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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

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Abstract

Identifying which factors lead to coral bleaching resistance is a priority given the global decline of coral reefs with ocean warming. During the second year of back-to-back bleaching events in the Florida Keys in 2014 and 2015, we characterized key environmental and biological factors associated with bleaching resilience in the threatened reef-building coral *Orbicella faveolata*. Ten reefs (five inshore, five offshore, 179 corals total) were sampled during bleaching (September 2015) and recovery (May 2016). Corals were genotyped with 2bRAD and profiled for algal symbiont abundance and type. *O. faveolata* at the inshore sites, despite higher temperatures, demonstrated significantly higher bleaching resistance and better recovery compared to offshore. The thermotolerant *Durusdinium trenchii* (formerly *Symbiondinium trenchii*) was the dominant endosymbiont type region-wide during initial (78.0% of corals sampled) and final (77.2%) sampling; >90% of the nonbleached corals were dominated by *D. trenchii*. 2bRAD host genotyping found no genetic structure among reefs, but inshore sites showed a high level of clonality. While none of the measured environmental parameters were correlated with bleaching, 71% of variation in bleaching resistance and 73% of variation in the proportion of *D. trenchii* was attributable to differences between genets, highlighting the leading role of genetics in shaping natural bleaching patterns. Notably, *D. trenchii* was rarely dominant in *O. faveolata* from the Florida Keys in previous studies, even during bleaching. The region-wide high abundance of *D. trenchii* was likely driven by repeated bleaching associated with the two warmest years on record for the Florida Keys (2014 and 2015). On inshore reefs in the Upper Florida Keys, *O. faveolata* was most abundant, had the highest bleaching resistance, and contained the most corals dominated by *D. trenchii*, illustrating a causal link between heat tolerance and ecosystem resilience with global change.

KEYWORDS
2bRAD, climate change, coral host genotype, *Durusdinium trenchii*, qPCR, *Symbiodinium*

1 | INTRODUCTION

The impacts of climate change on coral reefs have rapidly accelerated over the past 30 years from the first record of mass coral bleaching in the eastern tropical Pacific in 1982/1983 to global bleaching events in 1997/1998 and 2014–2017 (Baker, Glynn, & Riegl, 2008; Glynn, 1993; Hoegh-Guldberg et al., 2007; Hughes et al., 2017). Coral bleaching is the breakdown in the symbiosis between the coral host and its algal endosymbionts, which leaves corals white and energetically compromised (Glynn, 1993). Large-scale bleaching events are caused by sea temperatures 1–2°C greater than the maximum monthly mean for a month or more (Baker et al., 2008; Glynn, 1993; Hoegh-Guldberg et al., 2007). Coral bleaching prevalence and resultant mortality are a function of the magnitude and duration of the thermal anomaly (Glynn & D'Croz, 1990). Corals can survive bleaching if the stress is not too severe or abates soon, but they can become more susceptible to disease, as well as have depressed growth and reproduction for years after bleaching (Baird & Marshall, 2002; Cantin & Lough, 2014; Levitan, Boudreau, Jara, & Knowlton, 2014; Miller et al., 2009; Muller, Bartels, & Baums, 2018; Precht, Gintert, Robbart, Fura, & van Woesik, 2016).

Similar to the wider Caribbean, coral reefs in the Florida Keys have declined dramatically since the 1980s (Dustan & Halas, 1987; Porter & Meier, 1992). Coral bleaching and disease have been a major factor in this decline as there have been seven mass coral bleaching events since 1987 in the Florida Keys, with back-to-back events in 2014 and 2015 (Gintert et al., 2018; Manzello, 2015; Precht & Miller, 2007). An exception to this decline occurs on the inshore patch reefs of the Florida Keys, where coral cover has remained relatively high. Average coral cover on the patch reefs typically ranges from 15% to 35%, whereas values offshore are <5% (Lirman & Fong, 2007; Ruzicka et al., 2013). This is counter-intuitive because inshore sites experience environmental conditions that are perceived as marginal for coral survival: greater thermal variability, increased turbidity/depressed light, increased sedimentation, and elevated nutrients. In spite of this, coral growth and calcification are faster inshore relative to offshore and resilient to both cold and warm-water stress (Lirman & Fong, 2007; Manzello, Enochs, Kolodziej, & Carlton, 2015a,b; Manzello, Enochs, Kolodziej, Carlton, & Valentino, 2018).

Direct human impacts are unlikely to be driving the disparate cross-shelf trajectories in coral cover because the inshore sites are closer to human population centers and land-based sources of pollution (Lirman & Fong, 2007). As such, the higher coral cover on the inshore reefs has been hypothesized to be due to increased resistance and/or resilience of local corals to elevated temperatures and bleaching (Kenkel & Matz, 2016; Kenkel et al., 2013). In this case, resistance is defined as the ability of a coral to withstand elevated temperatures without bleaching and resilience is the ability to recover from bleaching. Two mechanisms that have been proposed for this inshore bleaching resistance/resilience are as follows: (1) coral host and/or symbiont adaptation and/or acclimatization to high and variable temperatures and/or (2) stress-mitigating environmental factors (lower light and elevated pH).

To address these hypotheses, we measured bleaching prevalence and took tissue samples from 179 *Orbicella faveolata* colonies across 10 inshore and offshore reef sites in the Upper and Lower Florida Keys during the second year of back-to-back coral bleaching in 2014 and 2015, and again during recovery in 2016. Colony condition was visually scored *in situ* as bleached, partially bleached, pale, or non-bleached according to established protocols (FRRP, 2011). Tissue samples were obtained to determine host genotype, as well as symbiont type and abundances using quantitative PCR (qPCR) and 2bRAD. Temperature, light, and pH sensors were deployed at the sample sites to characterize environmental conditions. One year after bleaching (August 2016), we measured the percent cover of all scleractinian corals, the *Orbicella annularis* species complex, and macroalgae at all sites to ascertain if differences in cross-shelf coral cover were maintained. For clarity, data are summarized by region as follows: Lower Keys Offshore (LKO, n = 2 sites), Lower Keys Inshore (LKI, n = 2), Upper Keys Offshore (UKO, n = 3), and Upper Keys Inshore (UKI, n = 3) (Figure 1, Table S1).

2 | MATERIALS AND METHODS

2.1 | Sites

Paired inshore–offshore sites were identified in the Upper (n = 6: 3 inshore, 3 offshore) and Lower (n = 4: 2 inshore, 2 offshore) Florida Keys (Figure 1). An attempt was made to find sites of similar depth, but we had difficulty finding shallow offshore sites in the Upper Florida Keys with enough colonies of *O. faveolata*. Thus, two of the offshore sites were > 10 m (Table S1). The remainder of the sites was 2.6–6.1 m.

2.2 | Physical environment

At each site, hourly sea temperature was measured from September 22–25, 2015, to May 22–25, 2016, with a Seabird SBE 56 thermistor fixed to a stainless steel stake that had been hammered into the substrate. Additional Seabird SBE 56 temperature probes were previously deployed in early December 2013 at LKI1 and UKO2, providing information on temperatures coincident with bleaching in 2014 and 2015. Temperature was measured every 3 h at the Cheeca Rocks Moored-Autonomous pCO_2 buoy ($MApCO_2$, depth = 1 m) over this same time period using a conductivity–temperature sensor (Model SBE-16 plus v. 2.2, Seabird Electronics). The $MApCO_2$ buoy is approximately 250 m from UKI1. To estimate conditions for LKO prior to September 2015, we used temperatures from a Seabird SBE 56 that was affixed to the Sand Key lighthouse at 1 m (Figure 1).

Photosynthetically active radiation (PAR, 400–700 nm) was measured hourly using an EcoPAR (Wet Laboratories) from September 21-22, 2015, to May 23, 2016, at LKI1 and LKO1. PAR data were collected inshore–offshore from October 8, 2015, to May 25, 2016, at UKI2 and UKO2. The EcoPAR sensors have a built-in wiper,

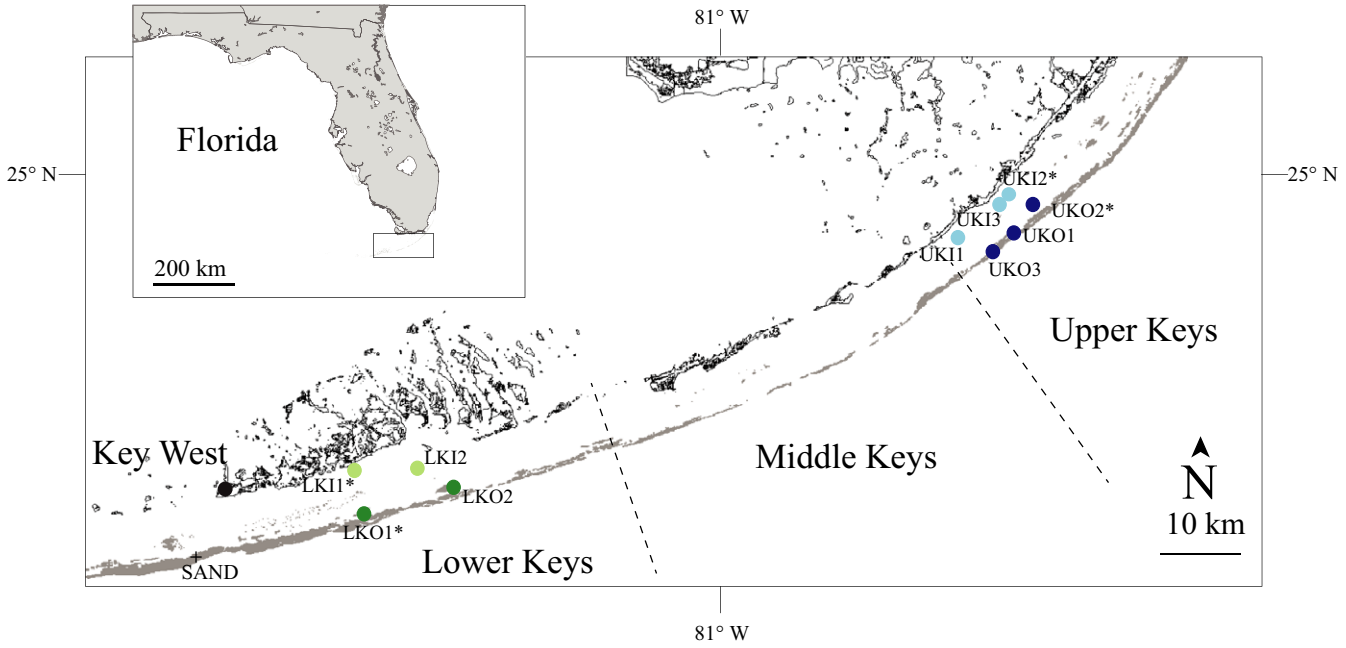

FIGURE 1 Map of 10 study sites in the Upper and Lower Florida Keys. Asterisks indicate deployment location of PAR and pH sensors. SAND, Sand Key Lighthouse

eliminating the need for regular cleaning of the sensor. PAR sensors were swapped at each site with new sensors on March 2, 2016, (LKI, LKO) and March 3, 2016 (UKI, UKO). The time period up to the swap in early March 2016 is referred to as deployment 1, whereas from March-May 2016 is referred to as deployment 2. PAR daily dose was calculated as described in Manzello et al. (2009).

