Global Change Biology

WILEY

Global Change Biology

RESEARCH ARTICLE

Legacy Effects of an Extreme Marine Heatwave on a Stress-Tolerant Coral

Benjamin H. Glass[1] | Hannah E. Aichelman[1] | Carsten G. B. Grupstra[1,2] | Maria Valadez-Ingersoll[1] | Ally Swank[1] | Viviana Guerra[3] | Plinio Gondola[3] | Aden Nagree[1] | James Schipfer[1] | Thomas D. Gilmore[1] | Sarah W. Davies[1]

[1]Department of Biology, Boston University, Boston, Massachusetts, USA | [2]Department of Biological Sciences, Florida Atlantic University, Boca Raton, Florida, USA | [3]Smithsonian Tropical Research Institution, Bocas del Toro, Panama

Correspondence: Benjamin H. Glass (bglass1@bu.edu) | Sarah W. Davies (daviessw@bu.edu)

Received: 3 December 2025 | **Revised:** 21 March 2026 | **Accepted:** 26 March 2026

Keywords: 16S rRNA | coral bleaching | ITS2 | marine heatwave | metabarcoding | microbiome | Symbiodiniaceae | symbiosis

ABSTRACT

During the 4th Global Coral Bleaching Event (GCBE4; January 2023–September 2025), an extreme marine heatwave occurred on the Bocas del Toro Reef Complex (BTRC) in Panama. We characterized how this heatwave impacted the health and holobiont communities of the stress-tolerant coral *Siderastrea siderea* at four sites across the BTRC. Tagged colonies at each site ($N = 30–53$ colonies per site) were visited before, during, and after the heatwave (early May 2022, mid-August 2023, and late April 2024, respectively), and images and DNA samples were collected at each time point. In situ temperature logger data showed that sites reached maxima of 32.1°C–33.9°C in October 2023, resulting in the accumulation of ~12–20 maximum degree-heating weeks (DHWs). Consequently, *S. siderea* colonies displayed widespread bleaching (i.e., the loss of algal endosymbionts), with an increase from 8.6% to 33% of colonies bleached per site in May 2022 to 33%–70% in August 2023, followed by a decline to 15%–63% by April 2024. Colony-level partial mortality increased significantly between 2022 and 2024 at three of the four sites, and was observed even in colonies that were not bleached in August 2023. Further, many corals hosting *Cladocopium* spp. algal symbionts in 2022 shifted towards less diverse communities dominated by heat-tolerant *Breviolum* and *Durusdinium* spp., and most of these corals continued to host modified symbiont communities for months. The heatwave also reshaped corals' bacterial microbiomes, including increases in α-diversity and abundances of potentially pathogenic taxa (e.g., Vibrionaceae), and these shifts were persistent following the heatwave. Together, these findings demonstrate that GCBE4 had lasting impacts on *S. siderea* holobiont health across the BTRC, underscoring that extreme heat events can compromise even stress-tolerant coral species and induce legacy effects that will likely affect their future resilience. Rapid action to minimize further ocean warming is thus necessary to safeguard reef ecosystems.

1 | Introduction

The marine heatwaves that occurred across the globe during January 2023–September 2025 were the longest and most intense since humans began to record ocean temperatures in the 1880s (Dong et al. 2025). These record-breaking marine heatwaves resulted in similarly unprecedented levels of coral bleaching, which is the breakdown of the symbiosis between tropical reef-building corals and their obligate algal endosymbionts (Hoegh-Guldberg et al. 2023; Reimer et al. 2024). As such, the United States (US) National Oceanic and Atmospheric Administration (NOAA) declared the occurrence of the 4th Global Coral Bleaching Event (GCBE4; National Oceanic and Atmospheric Administration 2025), the first of which occurred in the late 1990s (Goreau et al. 2000; Hoegh-Guldberg 1999). During GCBE4, degree-heating

weeks (DHWs)—a measure of bleaching-level heat stress on reefs—reached previously unobserved highs well above the common threshold for coral mortality of eight DHWs (Eakin et al. 2010; Kayanne 2017). Accordingly, corals experienced mass mortality on reefs worldwide, including in Florida (Manzello et al. 2025; Neely et al. 2024; Thompson et al. 2025), Little Cayman (Doherty et al. 2025), the US Virgin Islands (Dell'Antonio et al. 2025; Edmunds and Lasker 2025), Mexico (Birkart and Álvarez-Filip 2025), Martinique (Bon et al. 2025), Vietnam (Tkachenko et al. 2025), and Australia's Great Barrier Reef (Emslie et al. 2025). Indeed, after GCBE4, two coral species once dominant on Florida's coral reefs became functionally extinct in this region (Manzello et al. 2025), and species in other regions experienced extirpation (Birkart and Álvarez-Filip 2025; Thompson et al. 2025). Heatwaves do not, however, affect corals equally between or within reefs (Dixon et al. 2015; Drury 2020; de Souza et al. 2022; van Woesik et al. 2022), and understanding how genetic and local environmental factors interact to shape coral performance under stress remains a critical goal for guiding ecosystem management.

For several decades it has been clear that certain coral species and populations are more resistant to heat stress (reviewed in Drury 2020; van Woesik et al. 2022); however, the limits of this resistance remain unknown. For example, corals with massive growth forms have generally avoided the bleaching and mortality observed in species with other growth forms during past heatwaves, and are considered "winners" that may become increasingly important for reef function under ocean warming (Guest et al. 2023; Loya et al. 2001). One such example in the Caribbean is *Siderastrea siderea*, which has been observed to be highly stress-tolerant compared to other species (Jones et al. 2025), potentially owing to energy reserves in its thick tissues that can support survival under stress (Loya et al. 2001). Yet, heat tolerance in corals is influenced by genetic and environmental factors (Drury 2020; van Woesik et al. 2022), and whether evolved tolerance is sufficient to protect *S. siderea* and other resistant species from extreme (> 8 DHWs) heat stress is unclear. This is a particularly important question as massive corals including *S. siderea* are increasingly used in restoration efforts (Guest et al. 2023).

Local environmental factors also contribute to coral resistance and resilience. For example, high-frequency temperature variability has been associated with the reduction of coral bleaching at a global scale (Safaie et al. 2018). This is likely because corals inhabiting environments with high thermal variability can constitutively upregulate (i.e., frontload) stress-preventative proteins (e.g., heat shock proteins; Barshis et al. 2013; Brown et al. 2025; Da-Anoy et al. 2024) and/or display high levels of plasticity that support survival under acute stress (Kenkel and Matz 2016). Similarly, exposure to a stress event can modify responses during future exposures, a phenomenon referred to as "environmental memory" (Brown and Barott 2022; Hackerott et al. 2021), which can result from long-term "legacy effects" (here defined as effects of stress that persist after stress subsides) on coral physiology and symbiont communities (Starko et al. 2023; Strand et al. 2024; Wall et al. 2021). However, whether these environmentally mediated mechanisms can protect corals under heatwaves as extreme as those observed during GCBE4 remains an important unanswered question.

Coral bleaching results from the breakdown of an essential symbiosis between corals and their endosymbiotic algae (family Symbiodiniaceae; Helgoe et al. 2024; van Woesik et al. 2022), and environmental factors can further influence coral outcomes under stress by selecting for particular symbionts that promote tolerance or sensitivity. Corals hosting *Cladocopium* spp. symbionts are often more susceptible to bleaching than conspecifics hosting *Breviolum* and *Durusdinium* spp., and colonies can "shuffle" (i.e., change densities of preexisting symbiont types) or "switch" (i.e., gain new symbiont types *de novo*) to host larger populations of heat-tolerant symbionts during and after heatwaves (Buzzoni et al. 2023; Palacio-Castro et al. 2023; Sampayo et al. 2008). However, hosting heat-tolerant symbionts does not always protect corals from mortality (Brown et al. 2023), and can incur physiological costs (e.g., decreased growth) following the abatement of stress (Little et al. 2004; Matsuda et al. 2023). Further, many stable coral-Symbiodiniaceae associations are coevolved, and it is not known how the erosion of these evolved symbioses via heatwaves can affect corals long-term (Starko et al. 2023). It is therefore important to further characterize how symbiont community dynamics shift during and after extreme heatwaves and how these associations shape coral survival.

In addition to Symbiodiniaceae, other components of the coral holobiont (i.e., the coral host and associated microbial community) are also dynamic in response to heat stress (van Oppen and Blackall 2019; Voolstra et al. 2024). For example, the abundances of certain bacterial taxa have been positively associated with stress-resistance in corals (Palacio-Castro et al. 2022). By contrast, some bacterial taxa found in corals are pathogenic and have been associated with disease, which is often observed during stress events including heatwaves (Casey et al. 2015; Glasl et al. 2016). Changes in bacterial communities under heat stress have been associated with symbiont community changes, reflecting symbiont-mediated impacts on host microbiomes and/or direct effects on symbiont-associated bacteria (Camp et al. 2020; Chen et al. 2024; Gardner et al. 2023). Moreover, shifts in microbiome composition can occur in the absence of bleaching or mortality (van Oppen and Blackall 2019; Voolstra et al. 2024), potentially uncovering hidden impacts of stress on corals. Investigating whether these patterns are observed under extreme heatwaves will contribute key insights into our understanding of the complex role of the microbiome in shaping coral resilience.

To address these questions, we characterized how the 2023 marine heatwave impacted the relatively stress-tolerant coral *S. siderea* at four sites across Panama's Bocas del Toro Reef Complex (BTRC). Colonies were tagged and geo-located at each site before GCBE4 in early May 2022, allowing us to track the fates of individual corals over multiple years. Specifically, to characterize the impacts of the heatwave on holobiont (i.e., combined host and microbial) outcomes during stress and recovery, we quantified bleaching, mortality, and disease incidence in these corals, in addition to profiling symbiont and microbial communities at three time points: before, during, and after the heatwave. Together, these data provide key insights into how GCBE4 impacted *S. siderea* on the BTRC, with implications

for the future of typically stress-tolerant coral species under intensifying ocean warming.

2 | Materials and Methods

2.1 | Site Selection, Coral Tagging and Sampling, and Temperature Data Collection

In May 2022, study sites were established across Almirante Bay, Bocas del Toro, Panama at four locations: Cristobal Island (9°16.0962′N, −82°14.5368′W; 1–12 m depth), Hospital Point (9°19.9914′N, −82°13.059′W; 1–11 m depth), Punta Donato (9°21.507′N, −82°22.0824′W; 1–5 m depth), and STRI Point (9°20.9208′N, −82°15.762′W; 1–7 m depth). At each site, colonies of *S. siderea* ($N = 30–53$ colonies per site) were haphazardly selected, geo-located, and a metal tag with a unique identifying number was attached by a nail on or next to each colony. In early May 2022, mid-August 2023, and late April 2024, images were collected of each colony alongside a color standard (Olympus TG-6 camera; $N = 27–53$ colonies per site; Table S1), and a tissue sample (~1 cm^2) was collected from a central location of a healthy (i.e., not displaying signs of disease; see below) part of each colony via hammer and microchisel for in situ preservation in 100% ethanol. Due to the loss of some tags or samples, sample sizes for each metric quantified (see below) vary by site and year, and these are detailed in Table S1.

Temperatures were recorded continuously every 15–30 min with HOBO pendants (Onset) deployed at 1–4 m from May 2022 to April 2024 at all sites except for Punta Donato, where temperature data from October 2022 to August 2023 were not recorded due to a logger failure. Temperature data recorded every 15 min from January 2005 to December 2024 using a HOBO U22 logger (Onset) at a site ~1 km from STRI Point were downloaded from the Smithsonian Tropical Research Institute (STRI) website (https://striresearch.si.edu).

2.2 | Bleaching, Tissue Loss, and Disease Monitoring

Using the images collected at each time point (early May 2022, mid-August 2023, and late April 2024), each colony ($N = 27–53$ colonies per site; Table S1) was assigned a bleaching status, either pigmented (i.e., visually healthy), partially bleached, or fully bleached. To minimize bias, all images were classified by the same observer, and colonies showing any visually identifiable bleached tissue < 100% of their live tissue area were considered partially bleached. Differences in image angles and/or the size of some colonies prevented absolute quantification of bleaching severity for partially bleached colonies, and this is an important limitation of this approach. No colony comprised live tissue surface area < 15 cm^2 at any time point. Images of the same colonies ($N = 27–53$ colonies per site; Table S1) collected in August 2023 and April 2024 were compared to those from May 2022 to quantify tissue loss (i.e., partial mortality) using May 2022 as a reference. Differences in image angles between time points prevented the absolute quantification of tissue loss, which was instead estimated visually at 10% intervals by the same observer for all images. Colonies ($N = 27–53$ colonies per site; Table S1) were also designated as displaying signs of disease if they presented any dark purple tissue discoloration indicative of dark spot syndrome, which has a distinctive presentation and affects *S. siderea* in this region (Gochfeld et al. 2006).

