**Coral resilience to unprecedented heat stress**

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**Summary**

Coral reefs, which already live on the edge of their thermal tolerance [@Sampayo2016-vd], are under acute threat from ocean warming [@Hughes2003-aj; @Hoegh-Guldberg2007-fh; @Baker2008-ky]. Corals live in symbiosis with an extraordinarily diverse genus of photosynthetic dinoflagellates (Symbiodinium spp.; [@Muscatine1977-pn; @Rowan1992-lg]). The symbiotic association and diversity of various taxa of \*Symbiodinium\* can be flexible over time [@Baker2003-ks; @Little2004-tm], and individual \*Symbidoinium\* taxa can range from parasites to mutualists in their interaction with their coral host [@Lesser2013-dj]. Warming causes the breakdown of coral symbiosis, causing coral "bleaching" when symbionts are expelled and the white coral skeleton is visible through the coral tissue [@Brown1997-mf]. Coral bleaching can lead to mortality, although corals can regain their symbionts after heat stress has abated [@Douglas2003-nr; @Stat2009-qq]. The 2015/16 El Niño is the worst pulse warming event on record in terms of severity and longevity [@Eakin:2016vf; @Heron2016-am], yet despite massive coral mortality, some corals show resilience to this extreme event (@Bauminprep). Here, we track coral symbioses and survival at the epicenter of this bleaching event (Kiritimati, Central Pacific), and show, contrary to our current paradigm of coral bleaching and recovery dynamics, that some corals have the capacity to re-establish symbiosis before heat stress subsides. Furthermore, we demonstrate potential mechanisms for coral survival and recovery, including the lack of preferential symbiont expulsion, and the effect of local human disturbance on pre-bleaching symbiont community structure and the probability of coral survival. Together, these results show the potential for reef corals to survive extreme warming events, providing tentative hope for the survival of corals in the Anthropocene.

**Main text**

Global coral bleaching is increasing, and the 2014-2017 event caused a catastrophic loss of corals around the globe. WHAT IS CORAL BLEACHING. The 2014-2017 global coral bleaching event caused coral bleaching across the world's oceans (Eakin 2016, Normile 2016), with up to 75% bleaching on some reefs in Hawaii, and at least some level sof bleaching across 93% of the Great Barrier Reef (Minton et al 2015, GBRMPA 2016). The 2015-2016 El Niño, superimposed on nearly-ubiquitous tropical ocean warming, instigated the third global coral bleaching event (@Eakin:2016vf). Despite staggering losses caused by ocean warming at a global scale, some corals have the capacity to be resilient to increasingly frequent mass-bleaching events (Hughes et al 2017).

The symbiosis between coral and their single-celled photosynthetic dinoflagellate symbionts, *Symbiodinium*, is the foundation of coral reef ecosystems, supporting reef diversity and function at a global scale. There is much genetic, functional, and response diversity within the genus *Symbiodinium*. The *Symbiodinium* genus is divided into nine functionally distinct clades [@Stat2008-hk], and *Symbiodinium* associations can range from mutualistic to neutral to parasitic based on *Symbiodinium* type as well as environmental conditions [@Lesser2013-dj]. *Symbiodinium* types (a subdivision of clades), considered putative species [@Pochon2010-jm], have distinct geographic distributions, host associations, and environmental optima [@Fabina2012-mm]. NON SEQUITIR HERE… Recent advances in next-generation sequencing techniques have revealed cryptic genetic diversity within symbiotic *Symbiodinium* [@Quigley2014-zj; @Arif2014-kx; @Green2014-az], and has allowed for long-term genetic and ecological comparisons of symbiont community structure [@Edmunds\_undated-fd].