Seawater pH was measured hourly over the same time at the same sites as the PAR sensors. The pH sensors were also swapped with new instruments at each site in early March at the same time as the PAR sensors. During deployment 1, a SAMI pH sensor (Sunburst) was used at LKI1 and there are no data for LKO1 because the sensor at that site was lost. For all other sites and deployments, SeaFET pH sensors (Satlantic) were used. Seawater samples were collected in 500 ml borosilicate glass bottles and poisoned with 200 µl $HgCl_2$ when the instruments were initially collected and upon recollection. Samples were analyzed for total CO_2 and total alkalinity as described in Enochs et al. (2015). The calculated pH (total scale) values from these bottle samples were used to calibrate the pH sensors; offsets between the bottle values and sensor readings were applied. The pH sensors recorded quality data for different lengths of time, and thus, statistical comparisons were only performed for when data overlapped. For deployment 1, this was October 7, 2015, to November 29, 2015. For deployment 2, this was March 3, 2016, to May 3, 2016.

2.3 | Coral tissue sampling

During peak bleaching (22-25 September 2015), 20 colonies of *O. faveolata* were assessed for condition (nonbleached, pale, partially bleached, and bleached), tagged, photographed, and sampled with a hammer and chisel from each site (n = 200 total coral samples). All corals were sampled from the top of the colony given that symbiont types can change with colony orientation (Kemp et al., 2015). Samples were immediately preserved in 95% ethanol and placed on ice for genetic analysis. The same corals were relocated and sampled from May 22–25, 2016; 190 of the original 200 corals were resampled. Ten corals could not be relocated. We did not find any evidence of the original colony sampled (i.e., dead coral) as pictures of the sampled colonies were brought on the second set of dives to assist with relocation. It is most likely that human error in the original location mapping occurred rather than coral mortality. After careful consideration of all the photographs, it was determined that 11 of the corals sampled were either *Orbicella annularis* or *Orbicella franksi*, which was also supported by 2bRAD results. These corals were removed from the analysis, leaving a total sample size of 179.

2.4 | 2bRAD genotyping

2bRAD libraries were prepared generally following Wang, Meyer, McKay, and Matz (2012) with modifications described in the protocol hosted within the 2bRAD GitHub repository (https://github.com/z0on/2bRAD_denovo). Most importantly, the new protocol involves additional 12-fold in-read barcoding that considerably reduces library preparation effort and uses degenerate bases within ligated adaptors to remove PCR duplicates. We have included five groups of genotyping triplicates where we prepared three replicate 2bRAD libraries from the same coral sample. The replicates were originally intended to facilitate genotype quality filtering (Dixon et al., 2015), but proved to be most instrumental in identifying natural clones, as described in the next section. The reads were split by barcode, adaptor-trimmed, deduplicated, quality-filtered, and mapped to the *O. faveolata*

genome (Prada et al., 2016) as described in the documentation in the 2bRAD GitHub repository.

2.5 | Clonal and genetic structure

To identify clones, we used the single-read sampling approach in ANGSD (Korneliussen, Albrechtsen, & Nielsen, 2014) to compute identity-by-state (IBS). IBS is the proportion of times when two randomly sampled reads covering a SNP site match between the two compared individuals. The major advantage of this method of measuring pairwise genetic distance is that it is robust to variation in sequencing coverage among individuals. The data for this analysis were filtered requiring minimal mapping quality of 20, at least 85% of nonmissing genotypes, and minimum allele frequency of 0.05, leaving 14,166 SNPs. Pairwise IBS distances were clustered using function *hclust()* in R and displayed as a tree diagram (Figure 2). This identified groups of samples showing the same pairwise IBS level as our genotyping replicates; these samples were deemed natural clones. This analysis also revealed that 11 sampled corals were likely not from the target species, which was then confirmed by re-examining the photographs of these corals in the field. To explore genetic structure in the retained samples, the data were pruned to leave a single representative sample per genet (resulting in 107 samples). Genotype likelihoods were calculated in ANGSD with the following filters: p-value that SNP is true 1e-6, minimal mapping quality 20, minimal base quality 20, minimal number of genotyped individuals 90, minimal p-value for deviation from Hardy–Weinberg equilibrium 0.05, minimum *p*-value for strand bias 0.05, and minimum allele frequency 0.05. This filtering retained 6,947 SNPs. The results were analyzed using NGSadmix (Skotte, Korneliussen, & Albrechtsen, 2013), which performs ADMIXTURE analysis (Alexander, Novembre, & Lange, 2009) operating on genotype likelihoods data rather than on actual genotype calls. The resulting bar charts for K (number of genotypic clusters attempted) ranging from 2 to 6 were examined visually to conclude that there was no detectable genome-wide *O. faveolata* divergence throughout the Keys.

2.6 | Algal symbiont profiling based on 2bRAD data

The same 2bRAD sequencing data were mapped to a combination of coral reference genome and symbiont transcriptomes for the four Symbiodiniaceae genera (*Symbiodinium*, *Breviolum*, *Cladocopium*, and *Durusdinium* formerly assigned to clades A, B, C, and D, respectively: LaJeunesse et al., 2018). Transcriptomes for *Symbiodinium* and *Breviolum* were from Bayer et al. (2012), and transcriptomes for *Cladocopium* and *Durusdinium* were from Ladner, Barshis, and Palumbi (2012). We then counted the relative proportions of reads producing highly unique matches (with mapping quality 40 or better) to each symbiont transcriptome. To estimate relative overall abundance of algal symbionts, we have calculated the proportion of all such reads relative to number of reads matching to the longest coral host contig.

2.7 | Symbiont assemblage analysis based on qPCR

Genomic DNA was extracted using the organic extraction protocol described in Rowan and Powers (1991). Quantitative PCR (qPCR) assays were used to understand patterns of algal symbiont community structure and detect the presence of background symbiont types not detectable by traditional methods (Mieog, Van Oppen, Berkelmans, Stam, & Olsen, 2009). Assays targeted specific actin loci in *O. faveolata* of *Symbiodinium*, *Breviolum*, *Cladocopium*, and *Durusdinium* since *O. faveolata* has been shown to associate with members from all of these genera (Kemp et al., 2015). Assays for *O. faveolata*, *Symbiodinium*, and *Breviolum* were performed using the same primers and reactions as described in Cunning and Baker (2013), whereas assays for *Cladocopium* and *Durusdinium* were multiplexed and performed as described in Cunning, Silverstein, and Baker (2015). All assays were validated for target specificity and amplification efficiency as described in Cunning et al. (2015). Reactions were performed in duplicate in volumes of 10 μL (using 5 μL of Taqman Genotyping MasterMix and 1 μL of genomic DNA template) in a StepOnePlus Real-Time PCR System (Applied Biosystems, USA). Detection levels

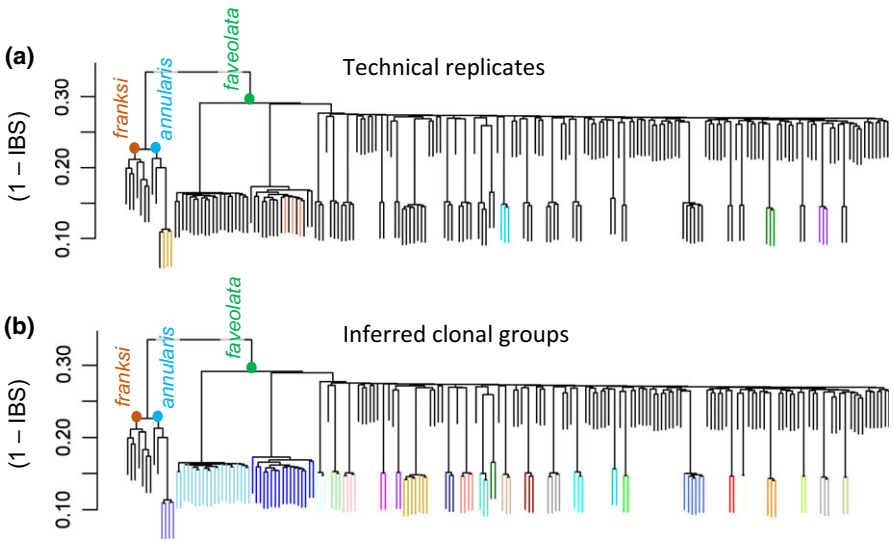

FIGURE 2 Identification of clonal groups using identity-by-state (IBS) analysis of 2bRAD data. (a) Hierarchical clustering of genotyped corals by genetic distance (1-IBS). Technical replicates (i.e., the same coral sample genotyped multiple times) are represented by branch tips of the same color. (b) The same dendrogram as in (a), with inferred clonal groups colored. Eleven samples (including one clonal group) that were notably dissimilar from the rest were identified as *O. franksi* or *O. annularis* after revisiting in situ photographs

were established with standard curves generated using known concentrations of target DNA. Cycle threshold (CT) values were calculated by the StepOnePlus software package using a fluorescence threshold of ΔR n = 0.01. Positive amplifications were counted when both technical replicates produced cycle threshold (CT) values <35, and there was no amplification in the negative controls.

Thirteen of the coral samples visually scored as bleached could not be amplified by qPCR. Therefore, we relied on the 2bRAD data for endosymbiont abundance (a quantitative measure of bleaching, see below) as well as proportion of *Durusdinium trenchii* (formerly *Symbiondinium trenchii* within clade D) within the endosymbiont population given its ability to resolve the most bleached corals. We used qPCR data to examine the trends in the relevant amounts of different symbiont genera during and after bleaching.

As proportion data do not conform to the assumptions of normality, coral colonies were categorized as being either *Symbiodinium*, *Breviolum*, *Cladocopium* or *Durusdinium* dominant (defined as the colony having >50% of the algal symbionts of that particular genera) to get a binomial response (either dominance or not). Differences in the proportions of symbiont dominance were then assessed between colonies using chi-squared tests to assess differences in community composition among regions (UKI, UKO, LKI, and LKO) per time point sampled (September 2015 and May 2016). To test the probability of a colony bleaching as a function of location and *Durusdinium* dominance, a nominal logistic regression was used with "thermal stress" (defined as any visible discoloration or bleaching) as the binomial response variable (0-no thermal stress, 1-thermal stress). This approach is similar to a linear regression with proportion of colonies bleached as the dependent variable; however, in this case, the logistic regression assumes that the probability distribution is binomial instead of normal (Quinn & Keough, 2002; Yee & Barron, 2010).

2.8 | Bleaching and recovery

Two independent measures of bleaching were analyzed: visual bleaching scores (bleached, partially bleached, pale, or nonbleached) and proportion of 2bRAD reads mapping to symbiont transcriptome (log-transformed). Every ramet (including unique genets) was given a unique number to be incorporated into mixed models as a random effect. To determine whether there was an effect of specific reef location or of inshore/offshore difference after accounting for the effect of the genet, ordinal mixed model incorporating bleaching scores as fixed effect and random effect of genet was fitted using function *clmm2*, package "ordinal" in R. The analogous model for the reads proportion data was fitted using function *lmer*, package "lme4" in R. To see whether being a part of the clonal group provided any benefit in terms of bleaching resistance, we have also fitted models with an additional two-level fixed factor "isclone." All these models were then compared via a likelihood ratio test to the corresponding null models containing only the random effect of genet. Point estimates and 95% credible intervals of per-location bleaching rates were obtained by fitting the same mixed models using *MCMCglmm* function (package "MCMCglmm" in R: Hadfield, 2010) and summarizing the posterior distribution of sampled parameter values. The ordinal model included a prior fixing the residual variation at unity, as recommended (Hadfield, 2010). Recovery was analyzed based on visual scores only (either "nonbleached" or "pale"), as no reads-based measures were available for recovering corals. We define "recovery" as when the coral colony was scored as "nonbleached" and having full pigmentation in the field. This comes with the caveat that visual determinations of coral health via color scoring have limitations as visual appearance does not always conform to physiological performance (See Fitt, Brown, Warner, & Dunne, 2001; Grottoli et al., 2014; Manzello et al., 2009). In spite of this known limitation, we did find a significant correlation between symbiont abundances using 2bRAD reads and visual scoring (Figure S1), but it is cautioned that fully pigmented corals may still have impaired physiological performance and reproductive output. Recovery was analyzed using Fisher's exact tests comparing (i) recovery of all corals inshore vs. offshore and (ii) recovery of clone-group members to recovery of unique genotypes, separately for inshore and offshore locations.