2.3 | Profiling of Algal Endosymbiont and Bacterial Communities

Tissue samples collected in situ (see above) were transferred to fresh 100% ethanol within 1–4 h of collection, then maintained at −20°C prior to transport to Boston University, where they were stored at −20°C until processing. DNA was isolated using RNAqueous Total RNA Isolation Kits (Invitrogen) or phenol:chloroform:isoamyl alcohol (25:24:1 v/v) according to established protocols (Davies et al. 2013), and a list of samples extracted using each method is in Dataset S1. Next, polymerase chain reaction (PCR) was used to amplify the V4 region of the bacterial 16S ribosomal RNA gene (515F and 806R primers; Apprill et al. 2015) or the ITS2 region of the Symbiodiniaceae ribosomal DNA (SYMVAR primers; Hume et al. 2013; $N = 24–37$ colonies per site; Table S1). Successful amplification was confirmed by visualizing each sample on a 1% agarose gel, and negative controls (no template DNA) were included in each PCR to confirm the absence of contamination. Amplified samples were then cleaned (GeneJET PCR purification kit; Thermo Fisher Scientific), barcoded via an additional PCR, verified again on a 1% agarose gel, pooled in an approximately equimolar ratio within amplicon type, quantified via a Qubit Fluorometer (Thermo Fisher Scientific), and finally pooled at a 1:3 M ratio of ITS2:16S. Final libraries were sequenced (paired-end 250 or 300 bp) on a MiSeq (Illumina) at the Tufts University Genomics Core Facility. Libraries (3 total) containing samples from 1 or 2 of the sampling time points (with corresponding negative controls) were sequenced in separate runs, and a list of samples in each run is in Dataset S1. PCR profiles are detailed in Table S2.

2.4 | Data and Statistical Analyses

RStudio running R version 4.2.1 was used for all analyses and visualizations (RStudio Team 2020). First, temperature data were used to calculate heat stress in units of DHWs as previously described (Eakin et al. 2010). Specifically, historical maximum monthly mean (MMM) temperatures for each site were determined from the thermal history products provided by National Oceanic and Atmospheric Administration Coral Reef Watch (Heron et al. 2016). These MMMs were used to calculate the "HotSpot" metric, defined as temperature anomalies above the MMM, and DHWs at a given time were calculated using HotSpot values ≥ 1°C for the preceding 12-week period (Eakin et al. 2010).

For bleaching and disease status data, the proportion of corals displaying each status was calculated for each site and year. For the tissue loss data, corals were classified as either having not bleached or bleached (partially or fully) in 2023, and a linear mixed-effects model was built relating percent mortality since 2022 to the fixed effect of year*site*bleaching status in 2023 with colony as a random effect. The significance levels ($p < 0.05$) of terms in the model were determined using an analysis of

variance (ANOVA) with type III sums of squares, and then the significance levels of pairwise comparisons of estimated marginal means generated from the model were determined using Tukey's honest significance difference *post hoc* tests. Means (± standard errors) were calculated for each group by site and year for visualization. Bleaching severity by site in 2023 and 2024 were correlated with maximum DHW, MMM, mean daily temperature, and mean daily temperature variability (Gantt et al. 2025), and these correlations were tested for statistical significance using *F*-tests.

Following demultiplexing, FASTQ files containing ITS2 reads were submitted to the *SymPortal* online portal for quality control and the identification of Symbiodiniaceae sequences (Hume et al. 2019). All negative control samples yielded no reads retained following *SymPortal* processing, so count tables of the relative and absolute abundances of sequences detected in each sample (following minimum entropy decomposition analyses; Hume et al. 2019) were used for downstream analyses without further modification. Using the relative abundances, the sequences identified in each coral were grouped by Symbiodiniaceae genus for plotting. Next, using the absolute abundances, a Shannon index (a measure of α-diversity) was calculated for each coral individual's symbiont community at each time point. A linear model was built relating Shannon index to the interaction of year and site, and the significance levels of model terms and pairwise comparisons of estimated marginal means were determined as described above. Additionally, a metric representing the degree of change in symbiont communities over time was generated for colonies by calculating Euclidean distances between points representing the same colony in different years in an *xyz*-coordinate system where x = relative abundance of *Breviolum* spp., y = relative abundance of *Cladocopium* spp., and z = relative abundance of *Durusdinium* spp. For example, a colony hosting 100% *Cladocopium* spp. in 2022 and 100% *Durusdinium* spp. in 2024 would lead to a value of $\sqrt{(0-0)^2+(0-1)^2+(1-0)^2}$ = ~1.41. This metric was calculated for each colony comparing each of 2023 and 2024 to 2022, and then these values were correlated with observed colony-level mortality since 2022 for each site and year, with the statistical significance of correlations assessed via *F*-tests.

For analysis of the 16S sequencing data, reads were first trimmed to remove primer sequences using *cutadapt* (Martin 2011), then the *DADA2* pipeline (Callahan et al. 2016) was used to further trim reads with low quality ($Q < 20$) bases and combine paired reads, to which taxonomy was then assigned using the Silva database (version 138.2; Quast et al. 2013). The count and taxonomy tables produced by *DADA2* were used to generate a *phyloseq* data object (McMurdie and Holmes 2013) for downstream analysis, which first entailed filtering to remove sequences originating from chloroplasts, mitochondria, and non-bacteria. Next, sequence relative abundances were calculated for each sample (i.e., colony), and any sequence not present with at least 5% relative abundance in a minimum of 5 samples was removed prior to grouping sequences by family for visualization. Absolute abundances were used to calculate a Shannon index for each coral's bacterial community, and these were compared by site and year as described above. A permutational analysis of variance (PERMANOVA) was used to relate community composition to the interaction of site*year*disease status. Next, absolute abundance data for both ITS2 and 16S sequences were combined into a single *phyloseq* object (v1.42.0), and a Bray–Curtis dissimilarity matrix generated from these data was then used for principal coordinates analysis (PCoA). The dissimilarity matrix was also used to test for differences in β-dispersion and group centroid positions using a permutation test of multivariate homogeneity and analysis of similarities (ANOSIM), respectively, both modeling the effect of year*site. The combined ITS2 and 16S data were also separated by site and year, and sequences not present with at least 5 reads in ~10% of the samples were removed prior to the generation of association networks using *phyloseq* (plot_net()), which uses a Bray–Curtis dissimilarity matrix to calculate edge widths and a Fruchterman-Reingold algorithm force-directed layout method. Networks were filtered to remove any edges representing maximum distances > 0.4 (Kajihara and Hynson 2024). Additional packages used included *lme4* (v1.1.30; Bates et al. 2015), *ggplot2* (v3.5.1; Wickham 2016), *emmeans* (v1.10.3; Lenth et al. 2023), *vegan* (v2.6.4; Dixon 2003), *psych* (v2.4.6.26; Revelle 2017), and *lubridate* (v1.9.3; Grolemund and Wickham 2011). Sequencing data were deposited in the National Center for Biotechnology Information's Short Read Archive under BioProject ID PRJNA1365718, and all other data and code were deposited in a Dryad repository (Glass and Davies 2026).

3 | Results

3.1 | The 2023 Marine Heatwave Brought Extreme Heat Stress to the BTRC, Leading to Bleaching and Mortality of *S. siderea*

Long-term temperature data from STRI showed that the 2023 marine heatwave was associated with record-high temperatures (maximum daily average 31.55°C) and accumulated heat stress (maximum 13.8 DHWs) on the BTRC (Figure 1A,B). Temperature data from loggers at the study sites also recorded exceptionally high levels of heat stress, although with variation between sites (Figure 1C,D). At Cristobal Island, Hospital Point, and Punta Donato, maximum DHWs reached 19.9, 17.7, and 18.8, respectively, while the maximum DHW observed at STRI Point was lower at 11.9 (Figure 1C,D). This accumulation of heat stress was associated with bleaching of *S. siderea* colonies at all sites (Figure 2A). Interestingly, while bleaching prevalence during the heatwave was highest at the hottest site, Cristobal Island (68% of colonies bleached in August 2023), the least warm site, STRI Point, displayed the second-highest bleaching prevalence (44%), surpassing bleaching observed at the warmer Hospital Point and Punta Donato sites (36% and 34%, respectively; Figure 2A). Further, while bleaching prevalence decreased by 10%–20% between 2023 and 2024 at the three warmest sites, bleaching prevalence increased by 19% in the same time frame at STRI Point (Figure 2A). Bleaching severity by site was not significantly related to DHW, MMM, mean daily temperature, or mean daily temperature variability ($p > 0.05$ for all; Figure S1A–D). Notably, these trends in bleaching severity were generally a stronger predictor of colony-level partial mortality (i.e., tissue loss; data summarized in Table S3) than DHWs (Figure 2A,B).

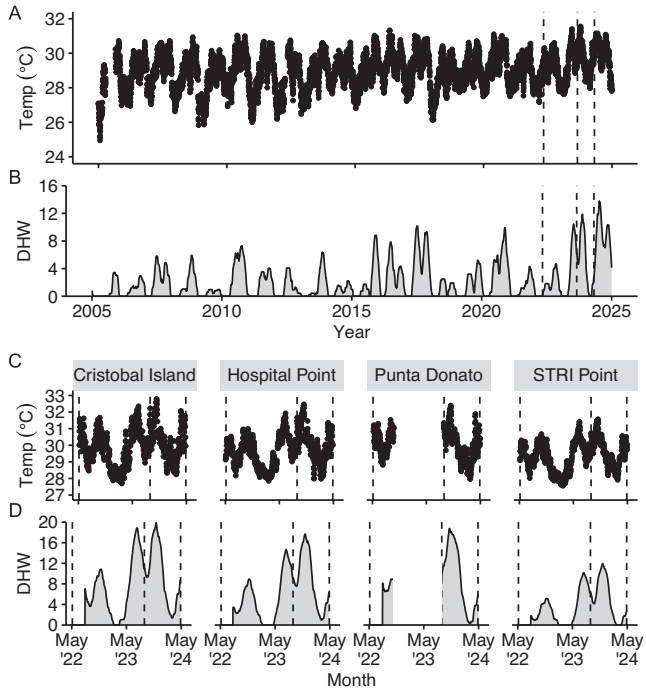

FIGURE 1 | Temperatures and accumulated heat stress at Bocas del Toro Reef Complex sites. (A) Daily average in situ seawater temperatures (Temp; °C) recorded at the Smithsonian Tropical Research Institute (STRI) between 2005 and 2025. (B) Accumulated heat stress expressed in degree-heating weeks (DHWs) derived from the temperature data in A. (C) Daily average in situ seawater temperatures (Temp; °C) at study sites (Cristobal Island, Hospital Point, Punta Donato, and STRI Point) between 1 May 2022 and 1 May 2024. Data for Punta Donato are incomplete due to a logger failure. (D) Heat stress expressed in DHWs derived from the temperature data in C. In all panels, vertical dashed lines indicate the timing of image/sample collection (early May 2022, mid-August 2023, and late April 2024).

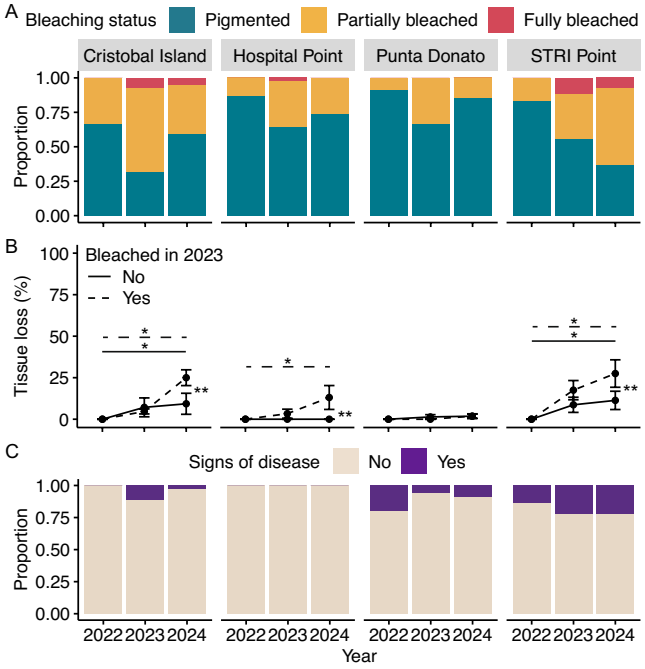

FIGURE 2 | Bleaching, mortality, and disease incidence of *Siderastrea siderea* at reef sites over time. (A) Proportion of *S. siderea* colonies at study sites displaying each bleaching status (color) at each time point. (B) Colony-level partial mortality (expressed as percent of tissue lost since 2022) for colonies at each site over time. Each point with error bars indicates mean ± standard error of the mean. Horizontal lines with single asterisks indicate significant ($p < 0.05$) differences in means between 2022 and 2024. For lines connecting data and indicating pairwise comparisons, line type indicates bleaching status in 2023 (solid = not bleached, dashed = bleached). Double asterisks indicate significant ($p < 0.05$) differences in mean mortality in 2024 for corals not bleached vs. bleached in 2023. (C) Proportion of colonies displaying no signs (beige) or signs (purple) of disease assumed to be dark spot syndrome at each time point. The *x*-axis in C applies to all of the panels, with year indicating the sampling time point (2022 = early May 2022, 2023 = mid-August 2023, and 2024 = late April 2024).

