

Decline of forereef corals in response to recent warming linked to history of thermal exposure

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Rising ocean temperatures have reduced rates of coral calcification and increased rates of coral mortality, thereby negatively impacting the health of coral reef ecosystems^{1,2}. Nevertheless, the response of corals to thermal stress seems to vary spatially across the reef environment^{3,4}. Here, we show that between 1982 and 2008 in the western Caribbean Sea, skeletal extension within forereef colonies of the reef-building coral *Siderastrea siderea* declined with increasing seawater temperature, whereas extension rates of backreef and nearshore colonies were not impacted. These results suggest that forereef *S. siderea* corals are more vulnerable to ocean warming than their backreef and nearshore counterparts. This may arise from backreef and nearshore coral colonies experiencing greater baseline diurnal and seasonal thermal fluctuations than forereef colonies, which may promote acclimatization and/or adaptation to more recent anthropogenic thermal stress. These findings reveal how corals have responded to recent anthropogenic warming, offer insights into how they are likely to respond to future warming and highlight the importance of understanding cross-reef differences in coral thermal tolerance for managing coral reef ecosystems in an era of rapid regional and global climate change.

The average surface temperature of the Earth has increased by about 0.2 °C per decade since the mid 1970s (ref. 5), with sea surface temperature (SST) rising by as much as 1.0 °C in the tropics and subtropics over the past century⁶. SST across the region where corals reside has increased by 0.3–0.4 °C over the past four decades⁷. The fourth assessment of the Intergovernmental Panel on Climate Change predicts that global SST will continue to increase owing to the rising partial pressures of greenhouse gases in the atmosphere⁸. Corals and their associated ecosystems seem to be particularly vulnerable to such thermal stress¹.

Tropical coral reefs exist near corals' upper thermal limits⁹. Thus, even a small rise in ocean temperature may have important consequence for their health. SSTs of 1–2 °C above the mean monthly summer maximum, even for only a few weeks^{10–12}, have been implicated in coral bleaching—the decrease in coral pigment concentration and/or ejection of the algal symbiont from the coral host. As reef-building zooxanthellate corals receive up to 95% of their energy from photosynthate translocated from their algal symbionts^{13,14}, disruption of this symbiotic relationship impairs key functions within the coral animal, such as light-enhanced calcification, tissue growth and reproduction.

Indeed, historical growth records obtained from coral cores reveal that skeletal extension of *Porites* spp. in the Coral Sea^{15,16},

Porites lutea in the Andaman Sea¹⁷ and *Diploastrea heliophora* in the central Red Sea², is negatively correlated with regional SST. However, these studies also show that the calcification response of corals to ocean warming is highly variable, both taxonomically and geographically. It is this variability in corals' response to warming that has compelled investigations of the ability of corals to acclimatize and/or adapt to recent and predicted future ocean warming³, and whether their unique acclimatization and/or adaptive capacities can be used to improve coral reef management in the face of rapid global climate change¹⁸.

Here, we investigate the relationship between skeletal extension and SST for forereef, backreef and nearshore colonies of the reef-building zooxanthellate scleractinian coral *S. siderea*. Specifically, we compare historical skeletal extension rates reconstructed from annual growth bands within cores obtained from this species with historical (about 30-yr) high-spatial-resolution SST records for the Mesoamerican Barrier Reef System in the western Caribbean Sea. Our objective was to determine whether the relationship between skeletal extension and SST for *S. siderea* colonies from the cooler and more thermally stable forereef environment differed from that of *S. siderea* colonies from the warmer and more thermally variable backreef and nearshore environments.

We investigated the slow-growing massive reef-building coral *S. siderea* because it is an important reef-building species commonly found in all three reef zones of interest: shallow forereef, backreef and nearshore habitats¹⁹. Additionally, the resilience of this species increases the likelihood that sublethal suppression of skeletal growth, rather than complete cessation of calcification and mortality, occurs when this coral is exposed to increased seawater temperatures, thereby leaving a more complete historical record of past environmental change than species more vulnerable to warming.