2.9 | Quantitative genetics

Broad-sense heritability (proportion of variation explained by clonal structure) was estimated for visual bleaching scores, log-transformed proportion of symbiont reads, and arcsine-square root of proportion of *Durusdinium* relative to other symbiont genera. Heritability models were fitted using MCMCglmm package in R (Hadfield, 2010); credible intervals were calculated from the distribution of parameter values sampled from the posterior. The models incorporated reef location as a fixed effect to control for variation due to environmental differences. This term would also absorb some of the genetic variation if populations were locally adapted; since this was likely the case our heritability estimates are conservative (it must be noted that omitting the location term results in only minor increase in heritability). Heritability was calculated as the proportion of residual variation after accounting for the fixed effect of location attributable to genet identity, which in this model setting essentially quantified variation due to differences between genets at the same location. This approach was possible because there were different clonal groups, including replicates for the same genets, at each location. Location UKI2 contained just a single genet; in this case, the effect of location was confounded with the effect of genet, resulting in omitting UKI2 from the ordinal analysis of visual color scores and broad credible interval in analysis of 2bRAD-derived symbiont abundances.

2.10 | Photograph transects

In August 2016, four 10 m transects were haphazardly placed at each site and photographs were taken of the benthos every meter from approximately 1 m above the substrate (n= 40 images per site). The percent cover of coral, macroalgae, *Orbicella faveolata*, *Orbicella franksi*, and *Orbicella annularis* was determined by overlaying 40 random points per image using CPCe (Kohler & Gill, 2006). Statistical analyses were conducted using the software JMP® Pro version 12

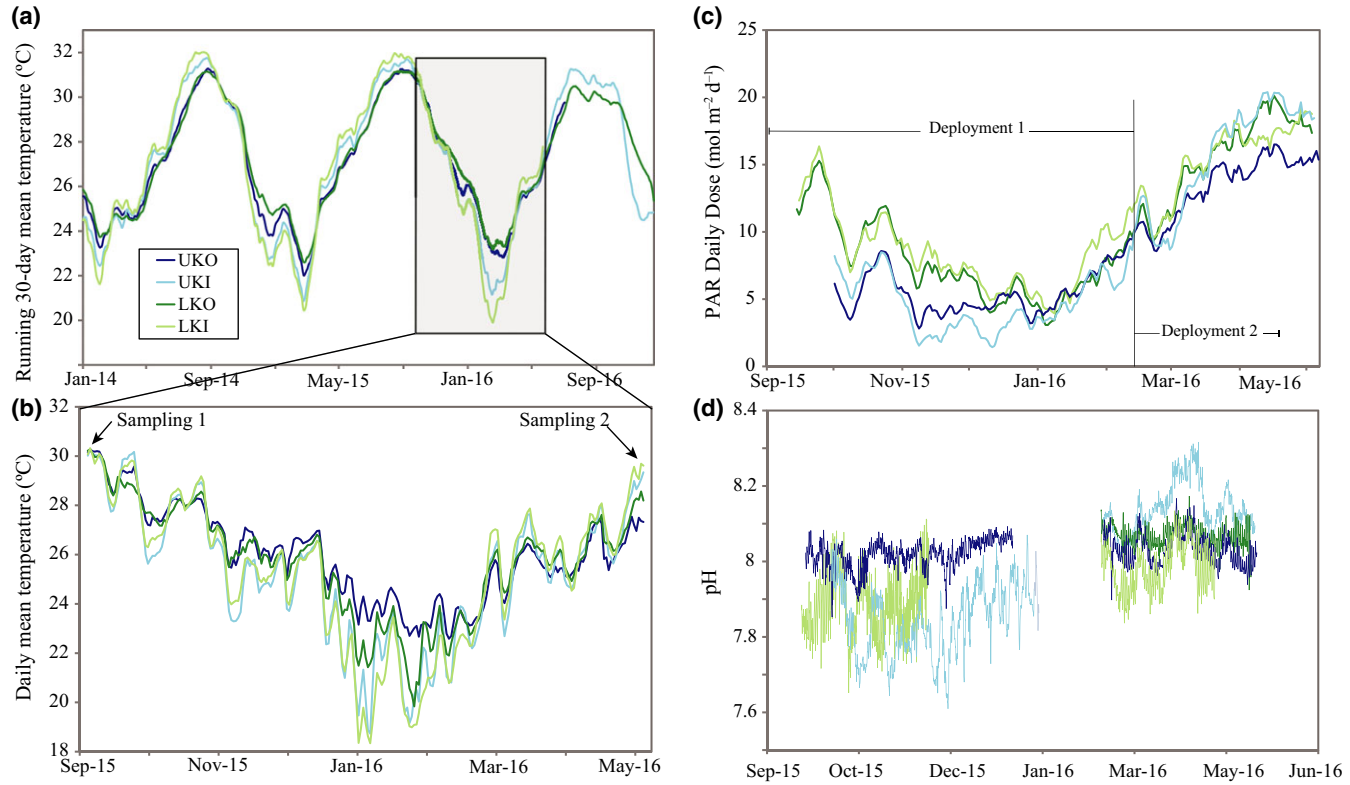

FIGURE 3 Environmental conditions for inshore and offshore sites in the Upper and Lower Florida Keys. (a) Running 30-day mean sea temperature from 2014 to 2016 and (b) daily average temperatures between the initial and final sampling in 2015 and 2016. (c) Daily dose of photosynthetically active radiation (PAR) and (d) 3-hourly seawater pH. UKO, Upper Keys Offshore; UKI, Upper Keys Inshore; LKO, Lower Keys Offshore; LKI, Lower Keys Inshore

TABLE 1 Mean, *SE*, maximum and minimum of daily average temperatures (°C) in the summer of 2014 and 2015. 30 d is maximum running 30-day mean temperature

	2014				2015			
	LKO	LKI	UKO	UKI	LKO	LKI	UKO	UKI
Mean	30.4	31.3	30.5	31.0	30.9	31.7	30.8	31.3
SE	0.08	0.10	0.07	0.09	0.05	0.08	0.06	0.06
30 d	31.2	32.0	31.3	31.8	31.2	32.0	31.2	31.7
Max	31.7	32.6	32.0	32.6	31.8	32.9	31.9	32.4
Min	28.5	28.3	28.8	28.7	29.8	29.2	29.7	29.1

(SAS Institute Inc., Cary, NC, USA), R Studio (R Core Team, 2015), and SigmaPlot 12.

3 | RESULTS

3.1 | Temperatures and bleaching prevalence

Inshore temperatures were significantly warmer (+0.5 to +0.9°C) than offshore during summer and cooler (−1.1 to −4.0°C) in winter (Kruskal–Wallis one-way ANOVA and Tukey Post hoc tests) (Figure 3, Tables 1 and S2). All sites were 0.3–0.4°C warmer in 2015 than 2014 (Mann–Whitney *U* tests, $p < .05$). LKI was the hottest of all regions (Tukey test, $p < .05$).

Inshore reefs bleached less (Likelihood ratio test, $p < .05$) and recovered significantly better than offshore reefs (Fisher's exact test, $p < .001$) (Figure 4). UKO exhibited the most evidence of thermal stress as 84% of corals were pale, partially bleached or bleached in September. The endosymbiont abundances measured as proportion of algal symbiont 2bRAD reads relative to coral host reads were well correlated with the visual scoring of bleaching ($r = .66$, $p < .001$, Figure S1), and differences in bleaching among sites inferred using these two methods (linear model of log-transformed read-based data and ordinal model for visual scores) were nearly identical ($r = .91$, $p < .001$, Figure 4e).

There was one outlier to this trend as there was high bleaching prevalence at one inshore site in the Lower Keys (LKI1, Jaap Reef) (Figure 4). However, all the corals at this site had full pigmentation by May 2016. Despite having significantly hotter temperatures than the offshore sites, none of the 60 colonies sampled at UKI were bleached and 70% had normal pigmentation; all corals at UKI had

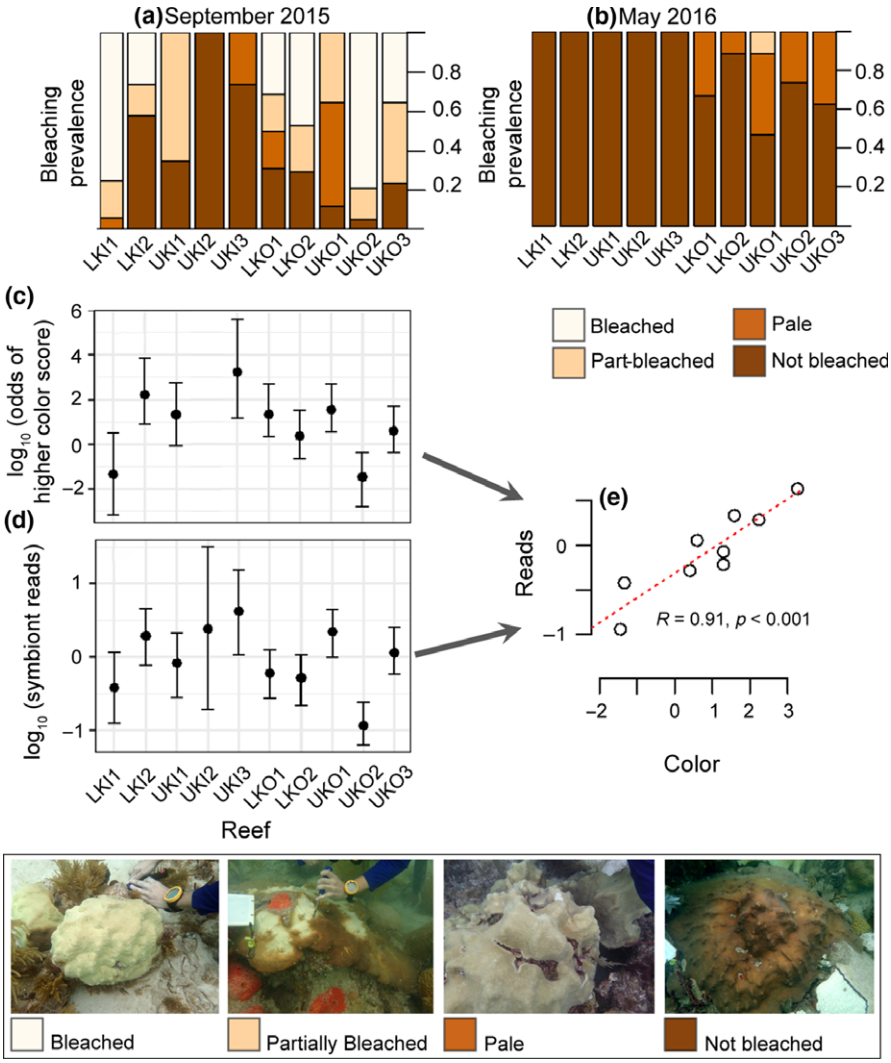

FIGURE 4 Coral colony condition of *O. faveolata* in September 2015 and May 2016 for inshore and offshore sites in the Lower and Upper Keys. (a) Stacked bar graph of visual bleaching scores assessed in September 2015 (peak bleaching) and (b) May 2016 (recovery). (c, d) Model-derived per-site bleaching rates, according to the ordinal mixed model based on visual scores (c) and linear mixed model based on proportion of symbiont reads (d). (e) Correlation between model-derived bleaching rates. Photographs taken during sampling in September 2015 from following sites: Bleached, UKO2; Partially bleached, LKI2; Pale, UKO1; Not bleached, LKI2

completely recovered by May (Figure 4). This quicker recovery inshore was significant (Pearson chi-square, $X^2 = 40.1$, $p < .001$). The offshore sites showed slower recovery as 23% of corals in LKO were still pale, whereas 40% in UKO were still pale or partially bleached.