For example, partial mortality in 2024 was highest at the two sites with the greatest bleaching prevalence, Cristobal Island (17% average tissue loss since 2022) and STRI Point (average 19%; Table S3; Figure 2A,B). Further, mortality was significantly higher in corals that bleached in 2023 compared to those that did not bleach at Cristobal Island, STRI Point, and Hospital Point (averages 0%–11% for non-bleached, 13%–28% for bleached; $p < 0.01$ for all sites; Table S3; Figure 2A,B). By contrast, there was no statistically significant increase in partial mortality observed between 2022 and 2024 for corals at Punta Donato (2% ± 1% in 2024; $p = 0.7745$; Table S3), where bleaching prevalence was consistently the lowest among the sites and no fully bleached colonies were observed at any time point (Figure 2A,B).

Interestingly, disease prevalence appeared uncoupled from both bleaching and mortality. The percentage of colonies showing signs of disease increased during the heatwave by 11% and 9% compared to 2022 for Cristobal Island and STRI Point, respectively, but decreased by 14% at Punta Donato, while no signs of disease were observed at any time point at Hospital Point (Figures 2C and 3A). Further, some corals displaying signs of disease in 2022 no longer had discernable tissue discoloration in 2023 and/or 2024, and this was likely not solely due to the mortality of diseased tissue, as some tissue areas with discoloration in 2022 were still alive but no longer discolored in subsequent years (Figure 3B).

3.2 | The 2023 Heatwave Shifted Symbiodiniaceae Communities Towards *Breviolum* and *Durusdinium* Dominance at the Three Warmest Sites, With Diversity Generally Decreasing

Before the heatwave in May 2022, most *S. siderea* colonies at Cristobal Island and STRI Point hosted symbiont communities comprising 90%–100% *Cladocopium* spp., with a few colonies at both sites hosting 100% *Breviolum* or *Durusdinium* spp. (Figure 4A). Mixed communities were also rare before the heatwave at Punta Donato, and *Breviolum* spp. were more common at this site compared to all other sites (Figure 4A). By contrast, corals at Hospital Point tended to host a more even mix of *Cladocopium* and *Durusdinium* spp. before the heatwave, although many colonies at this site also displayed 90%–100% dominance of just one of these genera (Figure 4A).

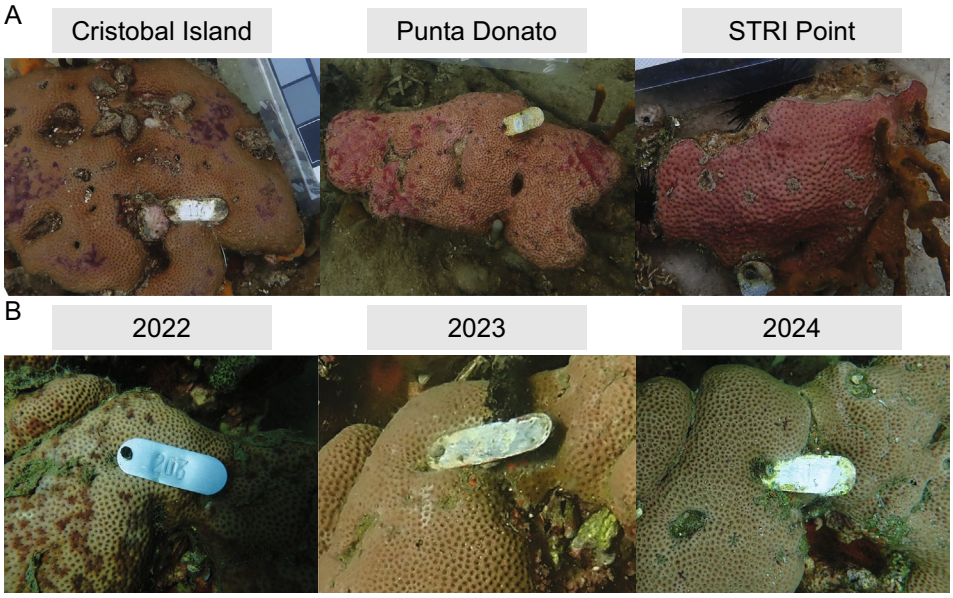

FIGURE 3 | Examples of corals displaying signs of disease and recovery. (A) Representative images of *S. siderastrea* colonies located at Cristobal Island, Punta Donato, and STRI Point displaying tissue discoloration indicative of dark spot syndrome. Images were collected in April 2024. (B) Representative images of a colony (203) in 2022, 2023, and 2024 displaying apparent recovery from dark spot syndrome.

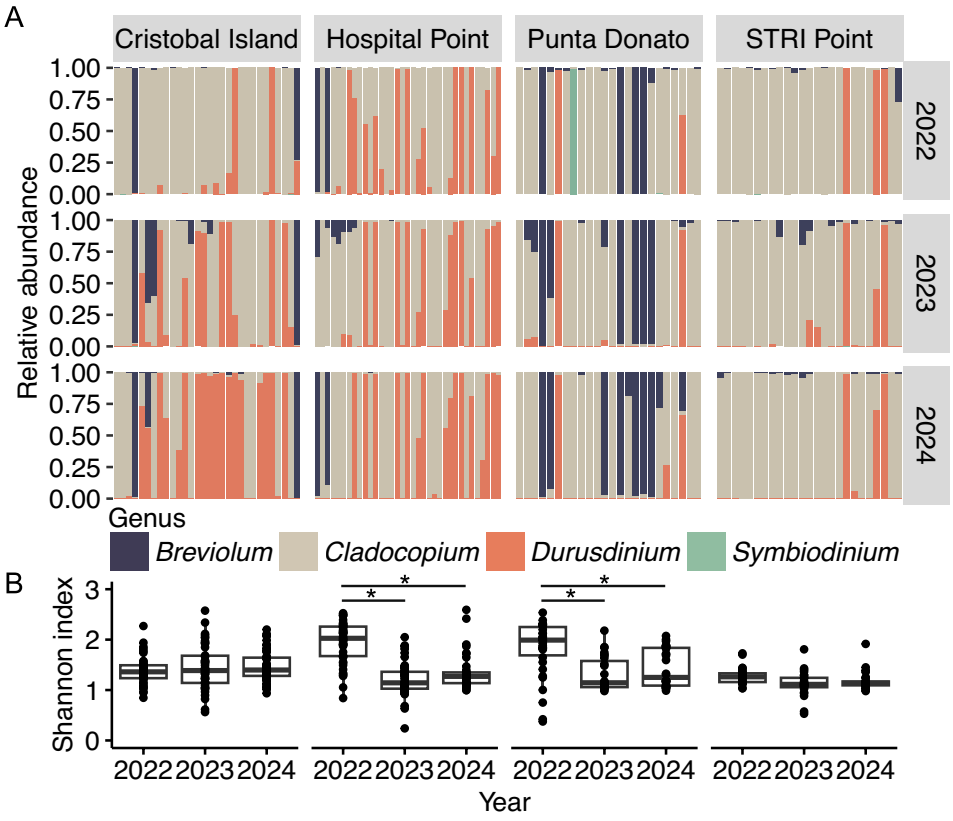

FIGURE 4 | Symbiodiniaceae community composition and α-diversity for *Siderastrea siderea* at reef sites over time. (A) Relative abundance of each Symbiodiniaceae genus (color) hosted by each coral (vertical bar) at study sites over time (2022 = early May 2022, 2023 = mid-August 2023, and 2024 = late April 2024) determined by ITS2 profiling. Each vertical bar represents one coral colony, and bars with the same horizontal alignment between years depict data from the same tagged colony sampled at each time point. (B) Shannon index (i.e., α-diversity) for each coral's (point) symbiont community at each time point. Horizontal lines with asterisks indicate significant ($p < 0.05$) differences in means.

The heatwave had significant impacts on symbiont communities at the three sites experiencing the highest accumulated heat stress (17–20 DHWs; Cristobal Island, Hospital Point, and Punta Donato), with evidence of both "shuffling" (i.e., increases in the abundances of previously low-abundance genera) and "switching" (i.e., the appearance of new genera;

Baker 2003). By contrast, algal communities at the cooler STRI Point (11.9 DHWs) were largely unaffected by the heatwave (Figure 4A). At Cristobal Island and Hospital Point, 18 colonies that hosted > 95% *Cladocopium* spp. before the heatwave hosted 50%–100% *Durusdinium* spp. in 2023 (Figure 4A). Similarly, at Punta Donato, six colonies that hosted > 90% *Cladocopium* spp. in 2022 displayed 25–100% abundance of *Breviolum* spp. in 2023 (Figure 4A). Notably, > 80% of colonies that displayed shifts in community composition between 2022 and 2023 retained these modified communities into 2024 (Figure 4A). However, multiple colonies at each of the sites also showed a different pattern, hosting > 95% *Cladocopium* spp. in 2022 and mostly retaining these symbionts while gaining small (1%–10%) populations of *Breviolum* spp. during the heatwave, but then losing these *Breviolum* populations between 2023 and 2024 (Figure 4A).

The described shifts in Symbiodiniaceae community composition were associated with significant decreases in α-diversity (Shannon index) for corals at Hospital Point and Punta Donato (Figure 4B). Corals at these sites hosted symbiont communities with the highest α-diversity among all sites prior to the heatwave, but this diversity was lost during the heatwave and remained significantly lower in 2024 compared to 2022 ($p < 0.001$ for all comparisons; Figure 4B). At Hospital Point, the homogenization of previously mixed communities likely contributed to this decrease in α-diversity (Figure 4B). Additionally, communities at Hospital Point and Punta Donato displayed a significant loss of *Cladocopium* diversity (Figure S2A), which was likely also a strong driver of decreases in overall α-diversity. No statistically significant relationship between the degree of change in symbiont communities and mortality was identified for any site (Figure S2B).

3.3 | The Heatwave Led to Restructuring of *S. siderea* Bacterial Microbiomes, Including Increases in Potentially Pathogenic Taxa and α-Diversity

Bacterial microbiomes of *S. siderea* varied over space and time, with some families present only at certain sites and/or time points, some changing over time in relative abundance, and others remaining relatively stable (Figure 5A). Accordingly, site, year, and their interaction were statistically significant predictors of community composition ($p < 0.05$ for all) in a PERMANOVA model, while disease status was not significant. Notable families included Amoebophilaceae, which was present in low-abundances at all sites in 2022 and displayed significant increases (10%–50%) in many corals at Punta Donato and STRI Point during and after the heatwave (Figure 5A). Also of note were Pseudomonadaceae and Spirochaetaceae, which were largely absent in all corals in 2022, but pervasive at 2%–10% abundance across sites during and after the heatwave (Figure 5A). Cyclobacteriaceae were also largely absent in 2022 and increased to 2%–5% abundance in many corals in 2023, but were then mostly absent again in 2024 (Figure 5A). Further, Vibrionaceae were present in low abundance (2%–5%) in many corals in 2022 and tended to increase by 3%–5% in 2023 before returning to lower levels in 2024 (Figure 5A). Other families displayed greater specificity by site, including Endozoicomonadaceae and Methylophagaceae (present almost exclusively at Hospital Point), Myxococcaceae (present only at Cristobal Island in 2023), and Xenococcaceae (presently almost exclusively at Hospital Point and Cristobal Island; Figure 5A). Strikingly, some families present in 2022 were absent in the latter years, including Burkholderiaceae and Rickettsiaceae (Figure 5A).