STILL NOT A SMOOTH TRANSITION HERE. Here we show that despite the unprecedented heat stress that occurred during the 2015-2016 El Niño event, some corals exhibited resilience and survived (Figure 1). Our study location, Kiritimati Atoll (Christmas Island, Kiribati, Central Equatorial Pacific, Coordinates: 2.0, -157.4), was at the epicenter of this extreme El Niño event. Thermal anomalies were severe on Kiritimati, rapidly exceeding NOAA Coral Reef Watch's Coral Bleaching Alert Level 1 and Alert Level 2 thresholds, reaching an unprecedented (@Hoegh-Guldberg2011-sl) 25.7 DHW over a year-long bleaching event, demolishing most of the reef (Figure 1a, @Baum\_inprep). Here, we assess coral symbiosis and survival during the massive 2015/2016 El Niño event. We tagged, sampled, and photographed the same coral colonies before, during, and immediately after the El Niño event. We determined bleaching condition and survival for each coral colony, and used Illumina MiSeq ITS-2 amplicon sequencing and 97% \*de novo\* OTU clustering to evaluate changes in *Symbiodinium* community structure. To investigate mechanisms underlying the ability of these corals to not only survive a year of continuous heat stress, but to recover in the interim, we assessed the relationship between human disturbance, pre-bleaching *Symbiodinium* community structure, and coral survival, as well as the timing of *Symbiodinium* community shifts throughout this El Niño event.

The current paradigm of coral bleaching and resilience is that as environmental stress (such as warming) increases, corals begin to lose their obligate symbionts (*Symbiodinium*) and "bleach" [@Gates1992-ew; @Douglas2003-nr]. Thermal stress is the primary cause for coral bleaching, and extreme or long-lasting warming causes a complete breakdown of symbiosis, leading to expulsion of all (or nearly all) *Symbiodinium* from the coral host tissue, often leading to coral mortality [@Hoegh-Guldberg1999-rb]. During bleaching, there is a window for recovery, that is, a certain amount of time during which the warming must cease and conditions must return to normal so that the coral can regain its symbionts. If the window for recovery passes without amelioration of environmental conditions, the coral will starve and die. (Cunning et al 2016, Putnam et al 2017). NEED BETTER SEGUE HERE Survival through such an extreme heat event provides an exceptional opportunity to understand how some corals can withstand intense heat stress, and how corals in general might survive long-term warming. Remarkably, we find that some coral colonies were able to survive this prolonged heat stress by regaining their symbionts after XX months of heat stress while temperatures were still elevated. Here, we provide the first evidence that corals have the capacity to not only survive, but to regain their symbionts and visibly recover from bleaching while still under intense thermal stress (Figure 1b, 2ab). These corals (Scleractinia family Merulinidae; *Platygyra* sp. and *Favites* *pentagona*) were bleached within two months of the onset of warming, but had visibly recovered after 10 consecutive months of intense warming (Fig. 1).WRAP UP AND TIE TO SYMBIO COMMUNITY?

It is thought that corals may be able to survive thermal stress by changing their complement of symbionts to better suit environmental conditions. The adaptive bleaching hypothesis suggests that corals bleach to expel environmentally sub-optimal symbionts, followed by switching (picking up new symbionts from the environment) or shuffling (an internal change in dominant symbiont type or overall symbiont community structure) [@Buddemeier2004-se; @Buddemeier1993-sx; @Baker2001-vc; @Baker2003-ks]. There is evidence for both *Symbiodinium* shuffling (Rowan 2004) and switching [@Boulotte2016-dy]. However, what remains unclear is if and how frequently bleaching events can actually be considered adaptive. Changes in symbiotic function ARE THESE + or - ? have been demonstrated due to shifts in the dominant *Symbiodinium* clade CAN I SAY SUCH AS C TO D?, and functional differences such as photosynthetic efficiency and bleaching resistance are also present among *Symbiodinium* types within a single clade [@Sampayo2008-tw; @Kemp2014-xj]. Clade D *Symbiodinium* are considered heat-tolerant symbionts [@Stat2010-zg]. Furthermore, repopulation of a coral host with clade D symbionts after a bleaching event is proposed to be a survival mechanism [@Berkelmans2006-rf; @Mieog2007-yy; @Silverstein2012-tm]. For example, one study showed that a history of thermal stress increased the prevalence of clade D *Symbiodinium* in one coral species, but did not instigate similar changes in two other coral species [@Stat2013-qp]. However, there is a trade-off to housing Clade D *Symbiodinium*, as corals that house clade D symbionts may have slower growth rates [@Little2004-tm] or lower capacity for energy storage [@Jones2011-nf]. WHAT WE FOUND FOR C VS D