We acquired daily, globally gridded SST records from the National Oceanic and Atmospheric Administration (NOAA)'s optimum interpolated SST (OI-SST) database (version 2)²⁰, which is available from 1982 to present. The OI-SST records were obtained for the interval 1982–2008 from paired 0.25° latitude/longitude sized grids spanning the reef zones from where the coral cores were extracted along the Mesoamerican Barrier Reef System of southern Belize (Fig. 1; fore-reef: 16° 07' 30" N–88° 07' 30" W and 16° 22' 30" N–87° 52' 30" W; backreef: 16° 07' 30" N–88° 22' 30" W and 16° 22' 30" N–88° 07' 30" W; and nearshore: 16° 07' 30" N–88° 37' 30" W and 16° 22' 30" N–88° 22' 30" W). Paired grids were used to provide more extensive and thus more representative coverage of SSTs within these three reef zones. To verify that OI-SST records matched the

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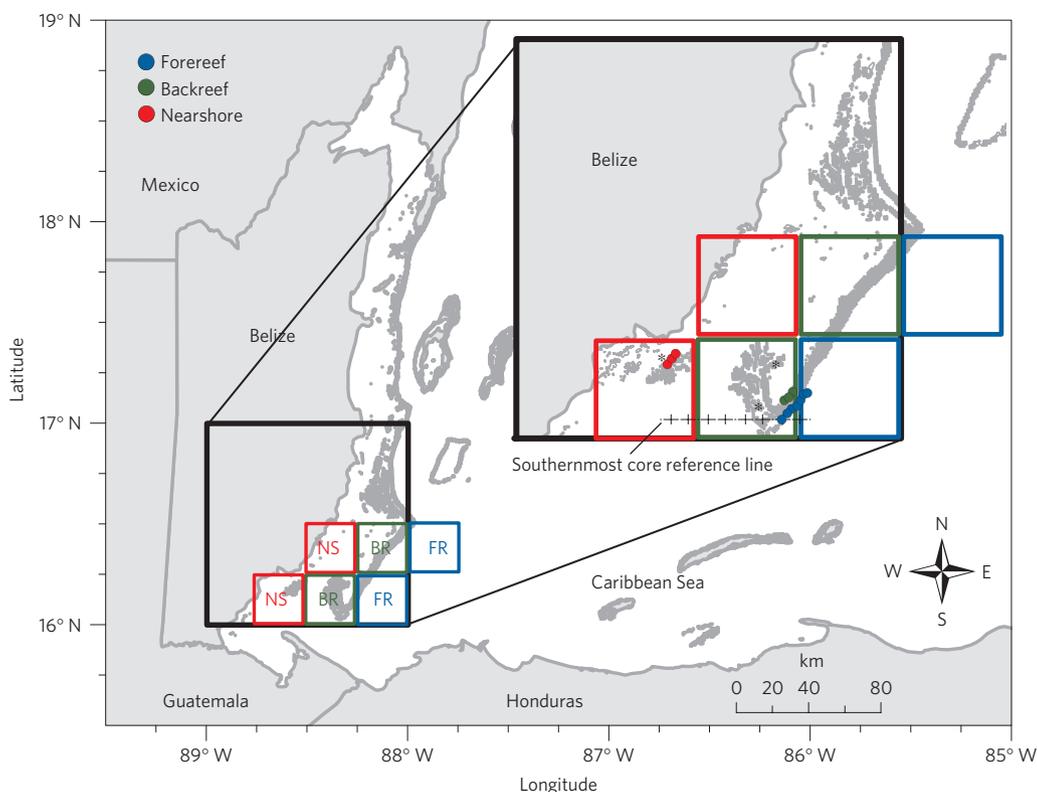


Figure 1 | Locations of core extraction sites, SST grids and *in situ* temperature loggers across reef zones in southern Belize. *S. siderea* core extraction sites within the forereef (blue), backreef (green) and nearshore (red) reef zones. Paired SST grids are for forereef, backreef and nearshore habitats. Cores ordered north to south for the forereef are FR-02, FR-04, FR-05, FR-13, FR-12, FR-11, FR-09; for the backreef are BR-06, BR-07, BR-08; and for the nearshore are NS-14, NS-15, NS-16. *In situ* temperature logger locations (installed June 2002) in offshore (forereef, backreef) and inshore (nearshore) habitats are marked with asterisks.