3.2 | Spatiotemporal patterns in algal symbiont community

Only 16.2% of the *O. faveolata* colonies hosted a single symbiont type, as most colonies hosted mixtures of 2, 3, or all 4 symbiont genera. Notably, *D. trenchii* was the dominant symbiont type both at the initial (78.0%) and final (77.2%) time points (Figure 5). The dominant symbiont genera remained the same from bleaching through recovery in 82.3% of the colonies (Figure S2). However, the number of colonies dominated by *Breviolum* did increase, while those dominated by *D. trenchii* decreased during recovery at UKO (Figure 5). Conversely, every coral at LKO became dominated by *D. trenchii* between September 2015 and May 2016. *Symbiodinium* (formerly clade A) and *Cladocopium* (formerly clade C) were no longer dominant within corals at any location after recovery except for UKO (Figure S2).

There was a strong relationship between *D. trenchii* abundance and bleaching in both the qPCR ($X^2 = 31.5$, $p < .001$) and 2bRAD data ($r = .52$, $p < .001$), as > 90% of the nonbleached corals were dominated by *D. trenchii*. The one outlier inshore site (LKI1), which had the highest bleaching prevalence of inshore sites, was also the inshore site with the least amount of *D. trenchii* (Figure 6c).

3.3 | Clonal and genetic structure

The frequency of host clonal ramets sampled from one genet was greater inshore (Figure 6a). At one of these locations, UKI2, all 20 sampled coral colonies were ramets of the same genet despite being up to 40 m apart and spanning an area sampled of 983 m^2. Interestingly, within a reef site, ramets were not spatially clustered (Figure S3); on average distances between them were only slightly smaller than between distinct genets (Figure S4). Still, no clonal groups spanned multiple reef sites. After removing all but one ramet of each genet from the dataset, essentially no genetic structure could be detected across the sampled locations (Figure S5).

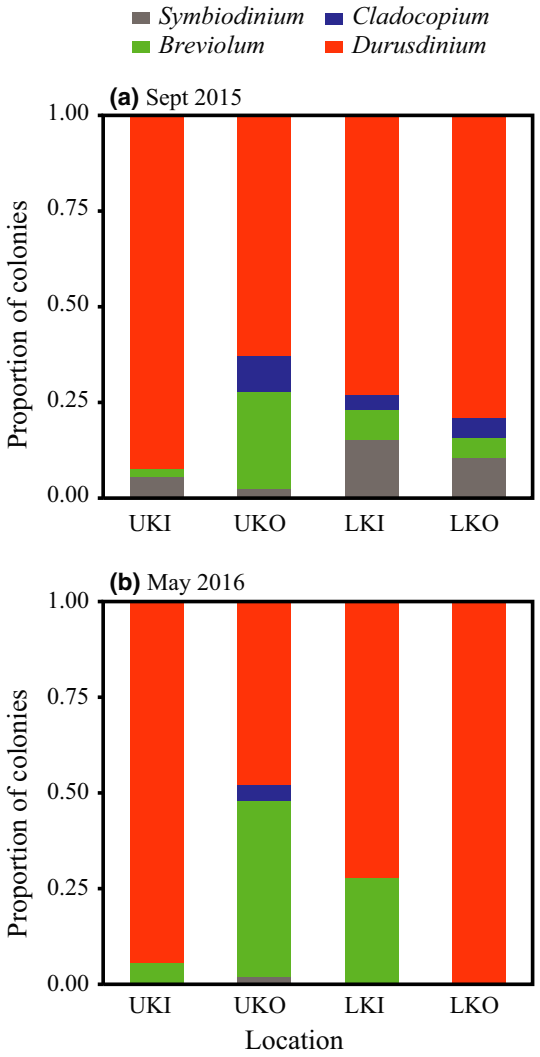

FIGURE 5 Proportion of colonies which were dominated by symbiont genera *Symbiodinium*, *Breviolum*, *Cladocopium*, and *Durusdinium* in (a) September 2015 and (b) May 2016

3.4 | Broad-sense heritability of bleaching resistance and proportion of *D. trenchii*

Both total symbiont density and proportion of *D. trenchii* making up the symbiont population within a colony varied greatly among genets, but were similar among ramets of the same genet (Figure 6). The proportion of variation attributable to coral's genet identity (i.e., broad-sense heritability, H^2) was nearly the same for the proportion of *D. trenchii* symbionts (H^2 = 0.73) as for total symbiont amount (H^2 = 0.71) (Table 2).

The models could not be improved by adding a fixed effect defining whether the coral colony was a member of a clonal group, which indicates that genets that are represented by multiple ramets are not inherently different in their bleaching resistance from other genets at the same reef site. Multi-ramet genets also did not recover better than their peers, after controlling for the difference in recovery between inshore and offshore sites.

3.5 | Light and pH during recovery

Photosynthetically active radiation (PAR, 400–700 nm) did not follow consistent cross-shelf trends by region or season. UKI had the highest PAR daily dose of all sites in spring, but lowest values in autumn and winter (Figure 3c, Table 3). UKO had the lowest PAR values of all sites in spring, and there were never any inshore–offshore differences in the Lower Keys (Tables 3 and S3). Seawater pH was highly variable inshore with UKI exhibiting a very large seasonal range (Figure 3d, Tables 3 and S3). UKI had the lowest pH of all sites in autumn/winter and highest pH in spring. At LKI, pH was similarly low to UKI in autumn, but there was no elevation during spring. There was little seasonal change in pH offshore, as mean pH increased 0.034 units from fall/winter to spring at UKO.

3.6 | Benthic cover after bleaching recovery

Total coral cover was significantly higher at the inshore sites, with mean values of 16.8% and 17.5% at UKI and LKI, respectively (Tables 4 and S4). The dominant benthic type in the Upper Keys was macroalgae (range of means: 56.4%–69.1%), whereas it was turf algae in the Lower Keys (35.5%–49.6%). All offshore sites had *Orbicella annularis* spp. coverage of <1% and low total coral cover. The two deeper offshore sites in the Upper Keys had the lowest total coral cover (1.5%–1.6%) and *O. annularis* species covered 0.1% of the benthos at each site. For the inshore sites, total coral cover was no different between the Upper and Lower Keys and overall coverage by the *O. annularis* species complex was similar (Table 4). *O. annularis* was the dominant coral at LKI, whereas at UKI it was *O. faveolata*.

4 | DISCUSSION

Despite having significantly hotter temperatures than the offshore sites, *O. faveolata* at the inshore sites bleached less and recovered faster. In fact, none of the 60 colonies sampled at UKI were bleached in September 2015, as 70% had normal pigmentation (Figure 4a). There was a strong relationship between *D. trenchii* abundance and bleaching, as >90% of the nonbleached corals were dominated by *D. trenchii*. UKI had the most corals dominated by *D. trenchii*. This correlation of bleaching resistance with the proportion of *D. trenchii* symbionts follows what has been observed in multiple previous works (e.g., Baker, Starger, McClanahan, & Glynn, 2004; Berkelmans & van Oppen, 2006; Jones, Berklemans, van Oppen, Mieog, & Sinclair, 2008).

An exception to the overall trend of high bleaching resistance and dominance by *D. trenchii* symbionts on the inshore reefs occurred at LKI1, or Jaap Reef. As previously mentioned, this site had the highest bleaching prevalence and least number of colonies dominated by *D. trenchii* of all inshore sites (Figure 6). In September 2015, 54% of the corals at LKI1 were dominated by *D. trenchii*, 31% by *Symbiodinium*, and 15% by *Breviolum*. In May 2016, the proportion of corals dominated by *D. trenchii* was nearly identical (53%) to