Stochasticity in the rare *Symbiodinium* biosphere may build or weaken a coral's capacity for resilience. Corals commonly host background *Symbiodinium* types in low levels (Correa et al 2009), but sub-dominant *Symbiodinium* communities are often unstable (Coffroth et al 2010). Despite their small numbers, rare microbial species have been demonstrated to be disproportionally important to maintaining functional processes during environmental change in other systems (Shade et al 2014). The importance of rare *Symbiodinium* types is currently under debate, and these rare types may be commensal (symbionts that pass through with no harm or gain for either partner), parasitic ("cheaters" (Yu 2001), or opportunistic symbionts that take more than they give), or mutualistic (symbionts which support host function) (Parkinson et al 2015). Some research suggests that low-abundance *Symbiodinium* types have minimal functional significance to corals (Lee et al 2016), while other evidence supports the idea that shifts in *Symbiodinium* community diversity may have a large influence on coral resilience (Baskett et al 2010), and that the rare *Symbiodinium* biosphere is important for corals' response to climate change (Boulotte et al 2016). We show that after two months of heat stress, fully-bleached corals retained approximately the same *Symbiodinium* community as they had before the bleaching event (Figure 2a). This suggests that a wholesale breakdown of symbiosis occurred in bleached corals during this event, indicating a lack of preferential symbiont expulsion or exodus. Furthermore, some coral colonies changed *Symbiodinium* communities drastically upon recovery, and recovered symbiosis with *Symbiodinium* types that were present in only a negligible amount before the bleaching event (Figure 2b). This supports recent evidence suggesting that symbionts present in even very low abundances can play a critical role in coral survival and recovery (CITE recent papers).

Global climate change is superimposed on a suite of local stressors on coral reefs ranging from overfishing to pollution. Coral reef management has typically focused on minimizing local stressors, through marine protected areas that restrict fishing pressure or limiting agricultural runoff and sewage inputs, rather than attempting to directly mitigate underlying climate stressorsbut see vanOppen et al. 2015 PNASetc.etc. Local management measures can significantly enhance reef recovery rates following bleaching events, for example, by protecting populations of herbivorous fishes which indirectly provision space for new coral recruits by mediating competition between coral and macroalgae. What is unclear is if local management can also influence coral resistance to heat stress, and if so via which mechanisms. Coral bleaching and mortality on the Great Barrier Reef during the 2015-2016 El Niño event occurred irrespective of local protection, with no detectable differences across water quality or fishing pressure levelsHughes et al. 2017. –plus Emily’s paper showing protection in Kenya didn’t matter either –describe other studies that may have provided evidence that local protection does enhance resistance (Carilli? Etc) – but the mechanism was still unknown. –then a sentence describing what is known about how local protection influences *Symbiodinium* communities. –then BOOM! Our findings (evidence PLUS the mechanism because we rock)!!!

Notes:

-it has been unclear via what mechanism local protection would enhance coral resistance to heat stress – Here, we show that it does enhance coral resistance to heat stress \*\*AND\*\* we show the mechanism of how it does so.

-~90% mortality on KI (cite bleaching paper), but different mortality for some species

We show that corals living at different levels of local human disturbance had distinct symbiont communities that corresponded tightly to survivorship. This is in contrast to a recent study which concluded that particulate and dissolved nutrients do not reduce coral health at a colony scale (Rocker et al 2017).

There is increasing evidence for local adaptation in corals (Howells et al 2012, Logan et al 2013, Dixon et al 2015). Our results suggest that some coral species may have the capacity to experience evolutionary rescue, defined as adaptation at a rate that allows an endangered population to survive the rate of environmental change (Orr & Unkless 2014, Carlson 2014). Our results suggest that the capacity for evolutionary rescue is tangibly related to local reef protection. Although massive bleaching events like this one will likely continue to cause catastrophic damage to coral reefs worldwide, mitigating local human disturbance can potentially help protect some coral species against a modest amount of ocean warming.

Methods

**Study Location**

Kiritimati Atoll (Christmas Island), Kiribati, is located in the Central Equatorial Pacific (1.9N 157W), at the center of the El Niño 3.4 region (a region which is used to quantify El Niño presence and strength). Kiritimati has a strong gradient of human disturbance around the island, with the majority of the human population residing in 3 villages on the West side of the atoll. Human use, including subsistence fishing and waste water runoff, are densely concentrated in this area, while the North, East, and South regions of the island are minimally impacted (Watson et al 2016). During the 2015/2016 El Niño event, Kiritimati experienced 10 months of sustained temperature stress, causing a mass bleaching and mortality event (@BauminPrep).