temperatures to which corals were exposed within each reef zone, we compared OI-SST records with high-temporal-resolution *in situ* instrumental seawater temperature measurements obtained from 2002 to 2008 in the offshore (forereef, backreef) and inshore (nearshore) reef environments²¹. Relative to *in situ* measurements, average monthly OI-SST has a positive bias of less than 0.6 °C during the warmer months of the year and a negative bias of less than 0.8 °C during the cooler months of the year for both inshore and offshore environments (Supplementary Fig. S1). Nevertheless, OI-SST is strongly correlated with *in situ* temperature measurements ($r = 0.982$ for both inshore and offshore reefs) and thus offers a reliable estimate of the temperatures to which the cored corals were exposed in the subsurface, and beneficially spans a longer historical interval (1982–2008) than our *in situ* instrumental record. Although we also explored longer-term SST data sets for comparison with our coral skeletal extension records, the spatial and temporal coarseness of these data resulted in substantially higher biases relative to our *in situ* instrumental record, thereby precluding meaningful comparisons with coral skeletal extension rates across reef zones. A thorough discussion of the comparison of *in situ* and satellite-based methods for assessing temperatures on coral reefs is available in a previous study²¹.

For each of the three reef zones, we calculated average annual summer (August, September, October) SST from NOAA OI-SST records. Because means were measured with varying precision, we used weighted regression, with weights that are reciprocals of the variances of the summer averages, to compare SST trends across reef zones. Since 1982, the average summer SST increased in all three reef zones by 0.32 °C per decade ($P < 0.001$; 95% confidence interval: 0.24 °C, 0.40 °C). These trends were statistically indistinguishable among reef zones ($P = 0.902$; Fig. 2a).

Summer SST spiked in 1998—a year characterized by mass coral bleaching on the Belize Barrier Reef²²—exceeding 30 °C in all three reef zones.

We also compared average summer SSTs across reef zones using a generalized least squares autoregressive model (to account for autocorrelation) of order eight, treating years as blocks and weighting the summer SST means by the reciprocals of their variances. The nearshore reef zone exhibited summer SSTs that were on average 0.097 °C higher than SSTs in the backreef environment (95% confidence interval: 0.065 °C, 0.129 °C), which were in turn 0.067 °C higher than SSTs in the forereef environment (95% confidence interval: 0.033 °C, 0.102 °C; Fig. 2a). Notably, backreef and nearshore reef habitats were frequently exposed to greater daily, monthly and annual variability in seawater temperature than the forereef habitat ($P < 0.001$ in all cases; Supplementary Figs S2–S4). The southern portion of the forereef study site also exhibited greater monthly and annual variability in SST than the northern portion ($P < 0.001$; Supplementary Fig. S5).

In February 2009, we extracted 13 *S. siderea* cores to obtain coral skeletal extension data for comparison with OI-SST records. Seven cores (FR-02, FR-04, FR-05, FR-09, FR-11, FR-12, FR-13) were extracted from the forereef, whereas three cores each were extracted from backreef (BR-06, BR-07, BR-08) and nearshore (NS-14, NS-15, NS-16) reef zones (Fig. 1). Skeletal extension rates were estimated from the thickness of high-density and low-density annual growth couplets using the Coral X-radiography Densitometry System software²³ (Coral XDS v. 3.0; Supplementary Fig. S6). Our previous analysis²⁴ reveals that only forereef *S. siderea* colonies exhibited a statistically significant decline in annual skeletal extension over approximately the past century ($P < 0.001$). The rates

