for RF\_GLOBAL, RF\_LOCAL, and RF\_CLIM models, respectively. A large increase in percentage MSE (%inc MSE) means that a variable is a better predictor of coccolithophore occurrence). Boxes highlight the ranking of  $\text{CO}_2$  parameters within each model. This is the marginal effect of the predictor on coccolithophore probability. (D to F) Partial dependence plots for  $\text{CO}_2$  parameters in RF\_GLOBAL, RF\_LOCAL,

and RF\_CLIM models, respectively. (G) Partial dependence plot for AMO, based on the probability of coccolithophore occurrence in each of the RF models. Global  $p\text{CO}_2$ , atmospheric  $p\text{CO}_2$  based on Mauna Loa records;  $\Delta p\text{CO}_2$ , climatological  $\Delta p\text{CO}_2$  (19); local  $p\text{CO}_2$ , estimate of local  $p\text{CO}_2$  based on the sum of spatial and long-term trends. U and Vcomp, zonal and meridional wind components; SST, sea surface temperature; tintinnid\_pres, tintinnid occurrence.

**Fig. 3. Long-term trends.** (A) Annual basin-averaged coccolithophore probability in CPR samples (sum of samples with coccolithophore records per year/total number of samples per year x 100). (B) Global atmospheric CO<sub>2</sub> measured from Mauna Loa. (C) AMO. (D and E) Annual mean basin-averaged diatom and dinoflagellate counts in CPR samples per year. Vertical lines marking years 1965 and 1997 are included for reference.



**Fig. 4. Relationship between CO<sub>2</sub> and coccolithophore growth rates based on 41 experiments from 16 publications and four species (details in the supplementary materials).** Results are binned in 50-ppm intervals, with minimum, quartiles, median, and maximum per interval used to construct box-and-whisker plots. Discontinuous lines represent schematic boundaries of this relationship depending on irradiance, nutrient, and temperature levels. Blue box, range of local oceanic pCO<sub>2</sub> values observed across the North Atlantic during this time period; red arrow, corresponding global atmospheric range.



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in the North Atlantic may represent a global trend. Contrary to the generalized assumption of negative effects of ocean acidification on calcifiers, coccolithophores may be capable of adapting to a high- $\text{CO}_2$  world (24), especially given evidence of highly calcified coccolithophores in areas with seasonally high  $p\text{CO}_2$  or low pH (7, 8). Coccolithophores show outstanding competitive abilities under the stratified, warm, nutrient-depleted conditions projected for the future ocean (6). Nevertheless, with increasing  $p\text{CO}_2$ , we might expect changes in community composition and a decrease in calcification, leading to changes in rain ratio, export efficiency, and trophic effects higher in the marine food web.

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#### SUPPLEMENTARY MATERIALS

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Materials and Methods  
Supplementary Text  
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References (25–47)

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## PALEOCEANOGRAPHY

# Dynamical excitation of the tropical Pacific Ocean and ENSO variability by Little Ice Age cooling

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Tropical Pacific Ocean dynamics during the Medieval Climate Anomaly (MCA) and the Little Ice Age (LIA) are poorly characterized due to a lack of evidence from the eastern equatorial Pacific. We reconstructed sea surface temperature, El Niño–Southern Oscillation (ENSO) activity, and the tropical Pacific zonal gradient for the past millennium from Galápagos ocean sediments. We document a mid-millennium shift (MMS) in ocean-atmosphere circulation around 1500–1650 CE, from a state with dampened ENSO and strong zonal gradient to one with amplified ENSO and weak gradient. The MMS coincided with the deepest LIA cooling and was probably caused by a southward shift of the intertropical convergence zone. The peak of the MCA (900–1150 CE) was a warm period in the eastern Pacific, contradicting the paradigm of a persistent La Niña pattern.

