i. **Title:** Elevated maximum temperatures and high-magnitude thermal variability drive low coral diversity on nearshore lagoonal reefs in Belize

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ABSTRACT

Aim Coral reefs are increasingly threatened by interactions of global and local anthropogenic stressors, two of the most prominent being rising seawater temperature and nutrient enrichment. We aim to determine how spatiotemporal variations of environmental stressors across a reefscape determine which coral species are most successful during this climate change interval.

Location Belize, Central America

Methods Thirteen lagoonal reefs on the Belize Barrier Reef System (BBRS) were surveyed to investigate the influence of temperature and nutrient history on coral community structure across reefscapes. A novel metric was developed using ultra-high resolution sea surface temperature (SST) records to classify reefs as enduring low temperature parameters (low_{TP}), moderate temperature parameters (mod_{TP}), or extreme temperature parameters (ext_{TP}) based on four thermal parameters known to be important drivers of overall reef health

Results Coral species richness, abundance, diversity, density, and percent cover were lower at ext_{TP} sites compared to low_{TP} and mod_{TP} sites, but these reef community traits did not differ between low_{TP} and mod_{TP} sites. Coral life history strategy analyses indicated that ext_{TP} sites were dominated by hardy stress-tolerant and fast growing weedy coral species, while low_{TP} and mod_{TP} sites included competitive, generalist, weedy, and stress-tolerant coral species.

Main Conclusions Coral community differences between ext_{TP} and low_{TP}/mod_{TP} sites were primarily driven by temperature differences. While the influence of nutrients on reef community traits was minimal, bulk nutrient concentrations likely affected percent coral cover. Lack of community scale differences between low_{TP} and mod_{TP} sites is likely driven by low-magnitude thermal variations in these reef locations. Dominance of weedy and stress-tolerant genera at ext_{TP} sites suggests that corals utilizing these two life history strategies may be better suited to cope with IPCC projected ocean warming conditions. Our results reveal that temperature is the primary driver of differences in coral community composition among these distinct reef environments.

INTRODUCTION

Coral reefs are threatened globally due to interactions of anthropogenic impacts such as warming from increasing greenhouse gas emission, excessive agricultural runoff, overfishing, and habitat destruction (Hughes *et al.*, 2003; Hoegh-Guldberg *et al.*, 2007; Frieler *et al.*, 2013). Of particular concern are increasing greenhouse gas emissions that are leading to significant warming of the oceans (Hughes *et al.*, 2003; Donner *et al.*, 2005). This warming trend is especially troubling in the Caribbean, where rates of warming are higher than in many other tropical basins (Chollett *et al.*, 2012), and where coral cover has declined up to 80% in recent decades (Gardner *et al.*, 2003). Elevated sea surface temperature (SST) is the major cause of the breakdown of essential coral-algal symbiosis, which can ultimately lead to mass coral bleaching (Jokiel & Coles, 1990; D'Croz *et al.*, 2001) and these bleaching events are projected to increase in frequency and severity as the climate continues to warm (Donner *et al.*, 2005; Wooldridge *et al.*, 2005). The Caribbean Sea is expected to be severely affected by warming as corals are extremely sensitive to even small temperature increases of less than 1°C (McWilliams *et al.*, 2005). In fact, the Caribbean is predicted to suffer bleaching events biannually within the next 20-30 years (Donner *et al.*, 2007) with predicted annual bleaching events occurring as soon as 2040 (van Hooidonk *et al.*, 2015). Caribbean-wide and global scale bleaching events are predicted to continue through the end of the century unless corals can increase their thermal tolerance at a rate of 0.2-1.0 °C per decade (Donner *et al.*, 2005).

Annual or daily thermal variability have recently been identified as important factors in coral thermal tolerance (Oliver & Palumbi, 2011; Soto *et al.*, 2011; Barshis *et al.*, 2013). Indeed, previous exposure to thermal variability increases a coral's tolerance to future stress events (Oliver & Palumbi, 2011; Carilli *et al.*, 2012; Castillo *et al.*, 2012; Pineda *et al.*, 2013), and

research suggests that Pacific corals living in areas with a high annual average SST are less susceptible to bleaching (van Woesik *et al.*, 2012; Fine *et al.*, 2013). A recent study has also shown that coral from both the mildest and the most extreme thermal environments can escape mortality during a bleaching event (Pineda *et al.*, 2013). Along the Belize Barrier Reef System (BBRS), corals historically exposed to less thermal variability exhibited slower growth rates and/or greater mortality in response to SST increases (Carilli *et al.*, 2012; Castillo *et al.*, 2012). In the Florida Keys, coral growth rates and cover were found to be higher in nearshore environments with more variable temperatures than on deeper reefs with more stable temperatures, in spite of higher nutrient concentrations nearshore (Lirman & Fong, 2007). While many studies suggest that extreme temperature variability (prolonged summer warming or extreme daily fluctuation) leads to higher coral resilience (Oliver & Palumbi, 2011; Barshis *et al.*, 2013; Pineda *et al.*, 2013), there is also evidence that corals experiencing moderate long term temperature variability (either average annual or daily variation) are better able to cope with stress (Soto *et al.*, 2011).

Temperature stress is not the only factor leading to Caribbean coral decline. Nutrient enrichment also plays a role and can lead directly to reef degradation (Fabricius, 2005; Kline *et al.*, 2006; Wooldridge, 2009; Wiedenmann *et al.*, 2013; DeCarlo *et al.*, 2015). Specifically, increased dissolved inorganic nitrogen (DIN) has been linked to a reduction of bleaching thresholds (Wooldridge, 2009; Wiedenmann *et al.*, 2013) and has been shown to increase disease and bleaching prevalence on Florida reefs (Vega Thurber *et al.*, 2014). Additionally, macrobioerosion can occur up to 10 times faster in corals in high nitrogen (N) waters compared to corals in low N waters (DeCarlo *et al.*, 2015). Kline et al. (2006) suggested that elevated levels of N, phosphorous (P), and ammonia did not cause substantial coral mortality in

Panamanian corals; instead, elevated levels of dissolved organic carbon (DOC) promoted coral mortality through acceleration of microbe growth on the surface layer of corals.