**Temperature quantification**

Temperature loggers (SBE 56, Sea-Bird Scientific) were deployed around the island at 10-12m depth from 2011-2016 to measure *in situ* thermal stress. Temperature measurements were sub-sampled to a consistent 1 hour sampling grid, and then averaged to determine ‘half week’ temperature (similar to NOAA’s DHW product, https://coralreefwatch.noaa.gov/satellite/dhw.php). Next, hotspot values were calculated, where a hotspot is defined as when (half-weekly temperature) – (baseline temperature) is a positive number (baseline temperature is the long-term maximum monthly mean, 28.14°C). For degree heating week calculations (DHW), the value of a hotspot is included if it is >1°C (values of 0-1°C are discarded). DHW is calculated as a rolling sum over 12 weeks, with each of the 24 half-week cumulative hotspot measurements divided by 2. As temperature profiles are similar among sites, and not all sites had temperature data for the full time period, DHW values were averaged across sites to create an island-wide *in situ* DHW metric.

**Coral tagging and sampling**

In August/September 2014, colonies of *Platygyra* sp. (n = 82) and *Favites pentagona* (n = 59) were tagged along a 60m transect at 10-12m depth at 15 different sites around Kiritimati atoll. A photo was taken of each coral to record colony measurements and bleaching. The tagged coral colonies were resampled twice more before (January/February 2015, April/May 2015), once during (July 2015), and once near the end (March 2016) of the El Niño warming. Some tagged coral colonies were lost due to storm damage, and new coral colonies were tagged to replenish the total number of surveyed colonies. Not all sites were visited during all field seasons, and some site surveys were only partially completed during some field seasons due to inclement weather conditions. Corals were sampled underwater using a small chisel, and stored in seawater on ice until preservation. Coral tissue samples were preserved in Guanidinium buffer (50% w/v guanidinium isothiocyanate; 50 mM Tris pH 7.6; 10 µM EDTA; 4.2% w/v sarkosyl; 2.1% v/v-mercaptoethanol) and stored at 4°C until extraction.

**Sample processing and sequencing**

*DNA Extraction*

DNA extraction was performed using a guanidinium-based extraction protocol [@Stat2009-qq; Cunning2017-sc; Cunning2015-mt] with the modification that the DNA pellet was washed with 70% ethanol three times rather than once. After extraction, DNA was cleaned using Zymo Genomic DNA Clean and ConcentratorTM -25 (Catalog Nos. D4064 & D4065) following the standard protocol (<http://www.zymoresearch.com/downloads/dl/file/id/638/d4064i.pdf>). DNA was measured using the dsDNA Qubit BR assay. Any samples that had concentrations below detection levels of this assay, were quantified using the dsDNA Qubit HS assay.

*ITS-2 Amplicon*

The ITS-2 amplicon was chosen because it is currently the standard region used for identification and quantification of *Symbiodinium* taxa. Although ITS-2 is a multi-copy marker, it can be phylogenetically (LaJeunesse, 2001), functionally, and ecologically (Cunning et al 2017) informative. To minimize misinterpretation of intragenomic data, we conducted 97% within-sample OTU clustering. Instead of combining all sequences together into one fasta file and clustering together, we cluster each sample independently, and then collapse identical taxa across samples. As described in Cunning et al 2017, this approach increases the likelihood of collapsing intragenomic variation within a sample, while maintaining what is more likely to be biologically and ecologically relevant interspecific variation among samples.