The tropical Pacific Ocean exerts a major influence on global climate through the interannual El Niño–Southern Oscillation (ENSO) (1) and Pacific Decadal Oscillation (PDO) (2). However, its role on centennial to millennial time scales remains unclear. Recent evidence that a cool eastern equatorial Pacific (EEP) played a key role in the global warming slowdown of the past ~15 years (3, 4) emphasizes the need to understand tropical Pacific climate in the recent past. During the last millennium, Northern Hemisphere (NH) climate evolved from a warm Medieval Climate Anomaly (MCA) (~900–1450 CE) into a substantially colder Little Ice Age (LIA) (~1450–1850 CE), followed by modern warming (5–7). In the tropics, the MCA-to-LIA transition exhibited a weakening of the East Asian summer monsoon (8, 9), a southward shift of the Atlantic and Pacific intertropical convergence zones (ITCZs) (10, 11), and sea surface cooling in the western Pacific warm pool (WPWP) (12, 13). Notably absent, however, are contemporaneous records of sea surface temperature (SST) from the ENSO-sensitive and dynamically important cold tongue of the EEP. Without such records, any dynamical connections between basin-scale tropical Pacific processes and NH climate cannot be properly diagnosed.

It has been hypothesized that an “ocean dynamical thermostat” (14) response of the EEP to solar and volcanic forcing induced a cool, La Niña-like mean state during the MCA and a warmer,

El Niño-like state during the LIA (6). This hypothesis has found some support in central Pacific corals (15), North American tree rings documenting medieval megadroughts (16), and multiproxy climate field reconstructions (6). In each of these cases, however, direct confirmation from the EEP has been lacking. Insights into past ENSO variability have also remained elusive and are mostly based on discontinuous corals and remote tree-ring records (15–18). Here we address these data limitations with climate reconstructions from the heart of the EEP cold tongue. We present continuous, multidecadally resolved estimates of local SST, basin-wide zonal SST gradient, and ENSO activity from Galápagos marine sediments over the period ~1000–2009 CE.

Our primary data sets were developed from an ocean multicore (KNR195-5 MC42C) retrieved in 2009 near Española Island in the Galápagos (01°15.18'S, 89°41.13'W, 615 m depth) (Fig. 1). Undisturbed recovery of the sediment-water interface and detection of bomb radiocarbon confirm that the core top is modern (19). Sedimentation rates averaged 13 cm/ky over the past millennium. Detection of a modern 0.3–per mil (‰) carbon isotope ( $\delta^{13}\text{C}$ ) depletion, or Suess effect (fig. S9), further corroborates the presence of a modern core top and core integrity and argues against substantial signal attenuation by bioturbation (19). The core was slabbed continuously in sub-centimeter slices representing ~20- to 80-year periods. We analyzed Mg/Ca ratios of the mixed-layer foraminifera *Globigerinoides ruber* (white) as a proxy for mean SST. We also analyzed  $\delta^{18}\text{O}_\text{c}$  (calcite) of individual *G. ruber* shells (~60 individual *G. ruber* analyses per sample horizon) to quantify population-level  $\delta^{18}\text{O}_\text{c}$  variance related to ENSO activity (20, 21). Benchmark tests comparing modern samples with instrumental data support the use of single-shell  $\delta^{18}\text{O}_\text{c}$  variance ( $\delta^{18}\text{O}_\text{c,V}$ ) as a proxy of the monthly SST variance of the real ocean and further show that large

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## Multidecadal increase in North Atlantic coccolithophores and the potential role of rising CO<sub>2</sub>

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### Passing an acid test

Calcifying marine organisms will generally find it harder to make and maintain their carbonate skeletons as increasing concentrations of atmospheric CO<sub>2</sub> acidify the oceans. Nevertheless, some types of organisms will be damaged more than others, and some may even benefit from higher CO<sub>2</sub> levels. Coccolithophores are a case in point, because their photosynthetic ability is strongly carbon-limited. Rivero-Calle *et al.* show that the abundance of coccolithophores in the North Atlantic has increased by up to 20% or more in the past 50 years (see the Perspective by Vogt). Thus, this major phytoplankton functional group may be able to adapt to a future with higher CO<sub>2</sub> concentrations.

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