Although much is known about the influence of temperature and nutrient enrichment on coral health, it is unclear exactly how these stressors interact to affect coral community structure. Community differences induced by anthropogenic stressors may lead to circumstances where reef calcification does not sufficiently counter reef erosion, leading to an overall flattening of reef structure, decline of coral reefs, and shifts from one dominant coral group to another, or from coral to algal dominance (Loya *et al.*, 2001; McManus & Polsenberg, 2004; Alvarez-Filip *et al.*, 2009; Alvarez-Filip *et al.*, 2013). Due to the variety of coral life history strategies and differential response to stress, an overall decline in coral cover and abundance can also be coupled with an increase in abundance of certain coral species (Loya *et al.*, 2001; Darling *et al.*, 2012), as seen in the Caribbean with the recent increase in abundance of 'weedy' species, including *Porites astreoides* (Green et al., 2008). Brooding, small, opportunistic corals (weedy) and fast growing (competitive) corals recover faster from stress events, but are more impacted by bleaching events than more stress-tolerant, slower growing species (Darling *et al.*, 2012; Darling *et al.*, 2013). Taken together, this evidence suggests that differential responses between coral species to temperature and nutrient stressors may lead to community scale shifts in composition.

The purpose of the current study was to investigate the influence of temperature and nutrients on coral community composition of lagoonal reefs across the Belize Barrier Reef System (BBRS). A novel GIS-based metric was developed to characterize lagoonal reefs across the BBRS into three thermally distinct regions. Within these three regions, thirteen reef sites were identified and benthic surveys were conducted to quantify coral community composition. Quantifying coral community differences amongst these thermally distinct reefs may help predict

how coral community structure may respond to climate change. In addition, identifying which areas and species are best able to cope with stress will allow for more targeted management strategies and for increased protection of vital reef areas that would otherwise be left unprotected.

MATERIALS AND METHODS

Novel Site Identification

SST Data Assembly

Daily 1-km horizontal resolution sea surface temperature (SST) data were acquired from JPL's Multi-Scale High Resolution Sea Surface Temperature (JPL MUR SST) via the Physical Oceanography Distributed Active Archive Center (PO.DAAC) at the NASA Jet Propulsion Laboratory, Pasadena, CA (http://podaac.jpl.nasa.gov). Conventional 1-km resolution satellite SST measurements (infrared, IR) are contaminated by clouds, creating data-void areas. Microwave (MW) data sets can penetrate clouds to gain better temporal coverage, but with a much coarser spatial resolution (25 km) (Chin *et al.*, 2013). MUR combines these two datasets to present a more comprehensive and complete SST product. MUR uses the multi-resolution variational analysis (MRBA) as an interpolation method to combine high resolution datasets with more conventional datasets, producing a product that contains no cloud contamination (Chin *et al.*, 2013). MUR reports foundation SST, or SST at the base of the diurnal thermocline (~5-10m depth). Comparison of in-situ temperature (recorded by HOBO® v2 data loggers) and MUR revealed that MUR showed an average negative bias of -0.495±0.01°C relative to in-situ loggers (Fig S1). Due to the comprehensive coverage, high resolution, range (2002-2012), and lack of contamination in this dataset, it was ideal for use in the current study.

Site Classification

Multiple thermal parameters were calculated at different temporal resolutions and examined across the thirteen reef sites. In the end, four parameters produced distinct thermal environments across the BBRS: average annual maximum temperature (Fig S2A in Supporting Information), average annual temperature range (Fig S2B), average annual number of days above the regional bleaching threshold of 29.7°C (Aronson *et al.*, 2002) (Fig S2C), and average annual consecutive days above the regional bleaching threshold (i.e., longest potential thermal stress events) (Fig S2D). A metric that combined all four thermal parameters was generated using ArcGIS© in order to assess thermal environments across the BBRS. Data from each of the four parameters in the metric were divided into 8-10 bins (0.5 standard deviations (SD) of the mean) and overlaid on a map of the BBRS (Table 1). Reefs were not present in areas where the value of any single variable was <1 SD below or >2 SD above the mean (across the entire data set from 2002-2012). For all four parameters, areas that were classified in bins ≥1 SD above the mean were designated extreme temperature parameter (ext_{TP}) sites (Fig.1A). Moderate temperature parameter (mod_{TP}) sites were classified as areas where all values were 0.5 to 1 SD above the average annual temperature range and average annual maximum temperature and within 1 SD of the average annual consecutive days and average annual number of days above the regional bleaching threshold (Fig 1A). Low temperature parameter (low_{TP}) sites were classified as bins that were 0.5 SD above the average to 2 SD below the average for annual temperature range and annual maximum temperature and below the average for consecutive and annual days above the regional bleaching threshold (Fig 1A). Using the metric presented in Fig 1A, 15 sites were selected. 13 of these sites were visited and surveyed in November 2014 (2 sites were not surveyed as no corals were located inside of the marked geographic area) (Table 1, Fig 1A).

Benthic surveys

In November 2014, benthic surveys we performed at the 13 sites described above. A team of three divers surveyed a total of 6 transects at each site following AGRRA methodology (AGRRA 2003). Genus and species of each coral was identified and the number and size of individual colonies of each species was recorded on underwater data sheets. After these data were collected, species diversity, abundance, species richness, and coral life history (following Darling *et al.*, 2012) were calculated for each site.

Six video transects (1 m x 20 m) were also performed at each site using GoPro® cameras attached to PVC stabilizing apparatuses allowing each diver to stabilize the camera while performing transects. Video transects were analyzed at UNC in a manner similar to the AGRRA method used in the field, except two additional parameters (percent coral cover and coral density) were calculated. Full details and a comparison of the methods employed are available in Appendix 1 of Supplementary Information.

Nutrient analysis

Chlorophyll a

Eight-day composite 4-km horizontal resolution chlorophyll a (*chl a*) measurements were obtained from NASA's Moderate Resolution Imaging Spectroradiometer (AQUA MODIS) via NOAA's Environmental Research Division's Data Access Program (ERDDAP) (Simons, 2011). Eight-day composite data were selected in order to minimize gaps in data from cloud cover. Unlike the MUR SST data used for temperature calculations, there is no integrated, high-resolution product for *chl a*. Similar to temperature calculations, monthly and yearly average *chl a* values were calculated for each survey site (Fig 1B, 2C). *Chl a* is a widely used proxy for both primary productivity and nutrient content in seawater (Bell, 1992), as it is the main

photosynthetic pigment present in phytoplankton (which can often quickly deplete nutrient concentrations below detectable limits). It has been shown that remotely sensed data, such as *chl a* concentration, yields better metrics for water quality than traditional measures such as distance from shore and distance from the nearest river (Polónia *et al.*, 2015). Here, *chl a* data are used as a proxy for bulk nutrient content across the BBRS. In addition to this reef scale coarse estimate of bulk nutrients, fine-scale in-situ nutrient sampling was conducted.