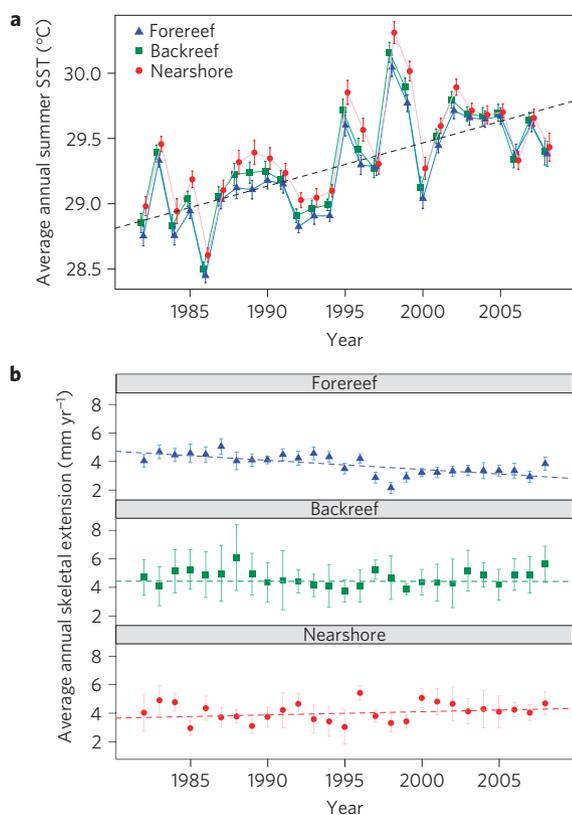


Figure 2 | Average summertime SST and average annual coral skeletal extension. **a**, Summer (August, September, October) SST time series for forereef, backreef and nearshore reef zones obtained from paired grids using OI-SST version 2. A simple linear regression line is shown for reference. **b**, Average annual skeletal extension (\pm standard error) for *S. siderea* corals from the forereef, backreef and nearshore reef zones. Regression lines show skeletal extension trends for each reef zone. Trend lines were estimated using mixed-effects models with random intercepts. Data shown are for the interval 1982–2008.

of change in annual skeletal extension for backreef ($P = 0.098$) and nearshore ($P = 0.231$) colonies over that time frame were not significantly different from zero. Detailed descriptions of coral core extraction procedures, chronology development and analysis are described in a previous study²⁴ and in the Supplementary Methods.

Here, we examine the correlation between average annual summer OI-SST (Fig. 2a) and annual skeletal extension rate of forereef, backreef and nearshore corals (Fig. 2b) over the interval 1982–2008 using a mixed-effects model with random intercepts. Skeletal extension within forereef corals declined ($P < 0.001$) with increasing summer SST over the 1982–2008 interval by $1.714 \pm 0.241 \text{ mm yr}^{-1}$. There was no significant effect of summer SST on skeletal extension for backreef ($P = 0.489$) and nearshore ($P = 0.566$) colonies over this interval (Figs 3 and 4a; Supplementary Tables S1 and S2).

Notably, separate estimation of the skeletal-extension–SST relationship (slope) for each forereef core varied systematically with latitude, such that the slope of the trend for forereef colonies became more negative from south to north, that is, with increasing distance from the Guatemala and Honduras coasts (Fig. 4b). We investigated this pattern by fitting a mixed-effects model with random intercepts, regressing skeletal extension against the two-year running mean of summer SST (level-one model) and using latitude (distance from the southernmost core) as a level-two predictor of the intercepts and slopes. The slope for

the southernmost forereef core was -1.138 (95% confidence interval: $-1.877, -0.398$). For each kilometre northward from this location the slope decreased by 0.296 (95% confidence interval: $-0.541, -0.051$; $P = 0.045$). It is worth noting that core FR-05 was not included in this analysis because the coral from which it was extracted was located in a tidal channel connecting the forereef and backreef environments (Fig. 4b). This north–south trend could not be assessed for the backreef and nearshore colonies as coral cores within these two reef zones were each collected at approximately the same latitude.

We also investigated the relationship between coral skeletal extension and annual accumulated thermal stress in degree-heating months (DHMs; $^{\circ}\text{C}\text{-months}$), which is similar in principal to NOAA's degree-heating weeks (DHWs; $^{\circ}\text{C}\text{-weeks}$): one week of SST that is 1°C greater than the maximum monthly mean SST of the hottest month of the year²⁵. Four DHWs are typically associated with moderate bleaching and eight DHWs predict mass coral bleaching and mortality²⁵. One DHM is equivalent to one month of SST that is 1°C greater than the maximum monthly mean SST of the hottest month of the year for that grid cell (August, September or October for most grid cells in the western Caribbean Sea)²⁶. A mixed-effects model with random intercepts was developed, which regressed skeletal extension against DHM as well as year in order to account for temporal autocorrelation. The model included interactions of year and DHM with reef zone to allow their effects to vary across reef zones. Both interactions were statistically significant at the 95% confidence level. Like the extension-rate–summer-SST analysis, the slope of the extension-rate–thermal-stress relationship was significantly different from zero for forereef colonies ($P = 0.0022$, $-0.249 \pm 0.081 \text{ mm yr}^{-1} \text{ per } ^{\circ}\text{C}\text{-month}$), but not for backreef ($P = 0.3768$, $-0.102 \pm 0.115 \text{ mm yr}^{-1} \text{ per } ^{\circ}\text{C}\text{-month}$) or nearshore colonies ($P = 0.3990$, $-0.090 \pm 1.06 \text{ mm yr}^{-1} \text{ per } ^{\circ}\text{C}\text{-month}$; Supplementary Fig. S7 and Table S3).