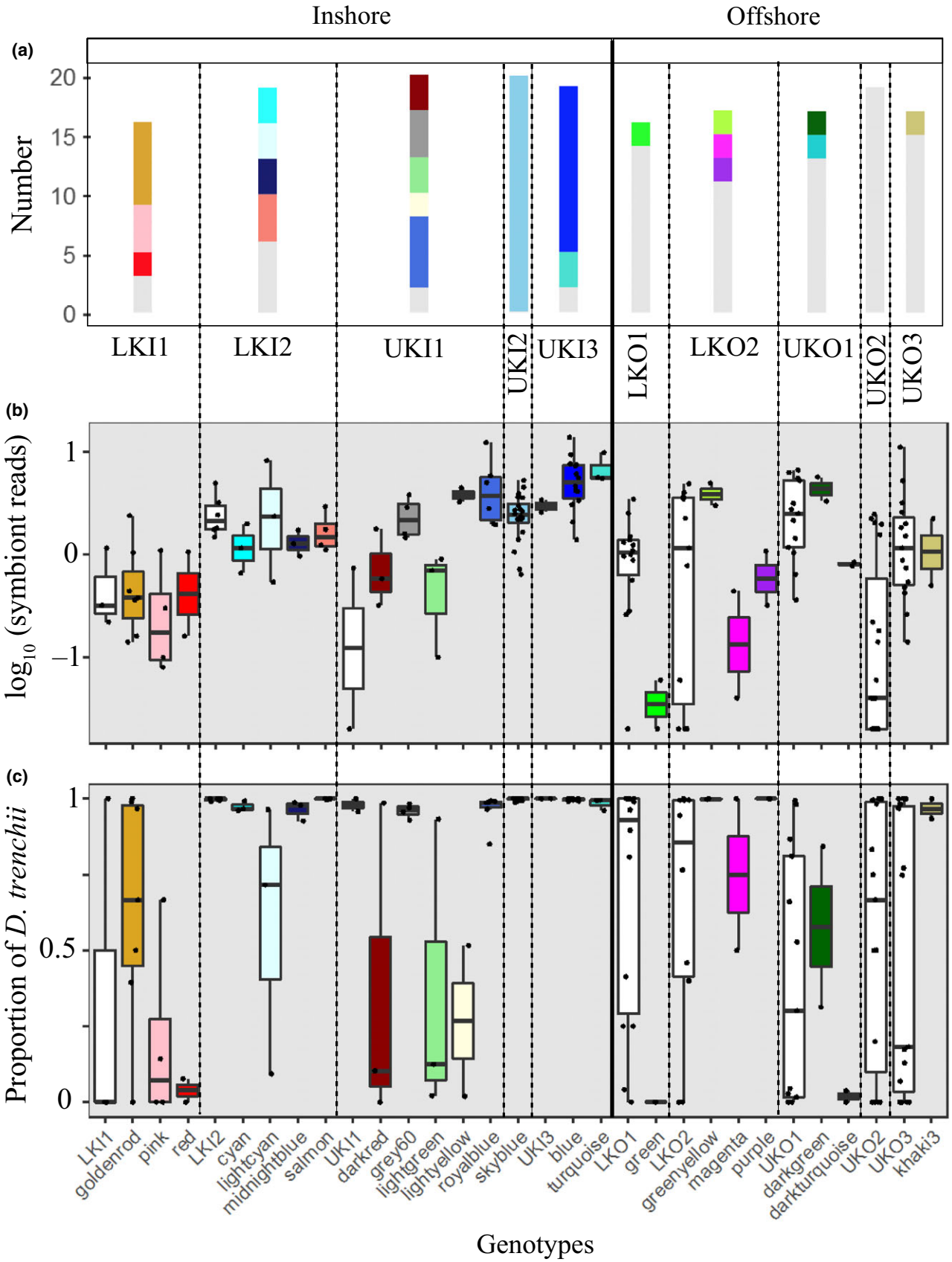

FIGURE 6 Host clonal structure, symbiont abundance, and proportion of *D. trenchii* symbionts within the symbiont population of *O. faveolata* across sites. (a) Stacked bar plot of coral counts at each site, colors representing distinct clonal groups and gray corresponding to unique genotypes. (b) Box plots of log-transformed proportions of 2bRAD reads relative to the coral host reads, and (c) proportions of *D. trenchii* relative to other genera. Colored boxes represent clonal groups as in panel (a), white boxes correspond to all unique genotypes from a given site

TABLE 2 Broad-sense heritability (H^2) of bleaching tolerance, estimated as proportion of trait variation explained by differences between genets. All models were fitted using MCMC and included location as fixed effect and genet as a scalar random effect

Trait	H^2 (95% CI)
Symbiont abundance during bleaching event, reads-based	0.71 (0.56–0.82)
Visual bleaching score (ordinal)	0.93 (0.87–0.98)
Proportion of *D. trenchii*	0.73 (0.62–0.83)

September, while the remainder of the corals were *Breviolum* dominated. Jaap Reef was the shallowest of all our sites (2.6 m) and had the highest PAR values of all sites in autumn, and high values again in spring, only slightly less than UKI1 (Table 3). This site also experiences the highest and lowest temperatures of all sites (Figure 3). *Symbiodinium* is a known high light and high temperature specialist (Kemp, Hernandez-Pech, Iglesias-Prieto, Fitt, & Schmidt, 2014), which may explain its abundance at Jaap Reef. *Symbiodinium* is rare in the Florida Keys and it has been hypothesized that this genus may be at a competitive disadvantage to *Breviolum* and *Cladocopium* due to cold sensitivity (Kemp et al., 2015). The fact that no corals were dominated by *Symbiodinium* in May, following the coolest part of the year, could be indicative of the cold sensitivity of this symbiont genus. Indeed, 75% of the corals that were *Symbiodinium* dominated in September 2015 later became *Breviolum* dominated, whereas the remainder became dominated by *D. trenchii*. This suggests that *D. trenchii* may be at a disadvantage when high light conditions co-occur with high temperatures. Summertime mean and maximum temperatures were 0.4–0.5°C higher at LKI versus UKI in 2015; thus, there could also be upper thermal limits whereby the bleaching resistance gained by hosting *D. trenchii* is lost.

To our knowledge, this is the first time it has been shown that both bleaching resistance and the proportion of *D. trenchii* symbionts were highly consistent among naturally occurring clonal ramets. Previous work has highlighted that ramets from one genet exhibit similar bleaching responses (Edmunds, 1994), but the symbiont types within the ramets were not investigated. Heritability is a measure of the genetic components of a trait or phenotype, as opposed to environmental factors, and ranges from 0 to 1 such that higher numbers indicate a greater degree of genetic influence and thus, potential for adaptation (Falconer & Mackay, 1996). Recent work has shown that the symbiont communities of corals are a heritable trait, even in a coral species that acquires symbionts environmentally (Quigley, Willis, & Bay, 2017). This means that host genetics factor into the resultant symbiont assemblages even when larvae do not acquire symbionts maternally. Our heritability estimates for bleaching resistance and the proportion of *D. trenchii* in the symbiont population were high, as were values obtained in a heat stress experiment on *O. faveolata* (Dziedzic, Elder, & Meyer, 2017). This suggests that the potential for adaptive responses to warming in *O. faveolata* do exist, but more work is required to better understand the real-world ramifications of these heritability estimates relative to the rate and magnitude of present-day warming and environmental degradation.

Different coral genotypes on the same reef whose symbiont populations were similarly dominated by *D. trenchii* exhibited differing degrees of bleaching resistance (see UKI1, Figure 6). Given that

	Fall/Winter				Spring			
PAR	LKO	LKI	UKO	UKI	LKO	LKI	UKO	UKI
Mean	7.47	8.20	5.70	5.07	15.98	16.02	13.77	16.16
Median	7.26	8.57	5.46	4.46	17.77	17.29	14.69	18.16
SE	0.359	0.384	0.274	0.331	0.610	0.597	0.477	0.684
Min	0.01	0.08	0.14	0.01	0.75	0.72	3.29	1.19
Max	18.63	18.90	12.49	15.19	23.15	22.91	19.66	24.18
pH								
Mean	n/a	7.893	8.005	7.819	8.072	7.979	8.039	8.145
Median	n/a	7.892	8.012	7.810	8.070	7.977	8.035	8.131
SE	n/a	0.003	0.002	0.003	0.001	0.003	0.002	0.003
Min	n/a	7.654	7.854	7.645	7.981	7.837	7.900	8.005
Max	n/a	8.112	8.078	8.059	8.171	8.134	8.167	8.316

TABLE 3 Daily dose of photosynthetically active radiation (PAR) and pH during 1st (October 2015–February 2016) and 2nd deployment (March–May 2016). PAR daily dose, mol m^{-2} d^{-1}. pH on total scale. SE, std. error of mean

Site	*n*	Total Coral	*O. annularis*	*O. faveolata*	Macroalgae	Turf Algae
LKI	2	17.5 (1.34)	10.0 (1.06)	1.0 (0.42)	15.2 (1.93)	49.6 (2.68)
LKO	2	7.4 (1.12)	0.0	0.8 (0.44)	6.5 (0.80)	35.5 (1.53)
UKI	3	16.8 (1.55)	0.7 (0.34)	11.3 (1.53)	56.4 (2.03)	17.0 (1.43)
UKO	3	3.3 (0.66)	0.0	0.3 (0.11)	69.1 (1.47)	10.4 (0.76)

TABLE 4 Percent cover of all scleractinian corals, *Orbicella annularis*, *Orbicella faveolata*, macroalgae, and turf algae. Values are means (± *SE*). *n*, number of sites

the degree of bleaching resistance was similar among clonal ramets, and ramets were haphazardly distributed among reefs (Figure S3), it seems unlikely that the differences in bleaching resistance between genets could be due to differences in microenvironment. Rather, this suggests an interaction of host genotype and algal symbiont, such that certain coral genotypes may garner more heat tolerance from *D. trenchii* than others. Different genotypes of *Acropora palmata* exhibited a 3.6-fold variance in photochemical efficiency with cold stress despite having clonal symbionts (Parkinson, Banaszak, Altman, LaJeunesse, & Baums, 2015). This is in line with recent work showing the importance of the coral host to bleaching resistance (e.g., Dixon et al., 2015; Howells, Abrego, Meyer, Kirk, & Burt, 2016; Kenkel & Matz, 2016; Kenkel et al., 2013; Palumbi, Barshis, Traylor-Knowles, & Bay, 2014).

We genotyped only the coral host and not the algal symbionts, thus it is unclear if the symbionts within clonal corals are also clonal. Unfortunately, our 2bRAD data did not contain enough symbiont reads to allow individual-level symbiont genotyping, so we can neither confirm nor exclude this possibility. If the clonal structure of the symbiont is aligned with the clonal structure of the host, it would remain unclear how much of the similarity in bleaching response between clonal coral colonies is due to genetically identical host versus genetically identical symbionts. Prior work from the Florida Keys showed that on a particular reef symbiont genotype was generally identical among different *O. faveolata* hosts and largely endemic to a site (Thornhill, Xiang, Fitt, & Santos, 2009). In other words, all colonies were dominated by the same symbiont genotype and that genotype was unique to a given site. *D. trenchii* has very low genotypic diversity in the Atlantic with a high degree of clonality, perhaps owing to its recent introduction to the Atlantic from the Indo-Pacific (Pettay, Wham, Smith, Iglesias-Prieto, & LaJeunesse, 2015). This suggests that genotypic variability at our sites was likewise low. If either of these scenarios were the case for the symbionts in our study, then this would suggest that the coral host is indeed playing the leading role in the degree of heat resistance gained from *D. trenchii*.

Finding (using two independent methods) that the majority of sampled colonies were dominated by *D. trenchii* was unexpected, since previous work consistently reported that *O. faveolata* from the Florida Keys were dominated by symbionts in the genus *Breviolum* (formerly clade B) (Baums, Johnson, Devlin-Durante, & Miller, 2010; Kemp et al., 2015; Thornhill et al., 2009). The shift in dominance from *Breviolum* to *D. trenchii* throughout the Keys is most likely the result of the back-to-back summer bleaching episodes in 2014 and 2015, since *D. trenchii* can become dominant during and after bleaching (Kemp et al., 2014; LaJeunesse, Smith, Finney, & Oxenford, 2009). We cannot rule out that this region-wide change was due to differential mortality, such that the corals dominated by *Breviolum* died, and we preferentially sampled the *D. trenchii*-dominated survivors. However, we argue that it is more likely that shuffling drove this change in region-wide symbiont dominance given that *O. faveolata* is well documented to host multiple symbiont genera simultaneously as well as readily shuffle to dominance by *D. trenchii* during and after bleaching (Kemp et al., 2014). Long-term monitoring at UKI1, a reef where *O. faveolata* is the most abundant coral, revealed that only 4 of 552 tracked colonies (<1%) died during the 2014–2015 bleaching (Gintert et al., 2018).

In previous studies, *D. trenchii* was competitively displaced, however, by less heat-tolerant symbiont genera after 2 years of recovery from bleaching (LaJeunesse et al., 2009; Thornhill, LaJeunesse, Kemp, Fitt, & Schmidt, 2006). During recovery at UKO, the number of colonies dominated by *Breviolum* did in fact increase, while those dominated by *D. trenchii* decreased suggesting a possible shift back to the symbiont assemblages previously measured for this species and location. However, every coral at LKO became dominated by *D. trenchii* from September 2015 to May 2016. Future work is necessary to determine if the endosymbiont populations within *O. faveolata* in the Florida Keys have indeed switched back to being dominated by other symbiont types as previously shown. Our result is intriguing in light of the fact that there was no change in the symbiont population structure within colonies of *O. faveolata* during the 2005 mass bleaching event in the Florida Keys, as *Breviolum* dominance was stable through time and bleaching (Thornhill et al., 2009). Therefore, the response to bleaching in *O. faveolata* in 2014 and 2015 appears to be different than the prior Keys-wide mass bleaching event in 2005. This difference may be because the bleaching in 2005 was less severe than 2014 and 2015, owing to less heat stress in 2005 (see Gintert et al., 2018).