In-situ nutrient sampling

125ml water samples (n=3-10) were filtered and collected in acid washed bottles from each survey site (n=13), flash frozen on dry ice, and transported to UNC for analysis. Fine-scale nutrient dynamics were quantified from dissolved inorganic nitrogen [(DIN) = nitrate plus nitrite (NO_x) and ammonium (NH_4)] and dissolved organic carbon (DOC). See Appendix 2 of the supplementary information for measurement and instrumentation details.

Statistical Analysis

Standard deviations used for temperature bins and site classification were calculated in ArcGIS©. All other statistical analysis were carried out in R 3.2.2 (R Core Team, 2014). Transect averaged survey data for species richness, abundance, Shannon diversity, coral cover, coral density, DIN, DON, DOC, and log-transformed *chl a* data were analyzed using analyses of variance (ANOVA). Three fixed factors were included in the ANOVA (survey method, site, and site type) for species richness, abundance, Shannon diversity, DIN, DON, and DOC. Only two fixed factors (site and site type) were included in the ANOVA for coral cover and coral density, since only data from video surveys were used to calculate these averages, and also for *chl a*

concentrations since they were calculated using satellite measurements and survey type did not factor in.

If factors were significant ($p<0.05$), a post-hoc Tukey's HSD test was used to evaluate the significance of each pair-wise comparison. To visualize coral community differences between site types non-metric multidimensional scaling (NMDS) ordination was implemented using Bray-Curtis similarity coefficients in the vegan package in R (Oksanen *et al.*, 2013). An optimal stress test was performed to determine the optimal k value (k=20). Resulting NMDS scores were visualized in two-dimensional ordination space. A PERMANOVA test was performed to analyze the site type differences using the *adonis* function in the vegan package in R (Oksanen *et al.*, 2013).

Linear mixed effects models with random intercepts, random slopes, or random slopes and random intercepts were created using the nlme package in R (Pinheiro *et al.*, 2007), and were used to analyze the effects of site type and temperature parameters on ecological measurements (species richness, abundance, Shannon diversity, coral cover, and coral density). The model that best described the effect of site type or each temperature parameter on each ecological parameter was chosen based on the Akaike Information Criterion (AIC), which scales estimated differences between the model equation and the actual equation (Burnham & Anderson, 2002). This criterion is based on goodness of fit of the data as well as a correction term that increases the AIC value as number of predictors increases, which optimizes the model with the lowest AIC for both fit and simplicity (Burnham & Anderson, 2002). Once the best fitting model was chosen using best AIC procedure for each ecological parameter vs. temperature parameter across site types, marginal R^2 (R^2m) and conditional R^2 (R^2c) were calculated using the *r.squaredGLMM* function of the MuMIn package in R (Nakagawa & Schielzeth, 2013). Marginal R^2 describes the proportion of

variance explained by fixed factors alone, while the conditional R^2 describes the variance explained by both random and fixed factors (Nakagawa & Schielzeth, 2013).

Linear models tested for the influence of temperature and nutrient parameters on the variation observed along NMDS1 and NMDS2 (within and between site type community variation) using the *lm* function in R (R Core Team, 2014). R^2 and *p* values were calculated for each parameter based on each linear model (Table S11.) For NMDS1, data were also divided by site type in order to assess within site type variation (Table S9).

RESULTS

Coral Community Composition

Combined results of AGRRA diver surveys and GoPro® video surveys of all 13 sites revealed that coral species richness varied as a function of site location as well as site type (low_{TP}, mod_{TP}, or ext_{TP}) (Table 3A). Coral species richness was significantly lower at ext_{TP} sites compared to low_{TP} and mod_{TP} sites, but was not significantly different between low_{TP} and mod_{TP} sites (Table 3B, Fig 3A). Coral abundance, Shannon diversity, percent coral cover, and coral density also followed these same trends (Table 3A, 3B; Fig S3 in Supporting Information). Nonmetric multidimensional scaling (NMDS) analysis showed the same patterns. Community structure was significantly different (stress=0.018, adonis test *p* value=0.006) between ext_{TP} sites and low_{TP}/mod_{TP} sites along the NMDS2 axis, but was not different between low_{TP} and mod_{TP} sites (Fig 3B).

Linear modeling of temperature and nutrient parameters against NMDS1 and NMDS2 revealed that average annual maximum temperature, average annual temperature range, average annual days above the bleaching threshold, average annual consecutive days above the bleaching

threshold, DOC, and DON all had significant effects on the NMDS1 variation and all four temperature parameters, as well as DON and *chl a*, also had significant effects on NMDS2 variation (S11; Fig S6). The parameter that explained the most variation for NMDS1 was DON (R^2=0.3414, *p value*=1.18x10^{-15}) and average annual consecutive days above the bleaching threshold explained the most variation in NMDS2 (R^2=0.6039, *p value*= 2x10^{-16}, S11; Fig S6).

Linear regressions of temperature and nutrients parameters within site types along NMDS1 revealed significant effects (p <0.05) of average annual maximum temperature, average annual days above the bleaching threshold, average annual consecutive days above the bleaching threshold, DOC, DIN, and DON for all site types, average annual temperature range for mod_{TP} and ext_{TP} sites, and *chl a* for ext_{TP} sites only (Table S9; Fig S5). Average annual days above the bleaching threshold yielded the highest R^2 for low_{TP} and mod_{TP} sites, while average annual temperature range yielded the highest R^2 for ext_{TP} sites (Table S9; Fig S5).

Linear mixed effects models of ecological parameters for species richness, abundance, Shannon diversity, coral cover, and coral density by site type reveal that random intercepts models best fit the trends in species richness, abundance, Shannon diversity, and coral cover the best (best AIC), while a random slopes and intercepts model works best for coral density (Table S10A). Models with the best AIC showed no significant difference between low_{TP} and mod_{TP} sites for any parameters, but a significant difference between low_{TP} and ext_{TP} sites for species richness, abundance, Shannon diversity, and coral density (Table S10B).