As with Symbiodiniaceae communities, corals at some of the sites displayed significant changes in α-diversity over time. Specifically, at Cristobal Island, Shannon indices were significantly higher in 2024 compared to 2022 ($p = 0.0134$), while diversity increased significantly for corals at Hospital Point in 2023 ($p = 0.0387$) before returning to levels comparable to 2022 after the heatwave ($p = 0.4708$; Figure 5B). At both Cristobal Island and Hospital Point, increases in α-diversity seemed to be largely driven by the novel appearance of and/or increases in Cyclobacteriaceae, Pseudomonadaceae, Spirochaetaceae, and Vibrionaceae during the heatwave (Figure 5B). These families were retained in microbiomes of corals at Cristobal Island in 2024, but were mostly lost at Hospital Point, explaining why α-diversity was significantly higher in 2024 compared to 2022 at Cristobal Island but not Hospital Point (Figure 5A,B).

3.4 | Impacts of the Heatwave on *S. siderea* Holobiont Community Structure Were Still Apparent After Months of Recovery

Holobiont communities were significantly different between years at all sites, as highlighted by the separation of corals by year along the first and second principal coordinates (8.6% and 5.2% variance explained, respectively) in combined PCoAs and the detection of significant differences in both β-dispersion and group centroid positions ($p < 0.001$ for both; Figure 6A). Moreover, communities in 2023 and 2024 were more similar to each other (i.e., higher overlap) than to those in 2022, and β-diversity increased between 2022 and 2024 at all of the sites (Figure 6A). Similarly, association networks were more sparse (i.e., fewer nodes and edges) in 2022 compared to 2023 and 2024 for all sites (Figure 6B, Figure S3). The connectedness within each network of symbiont and bacterial taxa was also variable between sites and years (Figure 6B). For example, symbiont taxa displayed significant associations with one another, but low associations with bacteria taxa, at all sites in 2022 (Figure 6B). However, during the heatwave, these taxa became broadly more integrated at all sites, with a group of symbiont taxa remaining in a separate network only at Punta Donato (Figure 6B). Interestingly, despite the overall lack of holobiont community recovery between 2022 and 2024 at all sites, symbiont taxa were again largely isolated in the networks for Hospital Point and Punta Donato in 2024 (Figure 6B). Overall, these data showed that communities in 2023 and 2024 were more similar to one another than to those in 2022. These and other findings are summarized in Figure 7.

4 | Discussion

Here, we describe widespread bleaching and associated mortality of *S. siderea* on the BTRC during and after a record-breaking

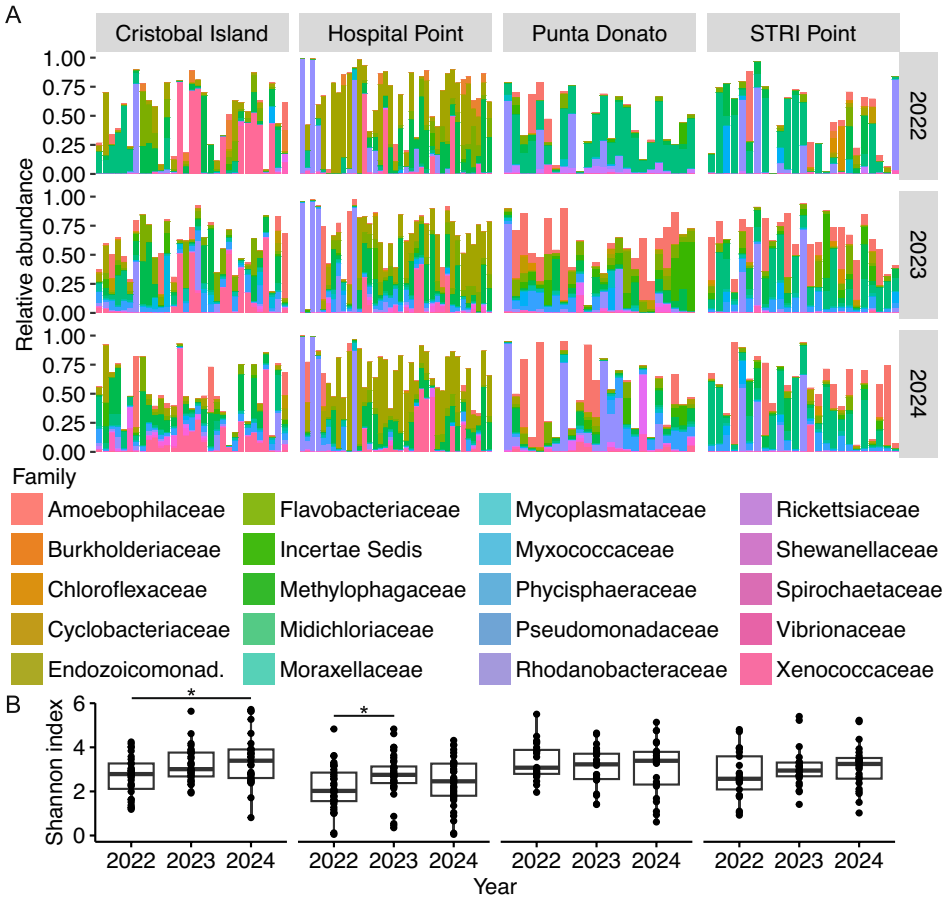

FIGURE 5 | Bacterial community composition and α-diversity for *Siderastrea siderea* at reef sites over time. (A) Relative abundance of each bacterial family (color) hosted by each coral (vertical bar) at study sites over time (2022 = early May 2022, 2023 = mid-August 2023, and 2024 = late April 2024). Each vertical bar represents one coral colony, and bars with the same horizontal alignment between years depict data from the same tagged colony sampled at each time point. Most bars depict total relative abundances < 1 due to filtering of low-abundance taxa. (B) Shannon index (i.e., α-diversity) for each coral's (point) bacterial community at each time point. Horizontal lines with asterisks indicate significant ($p < 0.05$) differences in means.

marine heatwave in summer 2023. These findings add to a growing body of evidence for the catastrophic effects of GCBE4 on coral reefs across the planet (Hoegh-Guldberg et al. 2023; Reimer et al. 2024). Through repeated microbial community profiling of fate-tracked colonies, our study also demonstrates persistent heatwave-induced restructuring of *S. siderea* holobionts, uncovering lasting impacts of heat stress that likely compromise coral health. These findings have implications for the coral communities of the BTRC and global reef ecosystems under intense periods of ocean warming.

4.1 | Unprecedented Heat Stress Turned a "Winning" Coral Species Into a Loser at Most, Though Not All, Reef Sites

The accumulation of ~12–20 DHWs resulted in up to 75% site-wide bleaching prevalence and 90% tissue loss in *S. siderea* colonies on the BTRC. This is particularly noteworthy given this species' high level of stress tolerance (Aichelman et al. 2021; Bove et al. 2019, 2022; Cramer et al. 2021) as well as the prior exposure of these colonies to heat stress, which can increase coral thermal tolerance through acclimatization and/or adaptation (Brown and Barott 2022; Hackerott et al. 2021). Notably, populations of *S. siderea* in Florida (Neely et al. 2024), Little Cayman (Doherty et al. 2025), and Martinique (Bon et al. 2025) displayed similar levels of bleaching and mortality to those observed in Panama during GCBE4. These findings demonstrate that increasingly intense marine heatwaves threaten even typically stress-tolerant coral species, at least at some reef sites, challenging the assumption that certain "winner" species will resist warming-induced population collapse (Grottoli et al. 2014; Hughes et al. 2017; Loya et al. 2001). Rather, these results underscore that tolerance of extreme heat is context-dependent, and determined by both genetic and environmental factors that are in need of further characterization. This is a particularly concerning finding given the long-term thermal history of the BTRC, which has entailed multiple incursions above 8 DHWs (a general threshold for coral mortality; Eakin et al. 2010; Kayanne 2017) in the past decade. Taken together, our results suggest that neither evolved heat tolerance nor prior exposure to heat stress can produce robustly resistant coral populations under intensifying marine heatwaves.

Among the sites monitored here, bleaching prevalence was the highest at Cristobal Island, the site with the greatest mean temperature and temperature variability, likely

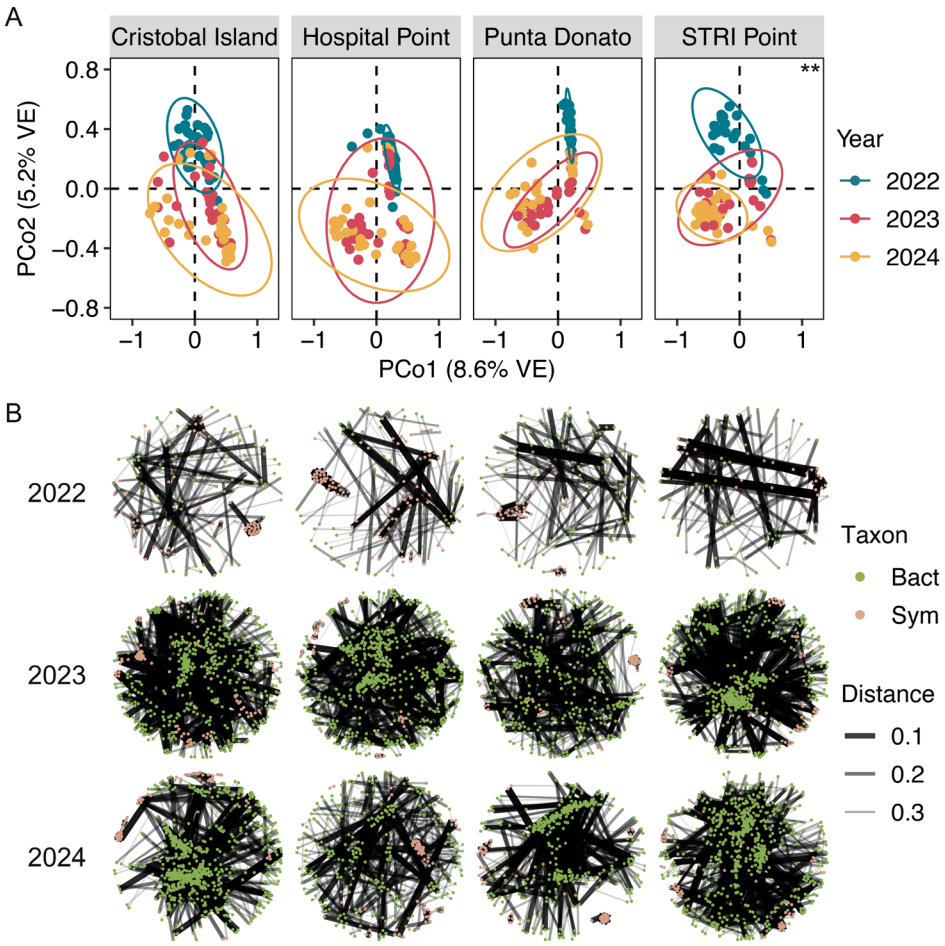

FIGURE 6 | Community dynamics of *Siderastrea siderea* holobionts at reef sites over time. (A) Depiction of principal coordinates (PCo) analysis performed using combined Symbiodiniaceae and bacterial community data for each coral holobiont (i.e., the coral host and associated microbial community; points), colored by year of sampling (2022 = early May 2022, 2023 = mid-August 2023, and 2024 = late April 2024). VE = variance explained. Ellipses represent 95% confidence intervals for centroid locations, and asterisks indicate statistical significance of β-dispersion and analysis of similarity tests. (B) Association networks for each site and year with nodes (points) representing taxa colored by taxon type (Bact = bacteria, Sym = Symbiodiniaceae) and edges (black lines) representing within-network distance (thresholded at 0.4).

due to heat stress being the highest at this site (19.9 DHWs). These findings complicate the hypothesis that particularly warm and thermally variable reef environments will host climate-resilient "super corals" (Camp et al. 2018). Instead, the same physical conditions that lead to such thermal regimes (e.g., high seawater residence times) can also contribute to greater heat stress in these environments during heatwaves, thus offsetting the benefits of local adaptation/acclimatization. Similar trends have also been observed in other reef systems such as the Great Barrier Reef, where warmer and more variable environments (e.g., reef flats) can accumulate more heat stress and so experience similar coral bleaching/mortality to cooler and more stable habitats (e.g., reef slopes) during heatwaves (Brown et al. 2022). However, these findings are complicated by the observation that corals at Punta Donato displayed relatively little bleaching and no significant mortality over GCBE4 despite exposure to extreme heat stress (18.8 DHWs). It is unclear why corals at this site did not experience greater declines. The lack of bleaching at Punta Donato may be due to a combination of local conditions. For example, this site has been shown to have relatively low irradiance (Rodas et al. 2020), which can act as a synergistic stressor with heat (Castro-Sanguino et al. 2024; Gonzalez-Espinosa and Donner 2021) and can also affect plankton communities that may promote coral survival through heterotrophy (Conti-Jerpe et al. 2020; Grottoli et al. 2006). In addition, Punta Donato is intermediate among the study sites with respect to mean temperature and variability, which may promote thermal tolerance. Indeed, intermediate thermal variability (relative to the local reefscape) has been shown to promote heat tolerance in other coral species (Brown et al. 2024; Marzonie et al. 2023). Genetic factors that were outside the scope of this study may have also contributed to site-specific outcomes, as *S. siderea* cryptic lineages on the BTRC display different responses to experimental thermal challenge (Aichelman et al. 2025), suggesting differential heat tolerance among lineages. Overall, it is clear that neither evolved heat tolerance nor acclimatization was sufficient to protect *S. siderea* on the BTRC and throughout the Caribbean during GCBE4, suggesting that typically heat-tolerant coral species will not be able to support robust reef ecosystems during future extreme heatwaves.