The negative correlation between summer SST (and accumulated thermal stress) and skeletal extension rate for forereef corals—but not for backreef and nearshore corals—may exist owing to differences in thermal tolerance owing to differential exposure to natural (that is, non-anthropogenic) long-term thermal stress among the three reef zones. The forereef environment is generally more thermally stable (diurnally and seasonally) than the backreef and nearshore environments. *In situ* instrumental measurements from 2002 to 2008 indicate that inshore environments have greater diurnal and seasonal variability in seawater temperature than off-shore environments (Supplementary Fig. S2 and Table S4). OI-SST records also indicate greater diurnal and seasonal fluctuations in SST for our nearshore and backreef study sites relative to our forereef study sites from 1982 to 2008 (Supplementary Figs S3 and S4 and Table S4). Thus, the increased thermal variability in the nearshore and backreef environments, relative to forereef environments, may have selected for *S. siderea* colonies with increased thermal tolerance in the nearshore and backreef environments. These results suggest that *S. siderea* inhabiting more thermally variable backreef and nearshore environments may be better acclimatized and/or adapted to thermal stress than corals inhabiting the more thermally stable forereef environment.

A similar pattern was observed within the forereef zone, where colonies from the more thermally stable northern portions of the forereef environment (more proximal to the open ocean) exhibited a more negative calcification response to recent seawater warming than colonies from the more thermally variable southern portions of the forereef environment (more distal from the open ocean; Fig. 4b and Supplementary Fig. S5 and Table S4). These observations of the responses of corals to thermal stress across reef zones, as well as within the forereef zone, collectively support the assertion that corals that have

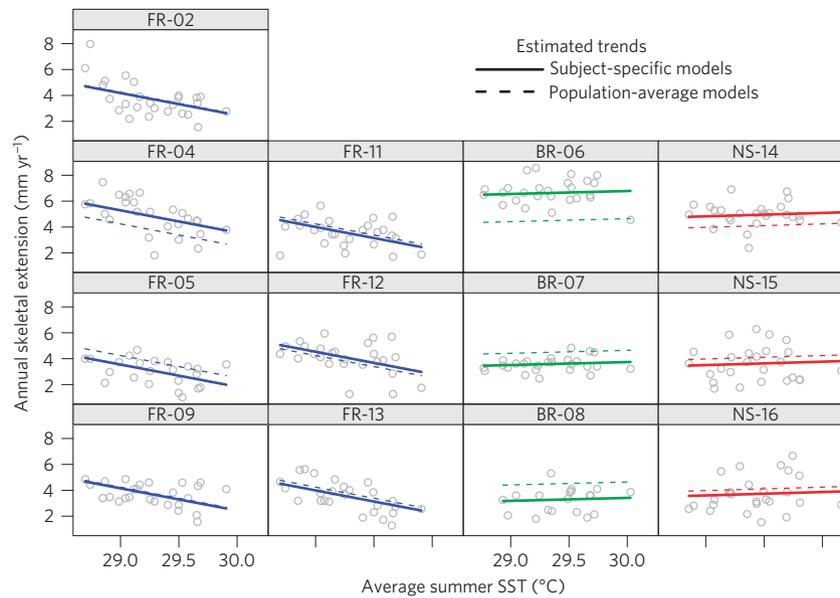


Figure 3 | Relationship between summertime SST and coral skeletal extension across reef zones. Estimated trends of the relationship between coral skeletal extension and summertime SST for individual *S. siderea* corals from foreeef (blue), backreef (green) and nearshore (red) reef environments. Dashed lines represent population-average models, which include estimates of the fixed effects only; solid lines represent subject-specific models, which include estimates of the fixed effects and best linear unbiased predictions of the random effects. The temperatures shown are two-year running averages.