There is debate as to whether the increased prevalence of *D. trenchii* during and after bleaching is a mechanism of acclimatization, or a symptom of stress (Pettay et al., 2015). On one hand, colonies dominated by *D. trenchii* are able to tolerate temperatures 1–2°C warmer than conspecifics hosting other symbiont types, and corals that become dominated by *D. trenchii* due to a bleaching event do gain increased heat tolerance (Silverstein, Cunning, & Baker, 2014). On the other hand, *D. trenchii* is associated with depressed calcification that could impact reef accretion (Pettay et al., 2015), as well as altered metabolic and immune activity indicative of suboptimal symbiosis in heterologous hosts (Matthews et al., 2017). Long-term monitoring data at one of the inshore sites sampled here (UKI1, Cheeca Rocks) revealed significantly less bleaching in 2015 versus 2014 despite the fact that 2015 was hotter (Gintert et al., 2018). Calcification in *O. faveolata* at Cheeca Rocks was depressed and similarly low following bleaching in 2014 and 2015 relative to non-bleaching years (Manzello et al., 2018). These observations are all in line with what is predicted to occur with a shift to *D. trenchii*. However, reef-scale carbonate production at Cheeca Rocks was resilient to bleaching and actually increased during the second year of bleaching, owing to a slight increase in coral cover (Manzello et al., 2018). Despite the fact that calcification did decline with bleaching, the community-wide bleaching resilience ultimately led to resilience in carbonate production. Clearly, more work is necessary to understand the ecosystem-scale ramifications of dynamic coral–algal symbiotic associations with thermal stress.

Annual bleaching scenarios are predicted to occur around the year 2050 for most reefs globally (Hoegh-Guldberg et al., 2007).

Recent predictions based on long-term, in situ temperature data suggest this may occur sooner, perhaps as early as the next decade in the Florida Keys (Manzello, 2015). It is generally assumed that repeated bleaching will result in compounded impacts, such that each successive bleaching event will have similar or worse impacts than the prior event. However, data on back-to-back bleaching events are limited and the studies that do exist have tended to yield nonintuitive results. At UKI1, there was a community-wide acclimatization response to back-to-back bleaching in 2014 and 2015, whereby bleaching prevalence, severity, and mortality were lower during the 2nd year of bleaching despite higher thermal stress (Gintert et al., 2018). Laboratory studies have shown that back-to-back bleaching can turn some coral species thought to be winners, or resistant to heat stress, into losers and vice versa (Grottoli et al., 2014). Multiple studies have shown that corals are often less impacted by a second bleaching event when events are separated by several or more years (Glynn, Maté, Baker, & Calderon, 2001; Guest et al., 2012; Maynard, Anthony, Marshall, & Masiri, 2008; McClanahan, 2017). Yet, other studies have observed the expected pattern of additive, negative impacts with multiple bleaching events (Neal et al., 2016; Riegl & Purkis, 2015). Warming is and will cause large-scale deleterious impacts to coral reefs (e.g., Hughes et al., 2017), but the details for how this will play out are less clear. One such outcome of repeated bleaching events could be region-wide switching to heat-tolerant symbionts in flexible coral species as we have shown here for the Florida Keys. If there are limited recovery periods as expected under annual bleaching, it seems likely that heat-tolerant symbionts will persist and not be competitively displaced.

Surprisingly, we saw no correlation of any of the examined environmental factors with bleaching. Turbidity has been associated with bleaching resistance and resilience elsewhere. Corals in the bays of Palau were more bleaching resistant than corals from offshore environments (van Woesik et al., 2012). These bays are warmer and have lower light, owing to higher levels of turbidity, and also have very low pH (Shamberger et al., 2014). A turbid reef in Singapore exhibited high resilience to bleaching, even in those species that are usually highly susceptible to bleaching (Guest et al., 2016). In our case, the more turbid inshore sites did not universally experience lower light than offshore, and the inshore site in the Upper Keys actually had the highest PAR values of all sites during spring. While we do not have light data leading up to bleaching, the patterns show that the hypothesis that inshore reefs suffer less from bleaching because shading (via increased turbidity) limits photooxidative stress may be too simplistic. The inshore sites tend to be shallower; thus, despite elevated turbidity they can still receive comparable or even greater PAR doses than the offshore sites. It has also been suggested that inshore bleaching resistance may be due to higher heterotrophic feeding as a result of the higher turbidity (Lirman & Fong, 2007). To date, there is no evidence for the hypothesis that elevated turbidity leads to increased heterotrophic feeding that could contribute to bleaching resilience of inshore reefs in the Florida Keys (Teece, Estes, Gelsleichter, & Lirman, 2011; Towle, Carlton, Langdon, & Manzello, 2015). Future research is required to better understand if there are any inshore–offshore differences in coral heterotrophy that may be linked to bleaching resilience.

High CO_2 in combination with high temperature has been reported to exacerbate bleaching (Anthony, Kline, Diaz-Pulido, Dove, & Hoegh-Guldberg, 2008), though this has been contradicted by other studies (Noonan & Fabricius, 2016; Wall, Fan, & Edmunds, 2013). The very low pH values at the inshore sites during recovery did not have a negative impact as every coral inshore, no matter the degree of bleaching severity in September 2015, completely regained normal pigmentation. In fact, the region with the lowest pH in the fall/winter and highest in spring exhibited the highest bleaching resistance. The data presented here confirm previously published patterns for seawater pH in the Florida Keys (Manzello, Enochs, Melo, Gledhill, & Johns, 2012). The large range of pH, in addition to temperature, at UKI could be stress hardening corals there, but future work is necessary to understand if there is any link between pH and bleaching, as well as if these sites are more or less susceptible to ocean acidification.

The high frequency of clonality for *O. faveolata* was unexpected, especially given that care was taken to avoid sampling coral colonies adjacent to one another that appeared to have been generated by fragmentation or fission. Recent work has also reported a high degree of clonality in *O. faveolata* from one of two sites in the Florida Keys (Miller et al., 2017). Clonality was greatest on the inshore reefs. Inshore reefs have elevated rates of macro bioerosion, corals with low skeletal density, and reef frameworks that are uncemented (James, Ginsburg, Marzalek, & Choquette, 1976; Risk & Sammarco, 1991; Sammarco & Risk, 1990). All of these factors contribute to the physical dislodgment and fracture of corals that could be facilitating the abundance of clones inshore. In this regard, it is notable that clonal groups are spatially intermixed (Figure S3), suggesting that broken-off fragments are being generated by wave action (Dubé, Boissin, Maynard, & Planes, 2017), perhaps as a result of storm or hurricane impacts (Foster, Baums, & Mumby, 2007; Foster et al., 2013). Hurricane frequency explained 26% of the variation in clone abundance in *O. annularis*, but the steepness of the reef slope was an equally good predictor (Foster et al., 2013). Conversely, hurricane frequency did not explain much of the variation in clonality observed in *A. palmata* across the Caribbean; instead, continental shelf area was the best predictor as wider shelves had more clones (Baums, Miller, & Hellberg, 2006). The rate of asexual reproduction likely depends on both the rate of fragmentation and the probability of fragments' reattachment and survival, which may be higher with the lower wave energies on inshore reefs that have little or no reef slope. Not a single clone was found at more than one reef site, indicating that the limit for this fragment dispersal is probably on the order of a few tens of meters.

Taken together, our results show that in the Florida Keys, *O. faveolata* coral–symbiont associations have adapted and/or acclimatized on inshore reefs to conditions up to ~1°C warmer than the offshore sites. Despite the fact that 2014 and 2015 were two warmest years on record for the Florida Keys (Gintert et al., 2018; Manzello, 2015), total coral cover at the inshore sites in August 2016

reflected prior patterns and was significantly higher than offshore (Lirman & Fong, 2007; Ruzicka et al., 2013). Thus, the inshore sites have still not undergone the decline seen offshore. In fact, the highest abundance of *O. faveolata* is where it was most bleaching resistant (UKI: Table 4), suggesting a causal link between heat tolerance and ecosystem resilience.

Although we did not detect genome-wide population structure in the coral host between our sites, it might be detectable in the symbionts upon their in-depth genomic analysis as previously shown for the Florida Keys (Baums, Devlin-Durante, & LaJeunesse, 2014; Thornhill et al., 2009). Even in the coral host, individual adaptive genetic variants (e.g., alleles affecting *D. trenchii* dominance) could be highly differentiated between locations due to spatially varying selection removing immigrants bearing locally maladaptive alleles of specific genes (the Levins, [1964)] model of adaptation). Even if such selection is very strong, killing 90% of all cross-habitat migrants every generation, the residual genome-wide gene flow would still be sufficient to prevent genetic differentiation between populations (Slatkin, 1987). Understanding if local genetic adaptation has taken place in this coral-zooxanthella system and identifying any locally adaptive genetic variants is a high priority task for the future.

The consistency of bleaching resistance among ramets of the same genet gives hope to restoration efforts based on clonal propagation of heat-tolerant coral genotypes to cooler offshore environments given that the inshore environments effectively represent a +1°C warming scenario for the offshore sites. Future work is necessary to determine if this increased bleaching resilience is a result of acclimatization or adaptation. If these inshore corals are acclimatized to the inshore conditions, they may lose their heat tolerance when transplanted to cooler offshore waters. If they maintain their heat tolerance, this provides some optimism for restoration activities, but it is not clear if it will be enough to cope with the anticipated warming over this century that is expected to exceed 1°C of warming.

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AUTHOR CONTRIBUTIONS

DPM conceived and designed the study. DPM, ICE, RDC, LV, GK conducted field sampling. RDC, GK, MJ conducted instrument calibration, deployment, and data recovery. Data analysis performed by DPM, MM, ICE, XS, EKT. DPM, MM prepared the manuscript with all authors contributing to its final form.

DATA ACCESSIBILITY

Physical and zooxanthellae qPCR data available from NOAA's National Center for Environmental Information (Accession #175572). Raw reads data have been deposited at the NCBI's Sequence Read Archive (SRA) database, under bio-project ID PRJNA508589. Bioinformatic walkthroughs, metadata, processed datasets, and R scripts with embedded instructions are available at the dedicated GitHub repository, https://github.com/z0on/ClonesAndClades_Ofav_Keys.