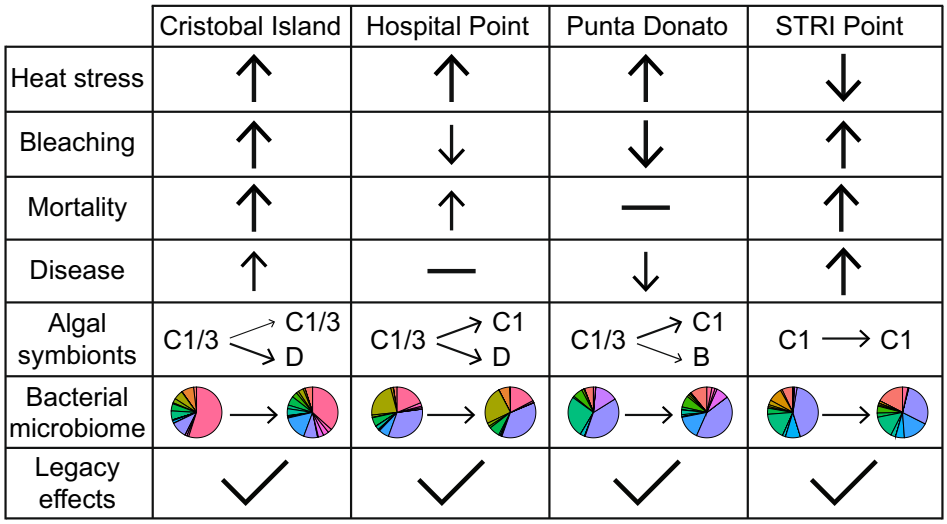

FIGURE 7 | Summary of key findings by site. Graphical summary of key findings by reef site (Cristobal Island, Hospital Point, Punta Donato, and STRI Point). Heat stress was lower at STRI Point compared to the other sites. Bleaching prevalence was highest at Cristobal Island and STRI Point, slightly lower at Hospital Point, and lowest at Punta Donato. Mortality was highest at Cristobal Island and STRI Point, slightly lower at Hospital Point, and not observed at Punta Donato. Disease incidence was highest at STRI Point, slightly lower but still increasing at Cristobal Island, decreasing at Punta Donato, and not observed at Hospital Point. Corals at all sites tended to host *Cladocopium* (C) 1/3 algal symbionts before the heatwave, and often shifted to hosting *Breviolum* (B) or *Durusdinium* (D) following the heatwave at all sites except STRI Point, where C1 remained common. In the algal symbiont boxes, letters indicate genera (B = *Breviolum*, C = *Cladocopium*, and D = *Durusdinium*), while numbers indicate *Cladocopium* taxa. Bacterial microbiomes differed between sites before the heatwave, and tended to show increases in α-diversity and abundances of potentially pathogenic taxa including Vibrionaceae (depicted in light pink; see Figure 5 for color key). In the bacterial microbiome boxes, pie charts represent average relative abundance across all corals at each site of bacterial families (colors) for 2022 (left) and 2024 (right), with family: Color mapping consistent across all charts. Legacy effects were observed at all sites. Across the figure, arrow size and thickness indicate relative scale of observations. For example, at Cristobal Island, fewer corals retained C1/3 algal symbionts than gained D, and the arrow pointing to D is thicker to indicate this.

4.2 | Disease Dynamics Were Uncoupled From Bleaching and Mortality Across Environments

Significant increases in dark spot syndrome incidence and colony-level mortality compared to before the heatwave were observed in *S. siderea* at two sites (Cristobal Island and STRI Point) irrespective of bleaching status in August 2023, demonstrating that bleaching resistance was not tantamount to maintenance of overall coral health. This finding corroborates previous reports that dark spot syndrome is positively associated with heat stress for *S. siderea* in the Carribbean (Borger 2005), and adds to a growing body of evidence that heat stress can have severe negative impacts on corals even in the absence of bleaching (Brown et al. 2023; Innis et al. 2021). As with dark spot syndrome, many coral diseases increase in prevalence during and after heatwaves, which is thought to reflect stress-induced weakening of the coral immune system resulting from the loss of symbiont-derived metabolic resources (Vega Thurber et al. 2025). However, our observations revealed that bleaching, disease, and mortality were not strongly correlated either within or between sites. For example, corals at Hospital Point displayed bleaching and mortality but no signs of disease at any time point, while those at Punta Donato did not experience mortality but showed the highest disease prevalence among the sites before the heatwave. Further, tissue areas on several corals that were diseased in 2022 no longer showed signs of disease in 2023 and 2024, suggesting that decreased disease prevalence following a heatwave can, in certain cases, be the result of stress-induced immune activation, which has been observed in corals and other cnidarians (Eliachar et al. 2022; Sharoni et al. 2025; van de Water et al. 2018). Overall, it remains unclear precisely what conditions determine the incidence and progress of *S. siderea* dark spot syndrome, as well as how heat stress influences coral immune function and disease dynamics. These are important questions for further investigation, particularly as stony coral tissue loss disease continues to spread across the Caribbean (Papke et al. 2024).

4.3 | Symbiont Community Shifts Imply Heatwave-Induced Changes in Holobiont Function, and Suggest That Environments Shape Plasticity

Many *S. siderea* colonies at the three warmest sites (Cristobal Island, Hospital Point, and Punta Donato) displayed shifts from *Cladocopium*-dominated algal symbiont communities before the heatwave to *Durusdinium* and *Breviolum* dominance during and after the heatwave, and these shifts likely impacted holobiont function. In agreement with these findings, similar shifts from *Cladocopium* to *Durusdinium* dominance have been observed in *S. siderea* exposed to experimental heat stress (Davies et al. 2018). Importantly, these changes may have promoted coral survival under extreme heat stress, as *Durusdinium* and *Breviolum* symbionts are generally more heat-tolerant and can support coral survival during heatwaves (Brown et al. 2023; Karp et al. 2025; Manzello et al. 2019; Palacio-Castro et al. 2023). However, there are trade-offs associated with hosting these genera compared to *Cladocopium*, including increased disease susceptibility

(Shore-Maggio et al. 2018), decreased growth (Little et al. 2004; Matsuda et al. 2023), and reduced photosynthate sharing under ambient conditions and during bleaching recovery (Allen-Waller and Barott 2023; Wall et al. 2020). Interestingly, nearly all colonies that gained 90%–100% *Durusdinium* or *Breviolum* in 2023 retained these symbionts at similar relative abundances into 2024, while several colonies that gained smaller populations (5%–10%) of these symbionts returned to ~100% abundances of *Cladocopium* after the heatwave. These findings suggest that *Cladocopium* symbionts possess a competitive advantage over the other genera in mixed communities, and/or that *S. siderea* hosts select for *Cladocopium* in the absence of stress. Reversions from *Durusdinium* to *Cladocopium* dominance were less common than *Breviolum* to *Cladocopium* transitions, potentially indicating that *Durusdinium* is competitively superior to *Breviolum* when either co-occurs with *Cladocopium*. Alternatively, *S. siderea* hosts may not be able to control the growth of *Durusdinium* populations after stress subsides, as has been previously suggested (LaJeunesse et al. 2009; Silverstein et al. 2017). Similar competitive dynamics have been observed in *S. siderea* algal symbiont communities in Florida, wherein populations of *Durusdinium* that surpassed a threshold abundance during bleaching were retained during recovery (Buzzoni et al. 2023). Yet, in the case of the 2023 heatwave in Panama, transitioning to heat-tolerant symbionts neither prevented bleaching nor mortality in *S. siderea* , suggesting that intensifying marine heatwaves preclude symbiont shuffling/switching as mechanisms supporting reef resilience, as has been previously suggested (Karp et al. 2025; Manzello et al. 2019; Palacio-Castro et al. 2023).

Corals that did not shuffle/switch towards the dominance of supposed heat-tolerant genera still displayed changes in symbiont community structure during the 2023 heatwave, most notably decreased diversity of *Cladocopium*, which drove significant decreases in α-diversity at the intermediately warm sites (Hospital Point and Punta Donato). These changes likely have important implications for *S. siderea* holobionts, as symbiont community diversity has been positively associated with holobiont community stability and resilience in corals (Baker 2003; Ziegler et al. 2018). Interestingly, this loss of diversity was mostly driven by the extirpation of C3 *Cladocopium* from coral hosts, and these symbionts have been shown to be less heat-tolerant than the C1 found more commonly in *S. siderea* at these sites (Aichelman 2023; Aichelman et al. 2025; Palacio-Castro et al. 2021). This was specifically true for C3 found in association with *S. siderea* cryptic lineage 2, which is the dominant lineage at Punta Donato (Aichelman et al. 2025). These findings suggest that heat-induced mortality of C3 taxa and/or that these symbionts were actively removed by *S. siderea* hosts. Notably, a similar loss in *Cladocopium* diversity following an extreme marine heatwave was observed in Kiritimati (Van Nynatten et al. 2025).

In contrast to all other sites, corals at STRI Point—the site with the lowest mean temperature yet second-highest bleaching prevalence—displayed little to no symbiont community changes over the 2-year study, indicating a lack of plasticity that may have contributed to the high bleaching and mortality observed in these corals. Environmental variables (e.g., temperature, nutrient availability) can promote or constrain the plasticity of coral symbiont communities (Baird et al. 2007; Baker 2003; Morris et al. 2019), and plasticity has been correlated with both stress tolerance and sensitivity (Howe-Kerr et al. 2020; Howells et al. 2020; Putnam et al. 2012; Zarate et al. 2024). In this case, STRI Point experienced the lowest mean temperature and variability among all of the sites, and these factors may have contributed to the lack of plasticity displayed by corals at this site. By contrast, corals at Cristobal Island, where temperature variability is high, displayed similar symbiont communities to those at STRI Point in 2022, yet significant plasticity was observed at Cristobal Island between 2022 and 2024, further supporting the hypothesis that local thermal regime may have been a strong driver of symbiotic flexibility. Nonetheless, mortality was comparable at these sites, again emphasizing that the dominant drivers of coral performance across reef environments are complex and in need of further investigation.

4.4 | Bacterial Microbiomes Showed Signs of Heat-Induced Restructuring That May Compromise Holobiont Health

Before the 2023 heatwave, bacterial microbiome compositions were variable both within and between sites, suggesting strong environmental structuring. This finding is consistent with previous observations that coral microbiomes can vary even for conspecifics on the same reef system (Galand et al. 2023; Osman et al. 2020), including *S. siderea* on the Mesoamerican Reef (Speare et al. 2020). Surprisingly, Endozoicomonadaceae were found almost exclusively in corals at Hospital Point, contrasting results from other coral species in which this family has been identified as dominant and highly stable in bacterial microbiomes (Neave et al. 2017; Pogoreutz and Ziegler 2024). Interestingly, in contrast to Symbiodiniaceae communities, which were variable at some sites but stable at others during the heatwave, nearly all colonies displayed significant temporal shifts in bacterial microbiomes, with both shared and site-specific patterns. For example, α-diversity increased significantly during and/or after the heatwave compared to 2022 at the two hottest sites (Cristobal Island and Hospital Point), suggesting a link between extreme heat stress and microbiome restructuring. However, increases in α-diversity were not observed at Punta Donato and STRI Point, which displayed lower mean temperatures and thermal variability than Cristobal Island and Hospital Point, supporting a potentially important role for these factors in determining how heat stress impacts bacterial communities. These results are consistent with previous observations that the effects of heat stress on coral microbiome α-diversity are context-dependent and influenced by synergistic interactions with other abiotic and biotic conditions (Maher et al. 2019, 2020; McDevitt-Irwin et al. 2019), as well as local thermal history (Ziegler et al. 2017).