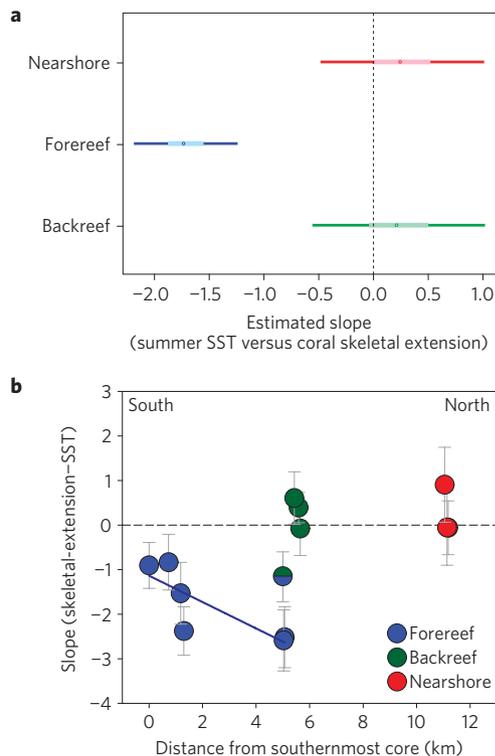


Figure 4 | Slopes of the relationship between summertime SST and coral skeletal extension for the three reef zones. **a**, Regression analysis of two-year running means of summertime SST and annual *S. siderea* coral skeletal extension. Shown are the 95% (light bars) and 50% (dark bars) confidence intervals for foreeef, backreef and nearshore colonies. **b**, Latitudinal (south-to-north) comparisons of the effect of summertime SST on *S. siderea* skeletal extension (shown as slopes) for foreeef, backreef and nearshore environments. The blue-green circle represents core FR-05, obtained from a foreeef coral inhabiting a tidal channel connecting the foreeef and backreef environments. Error bars represent standard error of the slope.

historically been exposed to more stable baseline seawater temperatures may ultimately be more vulnerable to recent and future warming resulting from the anthropogenic emission of greenhouse gases.

Methods

In situ seawater temperature. *In situ* instrumental seawater temperature measurements were acquired for the interval 2002–2008 using Hobo Water Temperature Pro loggers (Onset Computer Corporation, Pocasset Massachusetts) installed at 4–5 m depth in the offshore (foreeef, backreef) and inshore (nearshore) reef environments of southern Belize (Fig. 1). Logger installation methodology is described in the Supplementary Methods and in ref. 21.

SST and annual accumulated thermal stress. SST records for the foreeef, backreef and nearshore reef zones of southern Belize were obtained from NOAA's OI-SST database ($1/4^\circ$; ref. 20). This data set was shown to adequately characterize coastal environments²⁷. Two important thermal parameters calculated from the OI-SST database are the average annual summer (August, September, October) SST and the annual accumulated thermal stress measured in DHMs. Full descriptions of how these and other thermal parameters were calculated from the OI-SST records are described in the Supplementary Methods.

Core extraction and sclerochronology development. Coral cores were extracted at a water depth of 4–5 m using a pneumatic drill outfitted with a 5-cm-diameter diamond-tipped core bit²⁴. Six-millimetre-thick slabs were sectioned vertically from the centre of each coral core with a water-cooled trim saw. Coral slabs were then air dried and X-rayed. Skeletal extension rates were estimated from the thickness of high-density–low-density annual growth couplets using Coral XDS version 3.0 (ref. 23). In the western Caribbean Sea, the coral *S. siderea* deposits lower density skeletal growth bands from December to May and higher density growth bands from June to November²⁸. Core chronologies were established by counting annual growth bands backwards from the 2008 growth band at the top of the core, which corresponds to the last complete year of coral growth before extraction of the core.

Statistical analyses. Statistical analyses were carried out using the nlme package²⁹ of R 2.12.1 (ref. 30). We employed random intercept models with residual correlation structures to model the relationships between coral skeletal extension rates and summer SSTs and between coral skeletal extension rates and accumulated thermal stress (DHMs). This approach distinguishes observational units from sampling units and addresses the temporal autocorrelation structure that is inherently present in core data that are chronologically ordered. A comprehensive description of the statistical methods employed in this study is provided in the Supplementary Methods.

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Author contributions

K.D.C. and J.B.R. designed the experiment. K.D.C., J.B.R., J.M.W. and F.P.L. assembled the input data. J.M.W. carried out the statistical analysis with support from K.D.C. and J.B.R. K.D.C. and J.B.R. wrote the paper in collaboration with J.M.W. and F.P.L. All authors read and provided comments and feedback on the manuscript.

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 www.nature.com/reprints. Correspondence and requests for materials should be addressed to K.D.C.