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REFERENCES

Alexander, D. H., Novembre, J., & Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Research*, *19*, 1655–1664. https://doi.org/10.1101/gr.094052.109

Anthony, K. R. N., Kline, D. I., Diaz-Pulido, G., Dove, S., & Hoegh-Guldberg, O. (2008). Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences*, *105*(45), 17442–17446. https://doi.org/10.1073/pnas.0804478105

Baird, A. H., & Marshall, P. A. (2002). Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series*, *237*, 133–141. https://doi.org/10.3354/meps237133

Baker, A. C., Glynn, P. W., & Riegl, B. (2008). Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science*, *80*(4), 435–471. https://doi.org/10.1016/j.ecss.2008.09.003

Baker, A. C., Starger, C. J., McClanahan, T. R., & Glynn, P. W. (2004). Corals' adaptive response to climate change. *Nature*, *430*, 741. https://doi.org/10.1038/430741a

Baums, I. B., Devlin-Durante, M. K., & LaJeunesse, T. C. (2014). New insights into the dynamics between reef corals and their associated dinoflagellate endosymbionts from population genetic studies. *Molecular Ecology*, *23*, 4203–4215. https://doi.org/10.1111/mec.12788

Baums, I. B., Johnson, M. E., Devlin-Durante, M. K., & Miller, M. W. (2010). Host population genetic structure and zooxanthellae diversity of two reef-building coral species along the Florida Reef Tract and wider Caribbean. *Coral Reefs*, *29*(4), 835–842. https://doi.org/10.1007/s00338-010-0645-y

Baums, I. B., Miller, M. W., & Hellberg, M. E. (2006). Geographic variation in clonal structure in a reef-building caribbean coral. *Acropora Palmata*. *Ecological Monographs*, *76*(4), 503–519. https://doi.org/10.1890/0012-9615(2006) 076[0503:GVICSI]2.0.CO;2/

Bayer, T., Aranda, M., Sunagawa, S., Yum, L. K., DeSalvo, M. K., Lindquist, E., … Medina, M. (2012). *Symbiodinium* Transcriptomes: Genome Insights into the Dinoflagellate Symbionts of Reef-Building Corals. *PLoS ONE*, *7*(4), e3526. https://doi.org/10.1371/journal.pone.0035269

Berkelmans, R., & van Oppen, M. J. H. (2006). The role of zooxanthellae in the thermal tolerance of corals: A 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society of London B: Biological Sciences*, *273*(1599), 2305–2312. https://doi.org/10.1098/rspb.2006.3567

Cantin, N. E., & Lough, J. M. (2014). Surviving coral bleaching events: *Porites* growth anomalies on the Great Barrier Reef. *PLoS ONE*, *9*(2), e88720. https://doi.org/10.1371/journal.pone.0088720

Cunning, R., & Baker, A. C. (2013). Excess algal symbionts increase the susceptibility of reef corals to bleaching. *Nature Climate Change*, *3*, 259–262. https://doi.org/10.1038/nclimate1711

Cunning, R., Silverstein, R. N., & Baker, A. C. (2015). Investigating the causes and consequences of symbiont shuffling in a multi-partner reef coral symbiosis under environmental change. *Proceedings of the Royal Society of London B: Biological Sciences*, *282*(1809), 20141725. https://doi.org/10.1098/rspb.2014.1725

Dixon, G. B., Davies, S. W., Aglyamova, G. V., Meyer, E., Bay, L. K., & Matz, M. V. (2015). Genomic determinants of coral heat tolerance across latitudes. *Science*, *348*(6242), 1460–1462. https://doi.org/10.1126/science.1261224

Dubé, C. E., Boissin, E., Maynard, J. A., & Planes, S. (2017). Fire coral clones demonstrate phenotypic plasticity among reef habitats. *Molecular Ecology*, *26*(15), 3860–3869. https://doi.org/10.1111/mec.14165

Dustan, P., & Halas, J. C. (1987). Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida: 1974 to 1982. *Coral Reefs*, *6*(2), 91–106. https://doi.org/10.1007/BF00301378

Dziedzic, K. E., Elder, H., & Meyer, E. (2017). Heritable variation in bleaching responses and its functional genomic basis in reef-building corals (*Orbicella faveolata*). *bioRxiv*, *185595*, 0000–0000. https://doi.org/10.1101/185595

Edmunds, P. J. (1994). Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching-susceptible clones. *Marine Biology*, *121*(1), 137–142. https://doi.org/10.1007/bf00349482

Enochs, I. C., Manzello, D. P., Donham, E., Kolodziej, G., Okano, R., Johnston, L., & Price, N. N. (2015). Shift from coral to macroalgae dominance on a volcanically acidified reef. *Nature Climate Change*, *5*, 1083–1088. https://doi.org/10.1038/nclimate2758

Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to Quantitative Genetics*, 4th ed. (p. 480). Harlow, UK: Prentice Hall.

Fitt, W. K., Brown, B. E., Warner, M. E., & Dunne, R. P. (2001). Coral bleaching: Interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs*, *20*(1), 51–65. https://doi.org/10.1007/s003380100146

Florida Reef Resilience Program (2011) Coral Bleaching In-water Rapid Assessment Protocol 2011. Florida Reef Resilience Program, The Nature Conservancy. Available at frrp.org/DRM Training handouts/FRRP bleaching protocol 2011.pdf

Foster, N., Baums, I. B., & Mumby, P. J. (2007). Sexual vs. asexual reproduction in an ecosystem engineer: The massive coral *Montastraea annularis*. *Journal of Animal Ecology*, *76*(2), 384–391. https://doi.org/10.1111/j.1365-2656.2006.01207.x

Foster, N. L., Baums, I. B., Sanchez, J. A., Paris, C. B., Chollett, I., Agudelo, D. L., & Mumby, P. J. (2013). Hurricane-driven patterns of clonality in an ecosystem engineer: the Caribbean coral *Montastraea annularis*. *PLoS ONE*, *8*(1), e53283. https://doi.org/10.1371/journal.pone.0053283

Gintert, B. E., Manzello, D. P., Enochs, I. C., Kolodziej, G., Carlton, R. D., Gleason, A. C. R., & Gracias, N. (2018). Marked annual coral bleaching resilience of an inshore patch reef in the Florida Keys: A nugget of hope, aberrance, or last man standing? *Coral Reefs*, *37*(2), 533–547. https://doi.org/10.1007/s00338-018-1678-x

Glynn, P. W. (1993). Coral reef bleaching: Ecological perspectives. *Coral Reefs*, *12*(1), 1–17. https://doi.org/10.1007/BF00303779

Glynn, P. W., & D'Croz, L. (1990). Experimental evidence for high temperature stress as the cause of El Nino-coincident coral mortality. *Coral Reefs*, *8*(4), 181–191. https://doi.org/10.1007/BF00265009

Glynn, P. W., Maté, J. M., Baker, A. C., & Calderon, M. O. (2001). Coral bleaching and mortality in Panamá and Ecuador during the 1997-98 El Niño-Southern Oscillation event: Spatial/temporal patterns and comparisons with the 1982-83 event. *Bulletin of Marine Science*, *69*(1), 79–110.

Grottoli, A. G., Warner, M. E., Levas, S. J., Aschaffenburg, M. D., Schoepf, V., McGinley, M., & Matsui, Y. (2014). The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Global Change Biology*, *20*(12), 3823–3833. https://doi.org/10.1111/gcb.12658

Guest, J. R., Baird, A. H., Maynard, J. A., Muttaqin, E., Edwards, A., Campbell, S., & Chou, L. M. (2012). Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS ONE*, *7*(3), e33353. https://doi.org/10.1371/journal.pone.0033353

Guest, J. R., Low, J., Tun, K., Wilson, B., Ng, C., Raingeard, D., … Steinberg, P. D. (2016). Coral community response to bleaching on a highly disturbed reef. *Scientific Reports*, *6*, 20717. https://doi.org/https://doi.org/10.1038/srep20717

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*(2), 1–22. https://doi.org/10.18637/jss.v033.i02

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., & Hatziolos, M. E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, *318*(5857), 1737–1742. https://doi.org/10.1126/science.1152509

Howells, E. J., Abrego, D., Meyer, E., Kirk, N. L., & Burt, J. A. (2016). Host adaptation and unexpected symbiont partners enable reef-building corals to tolerate extreme temperatures. *Global Change Biology*, *22*(8), 2702–2714. https://doi.org/10.1111/gcb.13250

Hughes, T. P., Kerry, J. T., Alvarez-Noriega, M., Alvarez-Romero, J. G., Anderson, K. D., Baird, A. H., & Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*, 373–377. https://doi.org/10.1038/nature21707

James, N. P., Ginsburg, R. N., Marzalek, D. S., & Choquette, P. W. (1976). Facies and fabric specificity of early subsea cements in shallow Belize (British Honduras) reefs. *Journal of Sedimentary Research*, *46*(3), 523–544.

Jones, A. M., Berklemans, R., van Oppen, M. J. H., Mieog, J. C., & Sinclair, W. (2008). A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: Field evidence of acclimatization. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*(1641), 1359–1365. https://doi.org/10.1098/rspb.2008.0069

Kemp, D. W., Hernandez-Pech, X, Iglesias-Prieto, R., Fitt, W. K., & Schmidt, G. W. (2014). Community dynamics and physiology of *Symbiondinium* spp. before, during, and after a coral bleaching event. *Limnology and Oceanography*, *59*(3), 788–797. https://doi.org/10.4319/lo.2014.59.3.0788

Kemp, D. W., Thornhill, D. J., Rotjan, R. D., Iglesias-Prieto, R., Fitt, W. K., & Schmidt, G. W. (2015). Spatially distinct and regionally endemic *Symbiodinium* assemblages in the threatened Caribbean reef-building coral *Orbicella faveolata*. *Coral Reefs*, *34*(2), 535–547. https://doi.org/10.1007/s00338-015-1277-z

Kenkel, C. D., Goodbody-Gringley, G., Caillaud, D., Davies, S. W., Bartels, E., & Matz, M. V. (2013). Evidence for a host role in thermotolerance divergence between populations of the mustard hill coral (*Porites astreoides*) from different reef environments. *Molecular Ecology*, *22*(16), 4335–4348. https://doi.org/10.1111/mec.12391

Kenkel, C. D., & Matz, M. V. (2016). Gene expression plasticity as a mechanism of coral adaptation to a variable environment. *Nature Ecology and Evolution*, *1*, 0014. https://doi.org/10.1038/s41559-016-0014

Kohler, K. E., & Gill, S. M. (2006). Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences*, *32*(9), 1259–1269. https://doi.org/https://doi.org/10.1016/j.cageo.2005.11.009

Korneliussen, T., Albrechtsen, A., & Nielsen, R. (2014). ANGSD: Analysis of next generation sequencing data. *BMC Bioinformatics*, *15*, 356. https://doi.org/10.1186/s12859-014-0356-4

Ladner, J. T., Barshis, D. J., & Palumbi, S. R. (2012). Protein evolution in two co-occurring types of *Symbiodinium*: An exploration into the

genetic basis of thermal tolerance in *Symbiodinium* clade D. *BMC Evolutionary Biology*, *12*, 217. https://doi.org/10.1186/1471-2148-12-217

LaJeunesse, T. C., Parkinson, J. E., Gabrielson, P. W., Jeong, H. J., Reimer, J. D., Voolstra, C. R., & Santos, S. R. (2018). Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. *Current Biology*, *28*(16), 2570–2580. https://doi.org/10.1016/j.cub.2018.07.008

LaJeunesse, T. C., Smith, R. T., Finney, J., & Oxenford, H. (2009). Outbreak and persistence of opportunistic symbiotic dinoflagellates during the 2005 Caribbean mass coral 'bleaching' event. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*(1676), 4139–4148. https://doi.org/10.1098/rspb.2009.1405

Levins, R. (1964). The theory of fitness in a heterogeneous environment. 4. *Adaptive Significance of Gene Flow*. *Evolution*, *18*, 635–638. https://doi.org/10.1111/j.1558-5646.1964.tb01678.x

Levitan, D. R., Boudreau, W., Jara, J., & Knowlton, N. (2014). Long-term reduced spawning in *Orbicella* coral species due to temperature stress. *Marine Ecology Progress Series*, *515*, 1–10. https://doi.org/10.3354/meps11063

Lirman, D., & Fong, P. (2007). Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract. *Marine Pollution Bulletin*, *54*, 779–791. https://doi.org/10.1016/j.marpolbul.2006.12.014