Contrasting the site-specific dynamics observed for most bacterial families, temporal patterns for some families were highly conserved, indicating heat stress as a dominant factor influencing their abundance. For example, Pseudomonadaceae and Spirochaetaceae were virtually absent at all sites prior to the heatwave, but present in nearly every colony during and after the heatwave. Pseudomonadaceae have been found at higher abundances in the microbiomes of corals at sites more impacted by anthropogenic disturbance (Ostria-Hernández et al. 2022), potentially indicating a pathogenic role for this family. By contrast,

Spirochaetaceae abundances have been positively associated with survival under stress in other coral species (Palacio-Castro et al. 2022), and may have supported *S. siderea* performance under heat stress. During the heatwave, many corals also displayed increases in relative abundances of Vibrionaceae, which includes several species that are known coral pathogens (Ben-Haim et al. 2003), potentially indicating changes in immune processes, as has been observed in corals and other cnidarians under stress (Glass et al. 2026). As such, specific microbial taxa may play a role in the function of the coral holobiont and resilience to stress, which may affect population trajectories (van Oppen and Blackall 2019; Voolstra et al. 2024).

4.5 | Holobiont Community Structure Was Disrupted Months After the Heatwave, Demonstrating Legacy Effects of Heat Stress

Despite reductions in bleaching severity at most sites between 2023 and 2024, holobiont community structure in most corals continued to show signs of restructuring in 2024, as emphasized by multivariate and network analyses. This finding indicates legacy effects of heat stress on *S. siderea* that may contribute to holobiont instability. Moreover, the pre- and post-heatwave time points were season-matched, supporting the hypothesis that the heatwave, rather than seasonal variation, explains the shifts in holobiont community composition between 2022 and 2024. Prolonged recovery has also been observed in other coral species following marine heatwaves, with evidence of disrupted physiology and symbiotic communities for months to years (Brown et al. 2023; LaJeunesse et al. 2009; Strand et al. 2024; Wall et al. 2021; Vompe et al. 2024). This is a particularly concerning pattern given that the time between heatwaves is diminishing, and corals with a disrupted physiological state may be more sensitive to repeated exposure to heat and other stressors (Brown and Barott 2022; Hackerott et al. 2021). Moreover, legacy effects can impact the contribution of corals to reef function, including through disrupted reproduction (Johnston et al. 2020). Indeed, a legacy of stress exposure may explain why *S. siderea* at these sites were mostly producing sperm as opposed to energy-costly eggs in the years following the heatwave (Gantt et al. 2025), which could have detrimental consequences for fitness. On the other hand, certain changes in holobiont phenotypes such as increased abundance of heat-tolerant symbionts and specific bacterial taxa could promote coral resilience to future stress (Vompe et al. 2024; Ziegler et al. 2017). As marine heatwaves continue to increase in frequency and severity, it will be critical to determine the long-term fitness consequences of these legacy effects of heat stress.

5 | Conclusions

Overall, our findings indicate that the 2023 marine heatwave in Panama compromised the health of the heat-tolerant coral *S. siderea* across the BTRC, and induced legacy effects on physiology and symbioses that may influence resilience to future heatwaves. These findings demonstrate that ocean warming can threaten even generally stress-tolerant coral species, in which heat tolerance is determined by both genetic and environmental factors. These findings also highlight the value of long-term datasets and repeated sampling of fate-tracked colonies for uncovering the impacts of stress events that may otherwise be obfuscated by intraspecific, spatial, and temporal variability (Ziegler et al. 2021). Massive, long-lived corals like *S. siderea* are ideal for long-term observation, and these colonies can also be cored to examine historical patterns in phenotypes such as calcification and symbiont communities (Baumann et al. 2019; Grillo et al. 2025). Future research coupling such historical data with contemporary observations and considering the potential role of cryptic lineage would help clarify the complex factors shaping the performance of long-lived species like *S. siderea* . Finally, findings from GCBE4 from Panama and across the planet demonstrate that rapid reductions in anthropogenic environmental inputs are needed for the persistence of reef ecosystems.

Author Contributions

Viviana Guerra: investigation. **Plinio Gondola:** resources. **Maria Valadez-Ingersoll:** investigation, methodology, writing – review and editing. **Thomas D. Gilmore:** funding acquisition, resources, writing – review and editing. **Benjamin H. Glass:** data curation, formal analysis, investigation, methodology, software, validation, visualization, writing – review and editing, writing – original draft. **Hannah E. Aichelman:** conceptualization, investigation, methodology, project administration, writing – review and editing. **Carsten G. B. Grupstra:** conceptualization, investigation, methodology, writing – review and editing. **James Schipfer:** data curation, investigation, writing – review and editing. **Sarah W. Davies:** conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing – original draft, writing – review and editing. **Ally Swank:** data curation, investigation, writing – review and editing. **Aden Nagree:** data curation, investigation, writing – review and editing.

Acknowledgements

The authors thank Colleen Bove, Davey Kline, and Nicola Kriefall for assistance with the original tagging of colonies, Annabel Hughes for assistance with sequencing, the staff of the Smithsonian Marine Tropical Research Institute for assistance in the field, and Kristen Brown and Erick Geiger for assistance with extracting temperature data from the NOAA Coral Reef Watch thermal history products. Sequencing services were provided by the Tufts University Genomics Core Facility and all computational analyses were conducted on the Boston University Shared Computing Cluster. This work was supported by startup funding from Boston University to S.W.D. B.H.G. and M.V.-I. were supported by US National Science Foundation grant IOS-SDS 1937650 (to T.D.G. and S.W.D.). B.H.G. was also supported by NSF Ocean Sciences Postdoctoral Research Fellowship award 2506815 (to B.H.G.). Coral samples were collected and exported to the US under permits ARB-090-2021 and ARB-148-2023 (Ministry of the Environment, Panama).

Funding

This work was supported by Boston University, Startup to S.W.D. National Science Foundation, 1937650, 2506815.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All original data and code are available for open use in permanent, public repositories. Sequencing data are available through the National Center for Biotechnology Information's Short Read Archive under BioProject ID PRJNA1365718, and all other data and code are available through Dryad at https://doi.org/10.5061/dryad.573n5tbnv.

References

Aichelman, H. E. 2023. *Exploring Coral Symbiosis Under Climate Change Stress Across Spatial and Temporal Scales*. Boston University.

Aichelman, H. E., B. E. Benson, K. Gomez-Campo, et al. 2025. "Cryptic Coral Diversity Is Associated With Symbioses, Physiology, and Response to Thermal Challenge." *Science Advances* 11, no. 3: eadr5237.

Aichelman, H. E., C. B. Bove, K. D. Castillo, et al. 2021. "Exposure Duration Modulates the Response of Caribbean Corals to Global Change Stressors." *Limnology and Oceanography* 66, no. 8: 3100–3115.

Allen-Waller, L., and K. L. Barott. 2023. "Symbiotic Dinoflagellates Divert Energy Away From Mutualism During Coral Bleaching Recovery." *Symbiosis* 89: 173–186.

Apprill, A., S. McNally, R. Parsons, and L. Weber. 2015. "Minor Revision to V4 Region SSU rRNA 806R Gene Primer Greatly Increases Detection of SAR11 Bacterioplankton." *Aquatic Microbial Ecology* 75, no. 2: 129–137.

Baird, A. H., V. R. Cumbo, W. Leggat, and M. Rodriguez-Lanetty. 2007. "Fidelity and Flexibility in Coral Symbioses." *Marine Ecology Progress Series* 347: 307–309.

Baker, A. C. 2003. "Flexibility and Specificity in Coral-Algal Symbiosis: Diversity, Ecology, and Biogeography of *Symbiodinium*." *Annual Review of Ecology, Evolution, and Systematics* 34, no. 1: 661–689.

Barshis, D. J., J. T. Ladner, T. A. Oliver, F. O. Seneca, N. Traylor-Knowles, and S. R. Palumbi. 2013. "Genomic Basis for Coral Resilience to Climate Change." *Proceedings of the National Academy of Sciences of the United States of America* 110, no. 4: 1387–1392.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using LME4." *Journal of Statistical Software* 67: 1–48.

Baumann, J. H., J. B. Ries, J. P. Rippe, et al. 2019. "Nearshore Coral Growth Declining on the Mesoamerican Barrier Reef System." *Global Change Biology* 25, no. 11: 3932–3945.

Ben-Haim, Y., F. L. Thompson, C. C. Thompson, et al. 2003. "*Vibrio coralliilyticus* sp. nov., a Temperature-Dependent Pathogen of the Coral *Pocillopora damicornis*." *International Journal of Systematic and Evolutionary Microbiology* 53, no. 1: 309–315.

Birkart, L. V., and L. Álvarez-Filip. 2025. "2023 Global Heatwave Causes Mass Mortality of a Keystone Coral on Shallow Western Atlantic Reefs." *iScience* 28, no. 11: 113722.

Bon, M., M. Kayal, C. R. Dromard, and C. Desrosiers. 2025. "Impact of the 2023 Coral Bleaching Event in Martinique, Eastern Caribbean." *Coral Reefs* 20: 1–14.

Borger, J. L. 2005. "Dark Spot Syndrome: A Scleractinian Coral Disease or a General Stress Response?" *Coral Reefs* 24, no. 1: 139–144.

Bove, C. B., S. W. Davies, J. B. Ries, et al. 2022. "Global Change Differentially Modulates Caribbean Coral Physiology." *PLoS One* 17, no. 9: e0273897.

Bove, C. B., J. B. Ries, S. W. Davies, I. T. Westfield, J. Umbanhowar, and K. D. Castillo. 2019. "Common Caribbean Corals Exhibit Highly Variable Responses to Future Acidification and Warming." *Proceedings of the Royal Society B: Biological Sciences* 286, no. 1900: 20182840.

Brown, K. T., and K. L. Barott. 2022. "The Costs and Benefits of Environmental Memory for Reef-Building Corals Coping With Recurring Marine Heatwaves." *Integrative and Comparative Biology* 62, no. 6: 1748–1755.

Brown, K. T., Z. Dellaert, M. P. Martynek, et al. 2025. "Extreme Environmental Variability Induces Frontloading of Coral Biomineralisation Genes to Maintain Calcification Under pCO_2 Variability." *Molecular Ecology* 34, no. 2: e17603.

Brown, K. T., G. Eyal, S. G. Dove, and K. L. Barott. 2022. "Fine-Scale Heterogeneity Reveals Disproportionate Thermal Stress and Coral Mortality in Thermally Variable Reef Habitats During a Marine Heatwave." *Coral Reefs* 25: 2386.

Brown, K. T., E. A. Lenz, B. H. Glass, et al. 2023. "Divergent Bleaching and Recovery Trajectories in Reef-Building Corals Following a Decade of Successive Marine Heatwaves." *Proceedings of the National Academy of Sciences of the United States of America* 120: e2312104120.

Brown, K. T., M. P. Martynek, and K. L. Barott. 2024. "Local Habitat Heterogeneity Rivals Regional Differences in Coral Thermal Tolerance." *Coral Reefs* 43, no. 3: 571–585.

Buzzoni, D., R. Cunning, and A. C. Baker. 2023. "The Role of Background Algal Symbionts as Drivers of Shuffling to Thermotolerant Symbiodiniaceae Following Bleaching in Three Caribbean Coral Species." *Coral Reefs* 42: 1285–1295.

Callahan, B. J., P. J. McMurdie, M. J. Rosen, A. W. Han, A. J. A. Johnson, and S. P. Holmes. 2016. "DADA2: High-Resolution Sample Inference From Illumina Amplicon Data." *Nature Methods* 13, no. 7: 581–583.

Camp, E. F., T. Kahlke, M. R. Nitschke, et al. 2020. "Revealing Changes in the Microbiome of Symbiodiniaceae Under Thermal Stress." *Environmental Microbiology* 22, no. 4: 1294–1309.

Camp, E. F., V. Schoepf, and D. J. Suggett. 2018. "How Can 'Super Corals' Facilitate Global Coral Reef Survival Under Rapid Environmental and Climatic Change?" *Global Change Biology* 24, no. 7: 2755–2757.

Casey, J. M., S. Connolly, and T. Ainsworth. 2015. "Coral Transplantation Triggers Shift in Microbiome and Promotion of Coral Disease Associated Potential Pathogens." *Scientific Reports* 5: 11903.

Castro-Sanguino, C., D. Stick, S. Duffy, C. Grimaldi, J. Gilmour, and L. Thomas. 2024. "Differential Impacts of Light on Coral Phenotypic Responses to Acute Heat Stress." *Journal of Experimental Marine Biology and Ecology* 581: 152057.

Chen, B., Y. Wei, K. Yu, et al. 2024. "The Microbiome Dynamics and Interaction of Endosymbiotic Symbiodiniaceae and Fungi Are Associated With Thermal Bleaching Susceptibility of Coral Holobionts." *Applied and Environmental Microbiology* 90, no. 4: e0193923.