Further linear mixed effects modeling of ecological parameters vs. temperature and nutrient parameters revealed that variation in species richness and coral density across sites was best explained by the number of consecutive days above the bleaching threshold per year, while total days above the bleaching threshold per year best explained the variation in coral abundance and

Shannon diversity. Variation in coral cover was best explained by *chl a* concentration (Table S5 in Supporting Information). Each model selected as best AIC (model that explains the variation the best) had a significant *p* value (<0.05) (Table S6 in Supporting Information). A similar modeling approach completed for transects from low_{TP} sites only showed that average annual temperature range best explains the variation for all five ecological parameters, however *p* values are only significant for coral cover and coral density (Tables S7, S8 in Supporting Information).

Coral Life History

Coral life history proportions varied by site and differences were observed between site types (Table 3A). These trends, while not statistically significant across all sites (p=0.055), may still be ecologically interesting (Table 3A). low_{TP} sites and ext_{TP} sites had significantly different life history distributions (Table 3B, Fig 4). mod_{TP} sites did not differ significantly from low_{TP} or ext_{TP} sites. Overall, these data suggest a decrease in competitive and generalist species at ext_{TP} sites compared to low_{TP} and mod_{TP} sites (Fig 4).

Nutrients

Chlorophyll a

Chl a concentrations varied by year and differed by site and site type (Table 2A), but were consistently lowest at low_{TP} sites and highest at ext_{TP} sites regardless of year (Table 2B, Fig 2A). 13-year average *chl a* concentrations were significantly different between all three site types. low_{TP} sites had the lowest average *chl a* concentrations, mod_{TP} sites had average *chl a* values significantly higher than low_{TP} sites, but significantly lower than ext_{TP} sites, and ext_{TP}

sites had significantly higher average *chl a* values than both low_{TP} and mod_{TP} sites (Table 2B, Fig 2B).

In-Situ Nutrient Concentrations

In-situ values for DIN, DON, Total N, DOC, and C:N varied by site (Table S2, S4). However, there were no significant differences between site types in terms of average DON and C:N, while concentrations of DOC and Total N were significantly elevated at ext_{TP} sites compared to low_{TP} and mod_{TP} sites (Table S3 in Supporting Information, Fig S4A-E in Supporting Information). DIN concentrations were significantly higher in mod_{TP} sites compared to low_{TP} sites, but concentrations at low_{TP} and mod_{TP} were not significantly different than ext_{TP} sites (Table S3, Fig S4A).

DISCUSSION

Surveys revealed that ext_{TP} sites had lower species richness, abundance, diversity, coral cover, and coral density than low_{TP} and mod_{TP} sites, which did not significantly differ from one another (Fig 3A, 3B, S3). Differences between ext_{TP} sites and low_{TP}/mod_{TP} sites were largely driven by the temperature parameters used to define the three thermal environments (Table S6, S11; Fig S6). Ext_{TP} sites were dominated by weedy and stress tolerant coral species while corals of all four life history strategies (Darling *et al.*, 2012) were found at low_{TP} and mod_{TP} sites (Fig 4). Our data suggest that these coral community differences across site types are likely driven by temperature parameters and, to a lesser extent, nutrients. Higher bulk nutrient concentrations in ext_{TP} sites may play a role in observed decreased in coral cover (Table S6), while DOC, DON, and DIN appear to play roles in community differences within, but not among, site types (Table S11, Fig S5).

Coral community composition differed between ext_{TP} sites and low_{TP}/mod_{TP} sites

Coral species richness, abundance, diversity, coral cover, and coral density were all lower at ext_{TP} sites compared to low_{TP} and mod_{TP} sites, (Fig 3A, S3) suggesting that the coral community at ext_{TP} sites is different from the community at low_{TP} and mod_{TP} sites. This finding was further supported by NMDS and linear mixed effects models (Fig 3B, Table S10B) and is contrary to the results of Soto et al. (2011) which shows that sites with moderate temperature variability (mod_{TP}) have higher coral cover than sites at either extreme and Lirman and Fong (2007) which showed that nearshore reefs (Ext_{TP}) had higher coral cover than offshore reefs in the Florida Keys. Ext_{TP} sites were subjected to higher annual maximum temperatures, more extreme annual temperature variations, a higher number of days above the bleaching threshold per year, more consecutive days above the bleaching threshold per year, and higher *chl a* concentrations than low_{TP} and mod_{TP} sites. As variation between site types occurred along the NMDS2 axis (Fig 4), linear modeling of these parameters against NMDS2 revealed that temperature parameters had a much more significant effect on community differences between site types than did nutrient parameters (Table S11, Fig 3B). The average annual number of days above the bleaching threshold (R^2=0.5644) and the average annual consecutive days above the bleaching threshold (R^2=0.6039) (S11, Fig S6) were especially important in driving the observed community differences. Interestingly, these same two temperature parameters best explain the trends seen in coral species richness, abundance, diversity, and density between site type (Table S5, S6). This evidence suggests that coral community composition is strongly influenced by time spent above the regional thermal maximum. *Chl a* concentration was also significant, but produced an R^2=0.0434 (S11; Fig S6), indicating that while *chl a* may have some impact on coral community differences between site types; it is unlikely to be a primary driver. Taken

together with the fact that other nutrient parameters do not explain a significant proportion of the variation in NMDS2 (S11; Fig S6), it seems likely that nutrient parameters play a lesser role in determining overall differences in community structure between these three thermally distinct site types. Reef flattening may also play a role in decreased species richness between site types (Newman *et al.*, 2015), however in the current study 3-dimensional reef complexity was not quantified. Previous research shows that climate change has resulted in increased thermal stress, declines in coral cover, and shifts in coral community composition (Hughes *et al.*, 2003; Hoegh-Guldberg *et al.*, 2007). These results suggest that even without causing actual coral bleaching locally, thermal parameters have a strong influence on coral community composition.

In contrast, variation within site types appeared to be dependent upon both temperature and nutrient parameters and varied based on site type. In low_{TP}, mod_{TP}, and ext_{TP} sites, average annual days above the bleaching threshold explained the most variation within site types (R^2>0.95) (Table S9; Fig S5). Average annual maximum temperature explains 86% of variation at ext_{TP} sites, but only 11% at low_{TP} sites (Table S9; Fig S5), indicating that annual maximum temperature is more of a factor at warmer sites. Average annual consecutive days above the bleaching threshold showed a similar trend. However, nutrient parameters, such as DIN and DON appeared to play significant roles within site type variation at mod_{TP} and especially ext_{TP} sites (Table S9; Fig S5). Interestingly, linear mixed effects models of ecological parameters (species richness, abundance, diversity, coral cover, and coral density) among low_{TP} sites show that patterns within all of these parameters were most likely driven by annual temperature range (Table S7, S8). Overall, within site variation is different based on site type, but both temperature and nutrient parameters play a role. Variation among sites classified as low_{TP} was best explained by temperature parameters, however at mod_{TP} and ext_{TP} sites both temperature and nutrient

parameters show reasonably high R^2, suggesting that both play a role in variation within site type.