Manzello, D. P. (2015). Rapid recent warming of coral reefs in the Florida Keys. *Scientific Reports*, *5*, 16762. https://doi.org/10.1038/srep16762

Manzello, D. P., Enochs, I. C., Kolodziej, G., & Carlton, R. (2015a). Recent decade of growth and calcification of *Orbicella faveolata* in the Florida Keys: an inshore-offshore comparison. *Marine Ecology Progress Series*, *521*, 81–89. https://doi.org/10.3354/meps11085

Manzello, D. P., Enochs, I. C., Kolodziej, G., & Carlton, R. (2015b). Coral growth patterns of *Montastraea cavernosa* and *Porites astreoides* in the Florida Keys: The importance of thermal stress and inimical waters. *Journal of Experimental Marine Biology and Ecology*, *471*, 198–207. https://doi.org/10.1016/j.jembe.2015.06.010

Manzello, D. P., Enochs, I. C., Kolodziej, G., Carlton, R., & Valentino, L. (2018). Resilience in carbonate production despite three coral bleaching events in 5 years on an inshore patch reef in the Florida Keys. *Marine Biology*, *165*, 99. https://doi.org/10.1007/s00227-018-3354-7

Manzello, D. P., Enochs, I. C., Melo, N., Gledhill, D. K., & Johns, E. M. (2012). Ocean acidification refugia of the Florida Reef Tract. *PLoS ONE*, *7*(7), e41715. https://doi.org/10.1371/journal.pone.0041715

Manzello, D. P., Warner, M. E., Stabenau, E., Hendee, J. C., Lesser, M. P., & Jankulak, M. (2009). Remote monitoring of chlorophyll fluorescence in two reef corals during the 2005 bleaching event at Lee Stocking Island. *Bahamas. Coral Reefs*, *28*(1), 209–214. https://doi.org/10.1007/s00338-008-0455-7

Matthews, J. L., Crowder, C. M., Oakley, C. A., Lutz, A., Roessner, U., Meyer, E., … Davy, S. K. (2017). Optimal nutrient exchange and immune responses operate in partner specificity in the cnidarian-dinoflagellate symbiosis. *Proceedings of the National Academy of Sciences*, *114*(50), 13194–13199. https://doi.org/10.1073/pnas.1710733114

Maynard, J. A., Anthony, K. R. N., Marshall, P. A., & Masiri, I. (2008). Major bleaching events can lead to increased thermal tolerance in corals. *Marine Biology*, *155*(2), 173–182. https://doi.org/10.1007/s00227-008-1015-y

McClanahan, T. R. (2017). Changes in coral sensitivity to thermal anomalies. *Marine Ecology Progress Series*, *570*, 71–85. https://doi.org/10.3354/meps12150

Mieog, J. C., Van Oppen, M. J. H., Berkelmans, R., Stam, W. T., & Olsen, J. L. (2009). Quantification of algal endosymbionts (*Symbiodinium*) in coral tissue using real-time PCR. *Molecular Ecology Resources*, *9*, 74–82. https://doi.org/10.1111/j.1755-0998.2008.02222.x

Miller, M. W., Baums, I. B., Pausch, R. E., Bright, A. J., Cameron, C. M., Williams, D. E., … Woodley, C. M. (2017). Clonal structure and variable fertilization success in Florida Keys broadcast-spawning corals. *Coral Reefs*, *37*(1), 239–249. https://doi.org/10.1007/s00338-017-1651-0

Miller, J., Muller, E., Rogers, C., Waara, R., Atkinson, A., Whelan, K. R. T., & Witcher, B. (2009). Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. *Coral Reefs*, *28*, 925–937. https://doi.org/10.1007/s00338-009-0531-7

Muller, E. M., Bartels, E., & Baums, I. B. (2018). Bleaching causes loss of disease resistance within the threatened coral species *Acropora cervicornis*. *eLife*, *7*, e35066. https://doi.org/10.7554/elife.35066.001

Neal, B. P., Ken, A., Treibitz, T., Beijboom, O., O'Connor, G., Coffroth, M. A., & Kline, D. I. (2016). Caribbean massive corals not recovering from repeated thermal events during 2005-2013. *Ecology and Evolution*, *7*(5), 1339–1353. https://doi.org/10.1002/ece3.2706

Noonan, S. H. C., & Fabricius, K. E. (2016). Ocean acidification affects productivity but not the severity of thermal bleaching in some tropical corals. *ICES Journal of Marine Science*, *73*, 715–726. https://doi.org/10.1093/icesjms/fsv127

Palumbi, S. R., Barshis, D. J., Traylor-Knowles, N., & Bay, R. A. (2014). Mechanisms of reef coral resistance to future climate change. *Science*, *344*(6186), 895–898. https://doi.org/10.1126/science.1251336

Parkinson, J. E., Banaszak, A. T., Altman, N. S., LaJeunesse, T. C., & Baums, I. B. (2015). Intraspecific diversity among partners drives functional variation in coral symbioses. *Scientific Reports*, *5*, 15667. https://doi.org/10.1038/srep15667

Pettay, D. T., Wham, D. C., Smith, R. T., Iglesias-Prieto, R., & LaJeunesse, T. C. (2015). Microbial invasion of the Caribbean by an Indo-Pacific coral zooxanthella. *Proceedings of the National Academy of Sciences*, *112*(24), 7513–7518. https://doi.org/10.1073/pnas.1502283112

Porter, J. W., & Meier, O. W. (1992). Quantification of loss and change in Floridian reef coral populations. *American Zoologist*, *32*(6), 625–640. https://doi.org/10.1093/icb/32.6.625

Prada, C., Hanna, B., Budd, A. F., Woodley, C. M., Schmutz, J., Grimwood, J., & Medina, M. (2016). Empty niches after extinctions increase population sizes of modern corals. *Current Biology*, *26*(23), 3190–3194. https://doi.org/10.1016/j.cub.2016.09.039

Precht, W. F., Gintert, B. E., Robbart, M. L., Fura, R., & van Woesik, R. (2016). Unprecedented disease-related coral mortality in southeastern Florida. *Scientific Reports*, *6*, 31374. https://doi.org/10.1038/srep31374

Precht, W. F., & Miller, S. L. (2007). Ecological shifts along the Florida Reef Tract: The past as key to the future. In R. B. Aronson (Ed.), *Geological approaches to coral reef ecology* (pp. 237–312). New York, NY: Springer. https://doi.org/10.1007/978-0-387-33537-7

Quigley, K. M., Willis, B. L., & Bay, L. K. (2017). Heritability of the *Symbiodinium* community in vertically- and horizontally-transmitting broadcast spawning corals. *Scientific Reports*, *7*, 8219. https://doi.org/10.1038/s41598-017-08179-4

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. New Yor, NY: Cambridge University Press. https://doi.org/10.1017/CBO9780511806384

R Core Team (2015). *RStudio: Integrated development for R*. Boston, MA: RStudio, Inc.

Riegl, B., & Purkis, S. (2015). Coral population dynamics across consecutive mass mortality events. *Global Change Biology*, *22*(11), 3995–4005. https://doi.org/10.1111/gcb.13014

Risk, M. J., & Sammarco, P. W. (1991). Cross-shelf trends in skeletal density of the massive coral *Porites lobata* from the Great Barrier Reef. *Marine Ecology Progress Series*, *69*, 195–200. https://doi.org/10.3354/meps069195

Rowan, R., & Powers, D. A. (1991). Molecular genetic identification of symbiotic dinoflagellates (zooxanthellae). *Marine Ecology Progress Series*, *71*, 65–73. https://doi.org/10.3354/meps071065

Ruzicka, R. R., Colella, M. A., Porter, J. W., Morrison, J., Kidney, J. A., Brinkhuis, V., & Meyers, M. (2013). Temporal changes in benthic

assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. *Marine Ecology Progress Series*, *489*, 125–141. https://doi.org/10.3354/meps10427

Sammarco, P. W., & Risk, M. J. (1990). Large-scale patterns in internal bioerosion of *Porites*: Cross continental shelf trends on the Great Barrier Reef. *Marine Ecology Progress Series*, *59*, 145–156. https://doi.org/10.3354/meps059145

Shamberger, K. E. F., Cohen, A. L., Golbuu, Y., McCorkle, D. C., Lentz, S. J., & Barkley, H. C. (2014). Diverse coral communities in naturally acidified waters of a Western Pacific reef. *Geophysical Research Letters*, *41*, 499–504. https://doi.org/10.1002/2013GL058489

Silverstein, R. N., Cunning, R., & Baker, A. C. (2014). Change in algal symbiont communities after bleaching, not prior heat exposure, increases heat tolerance of reef corals. *Global Change Biology*, *21*(1), 236–249. https://doi.org/10.1111/gcb.12706

Skotte, L., Korneliussen, T. S., & Albrechtsen, A. (2013). Estimating Individual Admixture Proportions from Next Generation Sequencing Data. *Genetics*, *195*(3), 693–702. https://doi.org/10.1534/genetics.113.154138

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, *236*(4803), 787–792. https://doi.org/10.1126/science.3576198

Teece, M. A., Estes, B., Gelsleichter, E., & Lirman, D. (2011). Heterotrophic and autotrophic assimilation of fatty acids by two scleractinian corals, *Montastraea faveolata* and *Porites astreoides*. *Limnology and Oceanography*, *56*(4), 1285–1296. https://doi.org/10.4319/lo.2011.56.4.1285

Thornhill, D. J., LaJeunesse, T. C., Kemp, D. W., Fitt, W. K., & Schmidt, G. W. (2006). Multi-year, seasonal genotypic surveys of coral-algal symbioses reveal prevalent stability or post-bleaching reversion. *Marine Biology*, *148*, 711–722. https://doi.org/10.1007/s00227-005-0114-2

Thornhill, D. J., Xiang, Y., Fitt, W. K., & Santos, S. R. (2009). Reef endemism, host specificity, and temporal stability in populations of symbiotic dinoflagellates from two ecologically dominant Caribbean corals. *PLoS ONE*, *4*(7), e6262. https://doi.org/10.1371/journal.pone.0006262

Towle, E. K., Carlton, R., Langdon, C., & Manzello, D. P. (2015). In-situ measurement of metabolic status in three coral species from the Florida Reef Tract. *Regional Studies in Marine Science*, *2*, 145–153. https://doi.org/10.1016/j.rsma.2015.09.007

Wall, C. B., Fan, T.-Y., & Edmunds, P. J. (2013). Ocean acidification has no effect on thermal bleaching in the coral *Seriatopora caliendrum*. *Coral Reefs*, *33*(1), 119–130. https://doi.org/10.1007/s00338-013-1085-2

Wang, S., Meyer, E., McKay, J. K., & Matz, M. V. (2012). 2b-RAD: A simple and flexible method for genome-wide genotyping. *Nature Methods*, *9*, 808–810. https://doi.org/10.1038/nmeth.2023

van Woesik, R., Houk, P., Isechal, A. L., Idechong, J. W., Victor, S., & Golbuu, Y. (2012). Climate-change refugia in the sheltered bays of Palau: Analogs of future reefs. *Ecology and Evolution*, *2*(10), 2474–2484. https://doi.org/10.1002/ece3.363

Yee, S. H., & Barron, M. G. (2010). Predicting coral bleaching in response to environmental stressors using 8 years of global-scale data. *Environmental Monitoring and Assessment*, *161*, 423–438. https://doi.org/10.1007/s10661-009-0758-3

SUPPORTING INFORMATION

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