Conti-Jerpe, I. E., P. D. Thompson, C. W. M. Wong, et al. 2020. "Trophic Strategy and Bleaching Resistance in Reef-Building Corals." *Science Advances* 6, no. 15: eaaz5443.

Cramer, K. L., M. K. Donovan, J. B. C. Jackson, et al. 2021. "The Transformation of Caribbean Coral Communities Since Humans." *Ecology and Evolution* 11, no. 15: 10098–10118.

Da-Anoy, J., N. Posadas, and C. Conaco. 2024. "Interspecies Differences in the Transcriptome Response of Corals to Acute Heat Stress." *PeerJ* 12: e18627.

Davies, S. W., M. Rahman, E. Meyer, et al. 2013. "Novel Polymorphic Microsatellite Markers for Population Genetics of the Endangered Caribbean Star Coral, *Montastraea faveolata*." *Marine Biodiversity* 43, no. 2: 167–172.

Davies, S. W., J. B. Ries, A. Marchetti, and K. D. Castillo. 2018. "*Symbiodinium* Functional Diversity in the Coral *Siderastrea siderea* Is Influenced by Thermal Stress and Reef Environment, but Not Ocean Acidification." *Frontiers in Marine Science* 5: 348914.

de Souza, M. R., C. Caruso, L. Ruiz-Jones, C. Drury, R. Gates, and R. J. Toonen. 2022. "Community Composition of Coral-Associated Symbiodiniaceae Differs Across Fine-Scale Environmental Gradients in Kāne Ohe Bay." *Royal Society Open Science* 9, no. 9: 212042.

Dell'Antonio, E. C., L. Mahoney, and P. J. Edmunds. 2025. "Marine Heatwave Decimates Fire Coral Populations in the Caribbean." *Proceedings of the National Academy of Sciences of the United States of America* 122, no. 47: e2518506122.

Dixon, G. B., S. W. Davies, G. A. Aglyamova, E. Meyer, L. K. Bay, and M. V. Matz. 2015. "Genomic Determinants of Coral Heat Tolerance Across Latitudes." *Science* 348, no. 6242: 1460–1462.

Dixon, P. 2003. "VEGAN, a Package of R Functions for Community Ecology." *Journal of Vegetation Science: Official Organ of the International Association for Vegetation Science* 14, no. 6: 927–930.

Doherty, M. L., J. V. Johnson, and G. Goodbody-Gringley. 2025. "Widespread Coral Bleaching and Mass Mortality During the 2023–2024 Marine Heatwave in Little Cayman." *PLoS One* 20: e0322636.

Dong, T., Z. Zeng, M. Pan, et al. 2025. "Record-Breaking 2023 Marine Heatwaves." *Science* 389, no. 6758: 369–374.

Drury, C. 2020. "Resilience in Reef-Building Corals: The Ecological and Evolutionary Importance of the Host Response to Thermal Stress." *Molecular Ecology* 29, no. 3: 448–465.

Eakin, C. M., J. A. Morgan, S. F. Heron, et al. 2010. "Caribbean Corals in Crisis: Record Thermal Stress, Bleaching, and Mortality in 2005." *PLoS One* 5: e13969.

Edmunds, P. J., and H. R. Lasker. 2025. "A Long-Term Perspective to the Effects of the 2023 Marine Heat Wave on Stony Corals in the Caribbean." *Biology Letters* 21: 20250388.

Eliachar, S., G. A. Snyder, S. K. Barkan, et al. 2022. "Heat Stress Increases Immune Cell Function in Hexacorallia." *Frontiers in Immunology* 13: 1016097.

Emslie, M. J., D. M. Ceccarelli, M. Logan, et al. 2025. "Anthropogenic Climate Change Causes Substantial Loss of Coral on the Northern Great Barrier Reef During the 2024 Bleaching Event." *Coral Reefs* 25: 1–17.

Galand, P. E., H.-J. Ruscheweyh, G. Salazar, et al. 2023. "Diversity of the Pacific Ocean Coral Reef Microbiome." *Nature Communications* 14, no. 1: 3039.

Gantt, S. E., C. G. B. Grupstra, H. E. Aichelman, et al. 2025. "Sex Ratios and Gamete Production Vary Across Cryptic Coral Lineages and Thermal Environments." *Coral Reefs* 20: 2786. https://doi.org/10.1007/s00338-025-02786-8.

Gardner, S. G., W. Leggat, and T. D. Ainsworth. 2023. "The Microbiome of the Endosymbiotic Symbiodiniaceae in Corals Exposed to Thermal Stress." *Hydrobiologia* 850, no. 17: 3685–3704.

Glasl, B., G. Herndl, and P. Frade. 2016. "The Microbiome of Coral Surface Mucus Has a Key Role in Mediating Holobiont Health and Survival Upon Disturbance." *ISME Journal* 10: 2280–2292.

Glass, B., and S. Davies. 2026. "Data and Code for: Effects of an Extreme Marine Heatwave on Siderastrea siderea in Panama." *Dryad*. https://doi.org/10.5061/dryad.573n5tbnv.

Glass, B. H., T. Abraham, T. Siggers, S. W. Davies, and T. D. Gilmore. 2026. "NF-κB: A Diverse and Multi-Functional Transcription Factor in Holozoans." *Molecular Biology and Evolution* 25: msag059.

Gochfeld, D. J., J. B. Olson, and M. Slattery. 2006. "Colony Versus Population Variation in Susceptibility and Resistance to Dark Spot Syndrome in the Caribbean Coral *Siderastrea siderea*." *Diseases of Aquatic Organisms* 69, no. 1: 53–65.

Gonzalez-Espinosa, P. C., and S. D. Donner. 2021. "Cloudiness Reduces the Bleaching Response of Coral Reefs Exposed to Heat Stress." *Global Change Biology* 27, no. 15: 3474–3486.

Goreau, T., T. McClanahan, R. Hayes, and A. Strong. 2000. "Conservation of Coral Reefs After the 1998 Global Bleaching Event." *Conservation Biology* 14, no. 1: 5–15.

Grillo, J. F., V. Tirpitz, J. Reichert, et al. 2025. "Coral Skeletal Cores as Windows Into Past Symbiodiniaceae Community Dynamics." *Global Change Biology* 31: e70575.

Grolemund, G., and H. Wickham. 2011. "Dates and Times Made Easy With Lubridate." *Journal of Statistical Software* 40, no. 3: 1–25.

Grottoli, A. G., L. J. Rodrigues, and J. E. Palardy. 2006. "Heterotrophic Plasticity and Resilience in Bleached Corals." *Nature* 440, no. 7088: 1186–1189.

Grottoli, A. G., M. E. Warner, S. J. Levas, et al. 2014. "The Cumulative Impact of Annual Coral Bleaching Can Turn Some Coral Species Winners Into Losers." *Global Change Biology* 20, no. 12: 3823–3833.

Guest, J., M. V. Baria-Rodriguez, T. C. Toh, et al. 2023. "Live Slow, Die Old: Larval Propagation of Slow-Growing, Stress-Tolerant Corals for Reef Restoration." *Coral Reefs* 42, no. 6: 1365–1377.

Hackerott, S., H. A. Martell, and J. M. Eirin-Lopez. 2021. "Coral Environmental Memory: Causes, Mechanisms, and Consequences for Future Reefs." *Trends in Ecology & Evolution* 36, no. 11: 1011–1023.

Helgoe, J., S. K. Davy, V. M. Weis, and M. Rodriguez-Lanetty. 2024. "Triggers, Cascades, and Endpoints: Connecting the Dots of Coral Bleaching Mechanisms." *Biological Reviews of the Cambridge Philosophical Society* 99: 715–752.

Heron, S. F., J. A. Maynard, R. van Hooidonk, and C. M. Eakin. 2016. "Warming Trends and Bleaching Stress of the World's Coral Reefs 1985-2012." *Scientific Reports* 6, no. 1: 38402.

Hoegh-Guldberg, O. 1999. "Climate Change, Coral Bleaching and the Future of the World's Coral Reefs." *Marine and Freshwater Research* 50, no. 8: 839–866.

Hoegh-Guldberg, O., W. Skirving, S. G. Dove, et al. 2023. "Coral Reefs in Peril in a Record-Breaking Year." *Science (New York, N.Y.)* 382, no. 6676: 1238–1240.

Howe-Kerr, L. I., B. Bachelot, R. M. Wright, C. D. Kenkel, L. K. Bay, and A. M. S. Correa. 2020. "Symbiont Community Diversity Is More Variable in Corals That Respond Poorly to Stress." *Global Change Biology* 26, no. 4: 2220–2234.

Howells, E. J., A. G. Bauman, G. O. Vaughan, B. C. C. Hume, C. R. Voolstra, and J. A. Burt. 2020. "Corals in the Hottest Reefs in the World Exhibit Symbiont Fidelity Not Flexibility." *Molecular Ecology* 29, no. 5: 899–911.

Hughes, T. P., J. T. Kerry, M. Álvarez-Noriega, et al. 2017. "Global Warming and Recurrent Mass Bleaching of Corals." *Nature* 543, no. 7645: 373–377.

Hume, B., C. D'Angelo, J. Burt, A. C. Baker, B. Riegl, and J. Wiedenmann. 2013. "Corals From the Persian/Arabian Gulf as Models for Thermotolerant Reef-Builders: Prevalence of Clade C_3 Symbiodinium, Host Fluorescence and Ex Situ Temperature Tolerance." *Marine Pollution Bulletin* 72, no. 2: 313–322.

Hume, B., E. Smith, M. Ziegler, et al. 2019. "SymPortal: A Novel Analytical Framework and Platform for Coral Algal Symbiont Next-Generation Sequencing ITS2 Profiling." *Molecular Ecology Resources* 19, no. 4: 1063–1080.

Innis, T., L. Allen-Waller, K. T. Brown, et al. 2021. "Marine Heatwaves Depress Metabolic Activity and Impair Cellular Acid-Base Homeostasis in Reef-Building Corals Regardless of Bleaching Susceptibility." *Global Change Biology* 27, no. 12: 2728–2743.

Johnston, E. C., C. W. W. Counsell, T. L. Sale, S. C. Burgess, and R. J. Toonen. 2020. "The Legacy of Stress: Coral Bleaching Impacts Reproduction Years Later." *Functional Ecology* 34, no. 11: 2315–2325.

Jones, N. P., S. E. Leinbach, and D. S. Gilliam. 2025. "Interspecific Variation in Demographics Reveals Ecological Winners and Losers in a Highly Disturbed Coral Reef System." *Coral Reefs* 45: 1–15.

Kajihara, K. T., and N. A. Hynson. 2024. "Networks as Tools for Defining Emergent Properties of Microbiomes and Their Stability." *Microbiome* 12, no. 1: 184.

Karp, R. F., F. Lepiz-Conejo, S. B. Matsuda, et al. 2025. "Heat-Tolerant Algal Symbionts May Prevent Extirpation of the Threatened Elkhorn Coral, *Acropora palmata* , in Florida During Intensifying Marine Heatwaves." *Coral Reefs* 44, no. 3: 953–965.

Kayanne, H. 2017. "Validation of Degree Heating Weeks as a Coral Bleaching Index in the Northwestern Pacific." *Coral Reefs* 36, no. 1: 63–70.

Kenkel, C. D., and M. V. Matz. 2016. "Gene Expression Plasticity as a Mechanism of Coral Adaptation to a Variable Environment." *Nature Ecology & Evolution* 1, no. 1: 14.

LaJeunesse, T. C., R. T. Smith, J. Finney, and H. Oxenford. 2009. "Outbreak and Persistence of Opportunistic Symbiotic Dinoflagellates During the 2005 Caribbean Mass Coral 'Bleaching' Event." *Proceedings. Biological sciences* 276, no. 1676: 4139–4148.

Lenth, R. V., B. Bolker, P. Buerkner, et al. 2023. "emmeans: Estimated Marginal Means." *Github*. https://github.com/rvlenth/emmeans.

Little, A. F., M. J. H. van Oppen, and B. L. Willis. 2004. "Flexibility in Algal Endosymbioses Shapes Growth in Reef Corals." *Science (New York, N.Y.)* 304, no. 5676: 1492–1494.

Loya, Y., K. Sakai, K. Yamazato, Y. Nakano, H. Sambali, and R. van Woesik. 2001. "Coral Bleaching: The Winners and the Losers." *Ecology Letters* 4, no. 2: 122–131.

Maher, R. L., M. M. Rice, R. McMinds, D. Burkepile, and R. L. Vega Thurber. 2019. "Multiple Stressors Interact Primarily Through Antagonism to Drive Changes in the Coral Microbiome." *Scientific Reports* 9: 6834.

Maher, R. L., E. R. Schmeltzer, S. Meiling, et al. 2020. "Coral Microbiomes Demonstrate Flexibility and Resilience Through a Reduction in Community Diversity Following a Thermal Stress Event." *Frontiers in Ecology and Evolution* 8: 555698.