*Library Preparation and Sequencing*

Library preparation for Illumina MiSeq ITS-2 amplicon sequencing was performed following the Illumina 16S Metagenomic Sequencing Library Preparation (Illumina protocol, Part # 15044223 Rev. B) with the following modifications:

* ITS primers (ITS-forward: 5’-TCG TCG GCA GCG TCA GAT GTG TAT AAG AGA CAG GTG AAT TGC AGA ACT CCG TC-3’ and ITS-reverse: 5’-GTC TCG TGG GCT CGG AGA TGT GTA TAA GAG ACA GCC TCC GCT TAC TTA TAT GCT T-3’ [@Stat2009-qq]) were used instead of the 16S primers
* PCR 1 annealing temp was 52°C, PCR 1 was performed in triplicate, and PCR product was pooled prior to bead clean.
* 60 µl SPRI beads were used for PCR 1 clean up
* PCR 1 bead clean up elution buffer volume varied depending on the Qubit concentration of initial gDNA. Changes were as follows:
  + gDNA concentrations with 1 ng/ µl (or less) were resuspended in 12.5 µl elution buffer
  + gDNA concentrations between 2 ng/ µl to 4 ng/ µl were resuspended in 42.5 µl elution buffer
  + gDNA concentrations of 5 ng/ µl were resuspended in 52.5 µl elution buffer

Samples were sequenced on the Illumina MiSeq platform with 2x300 paired-end read chemistry. A total of 289 samples were prepared for sequencing, and 282 of these samples were successfully amplified, sequenced, and used in downstream analyses.

**Bioinformatics**

We conducted quality filtering of raw reads (in .fastq format) first using the iu-filter-quality-bokulich script implemented in Illumina-Utils [@Bokulich2013-cm; Eren2013-yg], followed by paired-end sequence merging via the iu-merge-pairs script (also in Illumina-Utils, [Eren2013-yg]), with a maximum mismatch of three bases between the forward and reverse reads. After quality filtering, sequence processing and identification was performed following all specifications of [@Cunning2017-sc]; chimeric sequences were removed, primers were trimmed, sequences from each sample were clustered independently at 97% similarity using UCLUST [@Edgar2010-zl] implemented in QIIME [@Caporaso2010-yl] and resulting OTUs were collapsed at 100% identity across samples, sequences were aligned using the Needleman-Wunsch global alignment algorithm (Biostrings package, [@Pages2017-ie]) in R [@R\_Development\_Core\_Team2008-sp], and *Symbiodinium* sequences were named using a reference database (Cunning et al 2015, Cunning et al 2017; reference database is archived, along with full bioinformatic pipeline at https://github.com/daniclaar/KI\_Platy).

The Phyloseq package [@McMurdie2013-hf] in R was used to store and analyze OTU tables, taxonomic information, and sample metadata. The phyloseq object was filtered to remove OTUs observed <5 times (n=33 OTUs removed and n=114 kept). The phyloseq object was further filtered to remove samples with very low sequence abundances due to amplification issues (<200 sequences, n=27 samples removed and n=262 kept). In 262 coral samples, there were a total of 1,977,124 sequences after quality filtering.

A *Symbiodinium* phylogenetic tree was built by aligning ITS-2 sequences from each clade separately (align\_seqs.py from QIIME, Caporaso et al 2011) using muscle (Edgar, 2004). After sequences were aligned within each clade, a distance matrix encompassing all sequences was created using nr28s-rDNA distances (divergence of the D1–D3 region of the 28S; Pochon and Gates 2010) to describe between-clade distances. A phylogenetic tree was created using upgma (R package phangorn v.2.2.0, Schliep 2011), and the resulting tree was imported into the phyloseq object before statistical analysis.

**Statistical Analysis**

Code for all analyses is available on GitHub (https://github.com/daniclaar/KI\_Platy).

*Symbiodinium clade summary*

Sequences were summarized to show overall clade abundance across the coral populations by calculating the percent of sequences for each sampling date that were identified as *Symbiodinium* clades A, C, D, and G. Not all corals were sampled at all time points, and new corals were sampled when previous corals died. Thus, changes in the percent of sequences for each *Symbiodinium* clade (Fig 2) can be due to either changes in *Symbiodinium* communities associated with individual coral colonies or due to selective mortality during the bleaching event.