Interestingly, and in contrast to our results, coral growth and coral cover were found to be higher in nearshore (ext_{TP}-like) environments in the Florida Keys than cooler and less thermally variable (low_{TP}-like) offshore reefs (Lirman & Fong, 2007). This difference may be due to the fact that corals living in warmer (Williams *et al.*, 2010; van Woesik *et al.*, 2012; Fine *et al.*, 2013) or more variable areas (Oliver & Palumbi, 2011; Barshis *et al.*, 2013) are less susceptible to bleaching stress due to adaptation/acclimatization to local conditions. However, here we observe that corals living in ext_{TP} environments were not visibly less healthy than corals at low_{TP} and mod_{TP} sites (data not shown). In fact, *Siderastrea siderea* in nearshore (ext_{TP}) environments have been shown to have higher growth and calcification rates than those on the forereef (low_{TP}) (Castillo *et al.*, 2011; Carilli *et al.*, 2012; Castillo *et al.*, 2012), suggesting that this species is locally adapted/acclimatized to more extreme temperature conditions and/or nutrients. These more extreme conditions may not be suitable for other coral species, which can lead to failed recruitment or inability of juveniles from more moderate sites to survive in these more extreme environments due to the influence of thermal history on limiting acclimatization (Howells *et al.*, 2013). Lack of differences in community variables between low_{TP} and mod_{TP} sites (Fig 3A, S3) indicates that although reefs subjected to moderate temperature variation have been shown to have higher coral cover (Soto *et al.*, 2011) differences in temperature and nutrient variables between these site types (Table 1) may not have been significant enough to elicit a community level response.

Influence of nutrients on coral community composition and life history strategies

Overall, bulk nutrients (*chl a*) increase with increasing temperature parameters, as *chl a* is highest at ext_{TP} sites and lowest at low_{TP} sites (Table 2B, Fig 2 A, B). As nutrient concentrations are highest in ext_{TP} environments, it is possible that nutrients are at least partially responsible for lower species richness, abundance, diversity, cover, and density at extreme sites compared to low_{TP} and mod_{TP} sites. In fact, linear mixed effects models show that *chl a* is a better explanatory variable for the change in percent coral cover across site types than any measured temperature parameter (Table S4). However, linear modeling of temperature and *chl a* against the NMDS2 axis was used to tease apart the independent contributions of temperature and *chl a* between sites and revealed that temperature is the primary driver of overall community composition between site types (Table S11, Fig 3B).

Preliminary in-situ nutrient sampling shows that concentrations of DOC and total N are higher in ext_{TP} sites relative to low_{TP} and mod_{TP} sites (Fig S4C, S4D). It is likely that these two nutrient types are responsible for driving the increase in bulk nutrients at extreme sites. Therefore, it is possible that accelerated microbe growth on corals (due to elevated DOC) (Kline *et al.*, 2006) and/or increased macrobioerosion (correlated with high N) (DeCarlo *et al.*, 2015) may play a role in lower coral species richness, abundance, diversity, cover, and density at ext_{TP} sites. However, based on linear modeling, it is unlikely that DOC or *chl a* play a large role in changing coral community ecology between site types (S11, Fig S6). Elevated *chl a* concentrations at mod_{TP} sites compared to low_{TP} sites were likely driven by DIN (Fig S4A). Increased DIN has been shown to cause a reduction in the bleaching threshold and induce a higher incidence of mortality (Wooldridge, 2009; Vega Thurber *et al.*, 2014). In this case, the above effect is unlikely to have occurred, as coral community composition did not differ between these site types. More frequent and consistent seawater nutrient sampling and manipulative

experiments are needed to fully understand the impacts of both bulk and individual nutrient pools on the dynamics of coral communities and individual coral physiology.

Extreme sites are dominated by weedy and stress tolerant coral species

Corals have previously been classified into 4 life history groups (Darling *et al.*, 2012). Competitive corals are large, quick growing, broadcast spawning, branching and plating species (i.e. *Acropora cervicornis*). These corals are dominant in ideal conditions and shade out competitors, but are sensitive to breakage. Weedy corals (i.e. *Porites sp.*) reproduce by brooding, have small colony sizes, and are opportunistic colonizers of recently disturbed habitat. Stress tolerant corals (i.e. *Siderastrea siderea*) are slow growing, massive, broadcast spawning species with long generation times and high fecundity. Generalists (i.e. *Orbicella sp.*) show overlap between these three groups (Darling *et al.*, 2012). In the current study, ext_{TP} sites were dominated by stress tolerant and weedy genera, while low_{TP} sites and mod_{TP} sites contained all 4 life history types (Fig 4). Low_{TP} sites contained all four life history strategies in mostly equal proportions, mod_{TP} sites were similar but with fewer competitive species than low_{TP} sites, and ext_{TP} sites had comparatively fewer of all four life histories, but were dominated by weedy and stress tolerant genera. Shifts toward weedy and stress tolerant genera under climate change conditions were predicted by Darling et al. (2012) and have been recorded in many areas of the world, including the Caribbean (Loya *et al.*, 2001; Aronson *et al.*, 2004; Green *et al.*, 2008; Alvarez-Filip *et al.*, 2011). Even in the face of region-wide decline in coral cover and competitively dominant species (Gardner *et al.*, 2003), some weedy species, such as *Porites astreoides*, are actually increasing in prevalence in the Caribbean (Green *et al.*, 2008). This weedy species is likely able to succeed under recent stressors due to its ability to brood and mature quickly, which allow it to quickly colonize a recently disturbed area. In contrast, stress-

tolerant species such as *S. siderea* are likely able to survive in ext_{TP} environments due to its slow growth rates and massive size, which allow them to be resistant to stress. These two contrasting strategies seem most effective in ext_{TP} environments, and are likely to be most effective in future conditions as the oceans continue to warm.