Manzello, D. P., R. Cunning, R. F. Karp, et al. 2025. "Heat-Driven Functional Extinction of Caribbean Acropora Corals From Florida's Coral Reef." *Science (New York, N.Y.)* 390, no. 6771: 361–366.

Manzello, D. P., M. V. Matz, I. C. Enochs, et al. 2019. "Role of Host Genetics and Heat-Tolerant Algal Symbionts in Sustaining Populations of the Endangered Coral *Orbicella faveolata* in the Florida Keys With Ocean Warming." *Global Change Biology* 25, no. 3: 1016–1031.

Martin, M. 2011. "Cutadapt Removes Adapter Sequences From High-Throughput Sequencing Reads." *EMBnet.journal* 17, no. 1: 10.

Marzonie, M. R., L. K. Bay, D. G. Bourne, et al. 2023. "The Effects of Marine Heatwaves on Acute Heat Tolerance in Corals." *Global Change Biology* 29, no. 2: 404–416.

Matsuda, S. B., M. L. Opalek, R. Ritson-Williams, R. D. Gates, and R. Cunning. 2023. "Symbiont-Mediated Tradeoffs Between Growth and Heat Tolerance Are Modulated by Light and Temperature in the Coral *Montipora capitata*." *Coral Reefs* 42, no. 6: 1385–1394.

McDevitt-Irwin, J. M., M. Garren, R. McMinds, R. Vega Thurber, and J. K. Baum. 2019. "Variable Interaction Outcomes of Local Disturbance and El Niño-Induced Heat Stress on Coral Microbiome Alpha and Beta Diversity." *Coral Reefs* 38, no. 2: 331–345.

McMurdie, P. J., and S. Holmes. 2013. "PHYLOSEQ: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data." *PLoS One* 8, no. 4: e61217.

Morris, L. A., C. R. Voolstra, K. M. Quigley, D. G. Bourne, and L. K. Bay. 2019. "Nutrient Availability and Metabolism Affect the Stability of Coral-Symbiodiniaceae Symbioses." *Trends in Microbiology* 27, no. 8: 678–689.

National Oceanic and Atmospheric Administration. 2025. "NOAA Confirms 4th Global Coral Bleaching Event." https://www.noaa.gov/news-release/noaa-confirms-4th-global-coral-bleaching-event.

Neave, M. J., R. Rachmawati, L. Xun, et al. 2017. "Differential Specificity Between Closely Related Corals and Abundant Endozoicomonas Endosymbionts Across Global Scales." *ISME Journal* 11, no. 1: 186–200.

Neely, K. L., R. J. Nowicki, M. A. Dobler, A. A. Chaparro, S. M. Miller, and K. A. Toth. 2024. "Too Hot to Handle? The Impact of the 2023 Marine Heatwave on Florida Keys Coral." *Frontiers in Marine Science* 11: 1489273.

Osman, E. O., D. J. Suggett, C. R. Voolstra, and D. T. Pettay. 2020. "Coral Microbiome Composition Along the Northern Red Sea Suggests High Plasticity of Bacterial and Specificity of Endosymbiotic Dinoflagellate Communities." *Microbiome* 8: 8059.

Ostria-Hernández, M. L., J. Hernández-Zulueta, O. Vargas-Ponce, et al. 2022. "Core Microbiome of Corals *Pocillopora damicornis* and *Pocillopora verrucosa* in the Northeastern Tropical Pacific." *Marine Ecology (Berlin, Germany)* 43, no. 6: e12729.

Palacio-Castro, A. M., C. E. Dennison, S. M. Rosales, and A. C. Baker. 2021. "Variation in Susceptibility Among Three Caribbean Coral Species and Their Algal Symbionts Indicates the Threatened Staghorn Coral, *Acropora cervicornis* , is Particularly Susceptible to Elevated Nutrients and Heat Stress." *Coral Reefs* 40, no. 5: 1601–1613.

Palacio-Castro, A. M., S. M. Rosales, C. E. Dennison, and A. C. Baker. 2022. "Microbiome Signatures in *Acropora cervicornis* are Associated With Genotypic Resistance to Elevated Nutrients and Heat Stress." *Coral Reefs* 41, no. 5: 1389–1403.

Palacio-Castro, A. M., T. B. Smith, V. Brandtneris, et al. 2023. "Increased Dominance of Heat-Tolerant Symbionts Creates Resilient Coral Reefs in Near-Term Ocean Warming." *Proceedings of the National Academy of Sciences of the United States of America* 120, no. 8: e2202388120.

Papke, E., A. Carreiro, C. Dennison, et al. 2024. "Stony Coral Tissue Loss Disease: A Review of Emergence, Impacts, Etiology, Diagnostics, and Intervention." *Frontiers in Marine Science* 10: 1321271.

Pogoreutz, C., and M. Ziegler. 2024. "Frenemies on the Reef? Resolving the Coral-Endozoicomonas Association." *Trends in Microbiology* 32, no. 5: 422–434.

Putnam, H. M., M. Stat, X. Pochon, and R. D. Gates. 2012. "Endosymbiotic Flexibility Associates With Environmental Sensitivity in Scleractinian Corals." *Proceedings of the National Academy of Sciences, India Section B: Biological Sciences* 279, no. 45: 4352–4361.

Quast, C., E. Pruesse, P. Yilmaz, et al. 2013. "The SILVA Ribosomal RNA Gene Database Project: Improved Data Processing and Web-Based Tools." *Nucleic Acids Research* 41: D590–D596.

Reimer, J. D., R. S. Peixoto, S. W. Davies, et al. 2024. "The Fourth Global Coral Bleaching Event: Where Do We Go From Here?" *Coral Reefs* 43, no. 4: 1121–1125.

Revelle, W. R. 2017. "The Psychiatrist: Procedures for Personality and Psychological Research." https://www.scholars.northwestern.edu/en/publications/psych-procedures-for-personality-and-psychological-research/.

Rodas, A. M., R. M. Wright, L. K. Buie, H. E. Aichelman, K. D. Castillo, and S. W. Davies. 2020. "Eukaryotic Plankton Communities Across Reef Environments in Bocas del Toro Archipelago, Panamá." *Coral Reefs* 39, no. 5: 1453–1467.

RStudio Team. 2020. "RSTUDIO: Integrated Development for R (Version 4.2.1)." http://www.rstudio.com/.

Safaie, A., N. J. Silbiger, T. R. McClanahan, et al. 2018. "High Frequency Temperature Variability Reduces the Risk of Coral Bleaching." *Nature Communications* 9, no. 1: 1671.

Sampayo, E. M., T. Ridgway, P. Bongaerts, and O. Hoegh-Guldberg. 2008. "Bleaching Susceptibility and Mortality of Corals Are Determined by Fine-Scale Differences in Symbiont Type." *Proceedings of the National Academy of Sciences of the United States of America* 105, no. 30: 10444–10449.

Sharoni, T., A. Jaimes-Becerra, M. Lewandowska, et al. 2025. "Heat Stress Drives Rapid Viral and Antiviral Innate Immunity Activation in Hexacorallia." *Molecular Ecology* 20: e70098.

Shore-Maggio, A., S. M. Callahan, and G. S. Aeby. 2018. "Trade-Offs in Disease and Bleaching Susceptibility Among Two Color Morphs of

the Hawaiian Reef Coral, *Montipora capitata*." *Coral Reefs* 37, no. 2: 507–517.

Silverstein, R. N., R. Cunning, and A. C. Baker. 2017. "Tenacious D: Symbiodinium in Clade D Remain in Reef Corals at Both High and Low Temperature Extremes Despite Impairment." *Journal of Experimental Biology* 220, no. 7: 1192–1196.

Speare, L., S. W. Davies, J. P. Balmonte, J. Baumann, and K. D. Castillo. 2020. "Patterns of Environmental Variability Influence Coral-Associated Bacterial and Algal Communities on the Mesoamerican Barrier Reef." *Molecular Ecology* 29, no. 13: 2334–2348.

Starko, S., J. E. Fifer, D. C. Claar, et al. 2023. "Marine Heatwaves Threaten Cryptic Coral Diversity and Erode Associations Among Coevolving Partners." *Science Advances* 9, no. 32: eadf0954.

Strand, E. L., K. H. Wong, A. Farraj, S. Gray, A. McMenamin, and H. M. Putnam. 2024. "Coral Species-Specific Loss and Physiological Legacy Effects Are Elicited by an Extended Marine Heatwave." *Journal of Experimental Biology* 227, no. 11: jeb246812.

Thompson, A. M., A. Stathakopoulos, K. J. Hollister, A. M. Lynch, J. C. Holder, and I. B. Kuffner. 2025. "Acute Heat Stress and the Extirpation of a Threatened Coral Species From a Remote, Subtropical Reef System." *Coral Reefs* 44, no. 3: 1023–1030.

Tkachenko, K. S., V. V. Dung, V. T. Ha, and H. H. Phong. 2025. "Unprecedented Coral Bleaching in Southern Vietnam in 2024: The Only Hope for Thermal Refuges?" *Coral Reefs* 44, no. 3: 881–894.

van de Water, J. A. J. M., M. Chaib De Mares, G. B. Dixon, et al. 2018. "Antimicrobial and Stress Responses to Increased Temperature and Bacterial Pathogen Challenge in the Holobiont of a Reef-Building Coral." *Molecular Ecology* 27, no. 4: 1065–1080.

Van Nynatten, A., R. Cunning, K. L. Tietjen, and J. K. Baum. 2025. "Marine Heatwaves Transform Coral Symbioses With Enduring Effects." *Ecology Letters* 28, no. 11: e70263.

van Oppen, M. J. H., and L. L. Blackall. 2019. "Coral Microbiome Dynamics, Functions and Design in a Changing World." *Nature Reviews. Microbiology* 17, no. 9: 557–567.

van Woesik, R., T. Shlesinger, A. G. Grottoli, et al. 2022. "Coral-Bleaching Responses to Climate Change Across Biological Scales." *Global Change Biology* 28: 4229–4250.

Vega Thurber, R. L., D. Silva, L. Speare, et al. 2025. "Coral Disease: Direct and Indirect Agents, Mechanisms of Disease, and Innovations for Increasing Resistance and Resilience." *Annual Review of Marine Science* 17, no. 1: 227–255.

Vompe, A. D., H. E. Epstein, K. E. Speare, et al. 2024. "Microbiome Ecological Memory and Responses to Repeated Marine Heatwaves Clarify Variation in Coral Bleaching and Mortality." *Global Change Biology* 30, no. 1: e17088.

Voolstra, C. R., J.-B. Raina, M. Dörr, et al. 2024. "The Coral Microbiome in Sickness, in Health and in a Changing World." *Nature Reviews. Microbiology* 22, no. 8: 460–475.

Wall, C. B., M. Kaluhiokalani, B. N. Popp, M. J. Donahue, and R. D. Gates. 2020. "Divergent Symbiont Communities Determine the Physiology and Nutrition of a Reef Coral Across a Light-Availability Gradient." *ISME Journal* 14, no. 4: 945–958.

Wall, C. B., C. A. Ricci, A. D. Wen, et al. 2021. "Shifting Baselines: Physiological Legacies Contribute to the Response of Reef Corals to Frequent Heatwaves." *Functional Ecology* 35, no. 6: 1366–1378.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag.

Zarate, D., J. Gary, and J. Li. 2024. "Flexibility in Coral-Algal Symbiosis Is Positively Correlated With the Host Geographic Range." *Ecology Letters* 27, no. 2: e14374.

Ziegler, M., A. Anton, S. G. Klein, et al. 2021. "Integrating Environmental Variability to Broaden the Research on Coral Responses to Future Ocean Conditions." *Global Change Biology* 27, no. 21: 5532–5546.

Ziegler, M., V. M. Eguíluz, C. M. Duarte, and C. R. Voolstra. 2018. "Rare Symbionts May Contribute to the Resilience of Coral-Algal Assemblages." *ISME Journal* 12, no. 1: 161–172.

Ziegler, M., F. O. Seneca, L. K. Yum, S. R. Palumbi, and C. R. Voolstra. 2017. "Bacterial Community Dynamics Are Linked to Patterns of Coral Heat Tolerance." *Nature Communications* 8, no. 1: 14213.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Sample sizes for each metric by site and year. **Table S2:** Polymerase chain reaction (PCR) profiles. **Figure S1:** Relationship between bleaching severity and reef site thermal characteristics. **Figure S2:** Relative abundances of Cladocopium sequences and relationship between symbiont community change and mortality by site and year. **Figure S3:** Microbial network feature counts by site and year. **Data S1**.