*Constrained ordination*

To assess the factors driving differences among *Symbiodinium* communities, a canonical analysis of principal coordinates (CAP) was performed. CAP is a constrained ordination method which allows for direct comparison of environmental variables and changes in *Symbiodinium* community composition by constraining ordination axes to linear combinations of the environmental variables. After exhausting all potential constrained axes, residual variability is addressed by fitting additional unconstrained axes (which represent linear variability which is caused by factors not included in the constrained axes. We conducted ordination with the function ‘ordinate’ (phyloseq, McMurdie and Holmes 2013), using weighted unifrac distances (Lozupone et al 2007), and included field season (timepoint during which each coral was collected), status (whether the coral survived the bleaching event (alive) or died (dead)), and local human disturbance level (very high, medium, low, and very low). After ordination, we conducted an ANOVA-like permutation test to determine if the defined model was significant. We confirm these results using an automatic stepwise model building tool to build and evaluate the significance of constrained axes using permutation P-values (ordistep tool, vegan package; Oksanen et al 2017). Furthermore, we tested the variance inflation factors (vif.cca, R package vegan) to test for redundant constraints, or for multicollinearity between model factors. Finally, we conducted two ANOVA-like permutation tests (anova.cca, R package vegan) to assess the significance of constraints by testing the full model as a whole, and the model terms individually.

*Indicator Taxa Analysis*

To test if any *Symbiodinium* taxa were associated with host coral survival after 10 months of heat stress, we conducted an indicator species analysis (multipatt, R package indicspecies, Caceres & Legendre 2009, (De Cáceres et al. 2010).

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**Author Contributions**: D.C.C., R.D.G.., and J.K.B. planned the project, D.C.C., K.L.T. and J.K.B. collected the data and conducted lab analyses. D.C.C. conducted the bioinformatics and statistical analyses. More to come here on interpreting results, writing, editing……

**Author Information**: The authors declare no competing financial interests.

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**Figure 1 | Thermal stress experienced by corals, and the transition of one such coral from healthy – bleached – recovered, at the epicentre of the 2015-2016 El Niño event. a.** Degree Heating Weeks (DHW), on Kiritimati Island over the course of the 2015-2016 El Niño event. Corals are sensitive to temperatures warmer than 1°C above their normal highest summertime mean sea surface temperature (SST), known as the bleaching threshold. DHW shows how much heat stress has accumulated in an area over the past twelve weeks by summing any temperature exceeding the bleaching threshold during that period. Horizontal lines show expected bleaching severity levels: 4°C (yellow line), NOAA Coral Reef Watch (CRW) Bleaching Alert Level 1 (significant bleaching likely); 8°C (light orange line), Bleaching Alert Level 2 (widespread bleaching and mortality may occur); 12°C (dark orange line), ‘mass coral mortality’ expected to occur (Hoegh-Guldberg 2011); 24°C (dark red line) ‘not experienced by reefs yet’ (Hoegh-Guldberg 2011). Solid black line indicates *in situ* calculated DHW, and fill colors correspond to bleaching severity levels. Dashed vertical gray lines show the six sampling time points. **b.** Photographs of the same tagged *Platygyra* coral colony (#99), from the six time points (dashed grey lines), showing the initially healthy colony (i-ii) bleached after two months of heat stress (iv), ‘recovered’ to a normal brown colour after ten months of heat stress (v), and still alive six months post heat stress (vi).

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**Figure 2 | Shift in *Symbiodinium* community composition from clade C to clade D dominance over the course of the 2015-2016 El Niño.** *Symbiodinium* community composition at each of five sampled time points for **i)** the entire pool of tagged coral colonies (solid lines, n=21-67 colonies per time point), and **ii)** a single representative tagged *Platygyra* colony (dashed lines).

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**Figure 3** **| Constrained ordination plot showing groupings of *Symbiodinium* communities from individual *Platygyra* colonies, grouping into two distinct areas according to level of local disturbance.** Ellipses show separation of the corals which survived the bleaching event (“Alive”, left side of plot) and those that did not (“Dead”, right side of plot). Values on x- and y- axes show per cent variation explained by each constrained axis.

**[insert extended data figure 1 here]**

**Extended Data Figure 1 | Transition of individual tagged coral colonies on Kiritimati Island from bleached – recovered over the course 2015-2016 El Niño event.** Photographs of **i-ii.** *Favites pentagona*, **iii-iv.** *Platygyra* sp., **v-vi.** *Favia matthaii* (*Dipsastrea matthaii*) taken two months into the heat stress (July 2015, left column) and at the conclusion of the heat stress (March 2016, right column), demonstrating the visual recovery of several coral species before the conclusion of the heat stress event.

**Extended Data Figure 2 |** Rank abundance plot for