Implications for conservation and management of reefs in the face of climate change

Lower coral community diversity and percent cover at ext_{TP} sites compared to low_{TP} and mod_{TP} sites are likely driven by temperature parameters (particularly the number of days and number of consecutive days above the bleaching threshold per year, as well as average annual temperature range and max temperature). While ecological differences between sites may be mainly driven by temperature parameters, bulk nutrients may still play a role. Lack of community scale differences between low_{TP} and mod_{TP} sites suggests that low magnitude variations in temperature (and nutrient) parameters are less likely to cause measureable, community-wide changes. The change in community structure between ext_{TP} and low_{TP}/mod_{TP} sites was accompanied by a change in the dominant coral genera. Low_{TP} and mod_{TP} sites contain all 4 coral life histories (competitive, generalist, weedy, and stress-tolerant) (Darling *et al.*, 2012), but ext_{TP} sites are dominated almost entirely by weedy and stress-tolerant species, suggesting that genera utilizing these two life history strategies may be better suited for survival under more extreme conditions. Future research is needed to examine the relative acclimatization/adaptation potential of corals at each of these site types as well as the relative contributions of thermal and nutrient stressors on coral health. Additionally, ext_{TP} sites may warrant further protection as they potentially harbor the coral genera and individuals that are most likely to thrive as the ocean continues to warm. These sites are not often protected and should be considered in future conservation management decisions.

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DATA ACCESSBILITY

Data will be archived on PANGAEA after acceptance and a DOI will be included here.

BIOSKETCH

Justin Baumann is a PhD student at the University of North Carolina at Chapel Hill working with Dr. Karl Castillo. His research focuses on the impacts of temperature and nutrients on coral reef ecosystems and the physiological response of the coral host and endosymbionts to climate change.

Tables

Table 1: Parameters used in Site Classification

Factor	Min	Mean	Max	Standard Deviation	low_{TP} Sites	mod_{TP} Sites	ext_{TP} Sites
Mean Annual Max Temp	30.192°C	30.624°C	31.286°C	0.273°C	30.192[1]-30.760 °C	30.760-30.897 °C	30.897-31.286[2] °C
Mean Annual Temp Range	4.35°C	5.168°C	7.065°C	0.692°C	4.350[3]-5.514 °C	5.514-5.860 °C	5.860-7.065[4] °C
Mean Annual Days Above Bleaching Threshold	20.000 days	40.105 days	78.4 days	14.333 days	20.000[5]-40.105 days	40.105-54.439 days	54.439-78.400[6] days
Mean Consecutive Days Above Bleaching Threshold	3.000 days	4.758 days	7.500 days	0.921 days	3.000[7]-4.750 days	4.750-5.680 days	5.680-7.500[8] days

[1]No corals below 30.352
[2]No corals above 31.169
[3]No corals below 4.476
[4]No corals above 6.552
[5]No corals below 25.772
[6]No corals above 68.772
[7]No corals below 3.837
[8]No corals above 6.600

Table 1: Values for the four factors included in site selection metrics. Values are all averages from 2002-2012 and include measurements for minimum, mean, maximum, and standard deviation for each factor. The range at which each factor was classified as low_{TP}, mod_{TP}, or ext_{TP} site is also shown. Note that these ranges vary for each factor because at both low and high extremes coral reefs were not present. Superscripts indicate ranges in which corals are not present.

Table 2A: Effects of site and site type on 13 year average (2002-2015) *Chl a* concentration

Site Variable	df	Sum Sq	Mean Sq	F value	*p*-value
Site	12	1350	112.75	131.5	**<0.0001**
Site Type	2	288	144.00	166.7	**<0.0001**

Table 2A: Results of analysis of variance (ANOVA) of the effect of site and site type on *chl a*. Significant effects are in bold ($p<0.05$). df= degrees of freedom.

Table 2B: Pair-wise comparisons of effects of site type on 13 year (2002-2015) *Chl a* concentration

Comparison	*p-value*
low_{TP}-mod_{TP}	**<0.0001**
low_{TP}-ext_{TP}	**<0.0001**
mod_{TP}-ext_{TP}	**<0.0001**

Table 2B: Results of Tukey's HSD tests evaluating the significance of the pair-wise comparisons of factors that had a significant effect on *chl a* concentration. Only significant pairwise comparisons ($p<0.05$) are included.

Table 3A: Effects of Survey Method, Site, and Site Type on Species Richness, Abundance, Shannon Diversity, Percent Coral Cover, Coral Density, and Life History

Community Parameter	Site Variable	df	Sum sq	Mean sq	F value	*p*-value
Species Richness	Survey Method	1	20.30	20.35	0.508	0.5
	Site	12	918.4	76.53	15.7	**<0.0001**
	Type	2	414.9	207.4	8.41	**0.002**
Abundance	Survey Method	1	16500	16500	1.37	0.3
	Site	12	238500	19890	3.80	**0.01**
	Type	2	116100	58010	7.06	**0.004**
Shannon Diversity Index	Survey Method	1	0.3010	0.3012	0.786	0.4
	Site	12	8.775	0.7312	13.1	**<0.0001**
	Type	2	5.274	2.637	14.4	**<0.0001**
Percent Coral Cover	Site	12	0.5666	0.04721	15.2	**<0.0001**
	Type	2	0.1172	0.05859	6.68	**0.002**
Coral Density	Site	12	263.5	21.96	20.7	**<0.0001**
	Type	2	142.1	71.07	39.8	**<0.0001**
Life History	Site	12	904.0	75.37	4.40	**<0.0001**
	Type	2	4311	2156	2.92	0.06

Table 3A: Results of three-way analysis of variance (ANOVA) of the effect of site variables on coral community parameters. Significant effects are in bold ($p<0.05$). df= degrees of freedom.

Table 3B: Pair-wise comparisons of effects of Site Type on Species Richness, Abundance, Shannon Diversity, Percent Coral Cover, Coral Density, Life History

Community Parameter	Factor	Comparison	*p*-value
Species Richness	Type	low_{TP}-ext_{TP}	**0.003**
		mod_{TP}-ext_{TP}	**0.02**
Abundance	Type	low_{TP}-ext_{TP}	**0.005**
		mod_{TP}-ext_{TP}	**0.02**
Shannon Diversity Index	Type	low_{TP}-ext_{TP}	**0.001**
		mod_{TP}-ext_{TP}	**0.0001**
Percent Coral Cover	Type	low_{TP}-ext_{TP}	**0.007**
		mod_{TP}-ext_{TP}	**0.003**
Coral Density	Type	low_{TP}-ext_{TP}	**<0.0001**
		mod_{TP}-ext_{TP}	**<0.001**
Life History	Type	low_{TP}-ext_{TP}	**0.049**

Table 3B: Results of Tukey's HSD tests evaluating the significance of the pair-wise comparisons of factors that had a significant effect on species richness, abundance, Shannon diversity index, percent coral cover, coral density, or life history. Only significant pairwise comparisons ($p<0.05$) are included.

Figure Legends

Figure 1: The Belize Barrier Reef System (BBRS) classified by site type (A), and 13 year average log-transformed [*chl a*] (B). Stars indicate survey and sampling sites. Numbers represent site labels (see statistical tables below).

Figure 2: Annual (2003-2015) average *chl a* concentration by site type (+/- SE) (A). Panel B shows overall average *chl a* (D). The letters a, b, and c indicate results of post hoc Tukey tests that show significant differences between site types ($p<0.05$).

Figure 3: Species Richness (# of species present) at each site type (A). Statistically significant differences ($p<0.05$) are marked with an *. This trend is consistent among other community variables, including: coral abundance (# of corals), percent coral cover, Shannon diversity, and coral density (# of coral/ m^2) (Fig S2). B.) Nonmetric multidimensional scaling (NMDS) plot of coral community differences clustered by site type (B).

Figure 4: Abundance of coral (±1 SE) grouped by life history (Darling et al. 2012). Letters a and b indicate results of post hoc Tukey tests that show significant differences between site types ($p<0.05$).

Figures

Figure 1: Site location, temperature parameter, and *chl a* maps

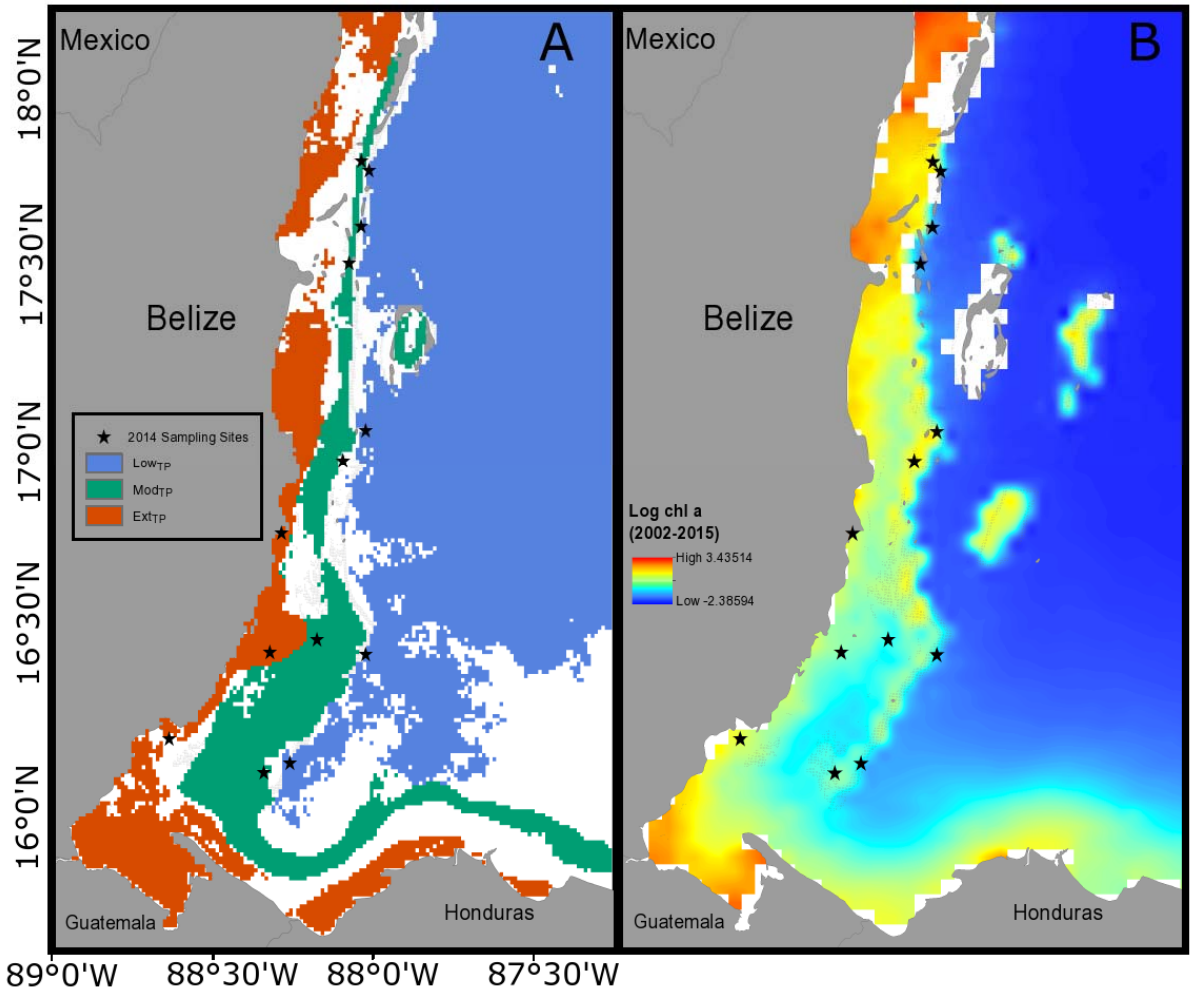

Figure 2: Average *chl a* by site type

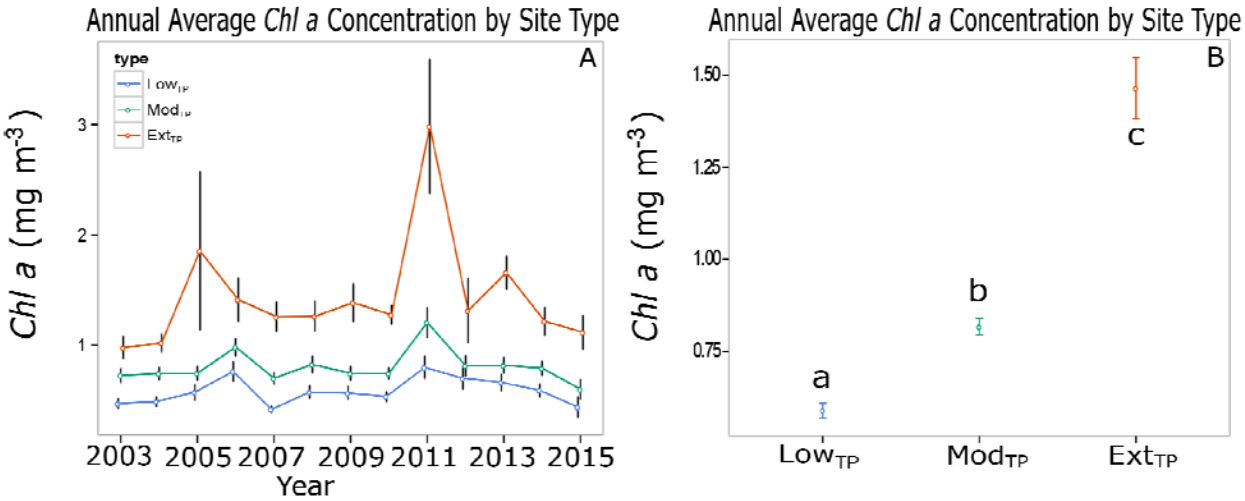

Figure 3: A.) Average coral species richness by site type and B.) NMDS of coral community variables by site type

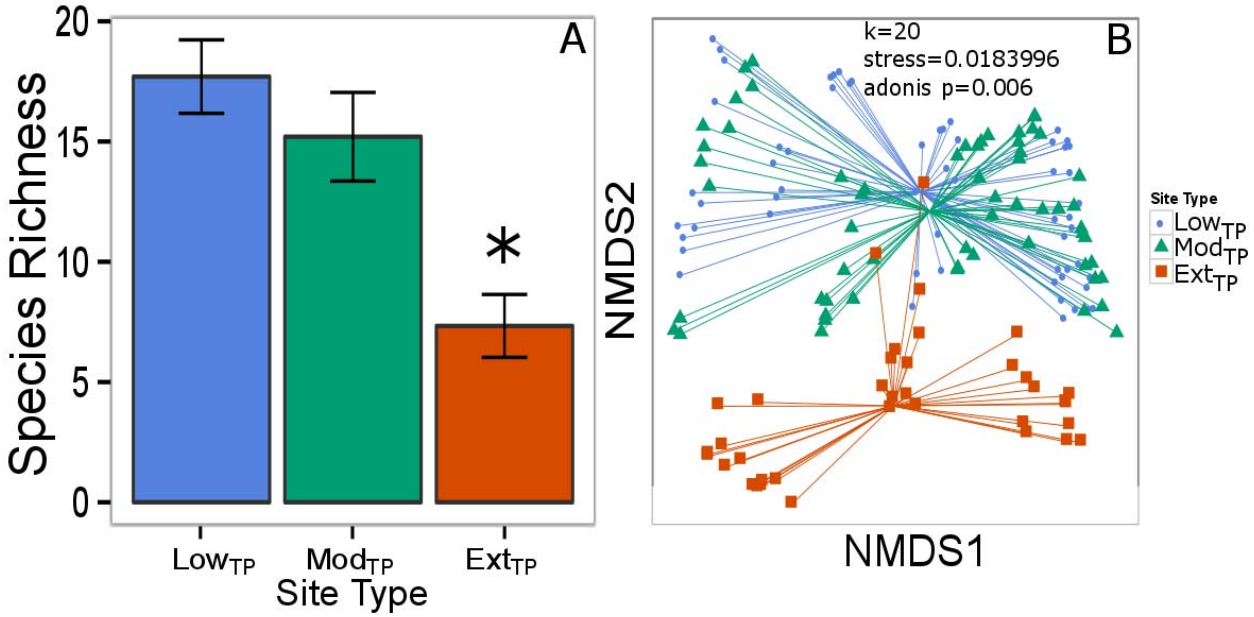
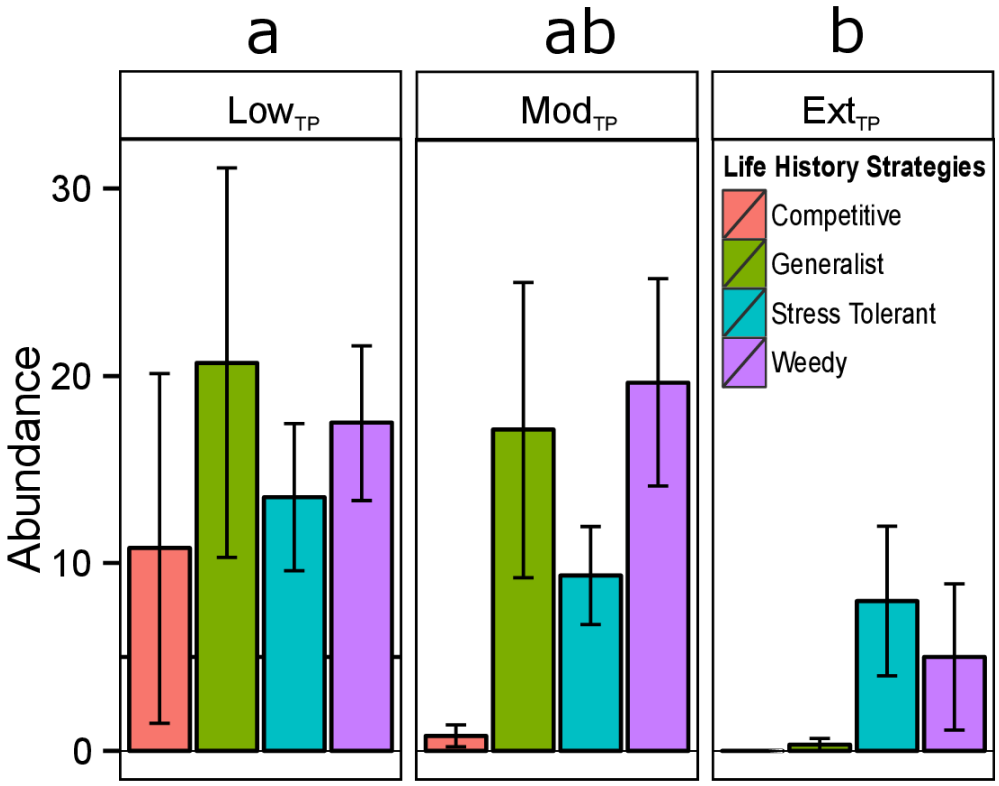
Figure 4: Coral life history strategy by site type