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Temperature regimes impact coral assemblages along environmental gradients on lagoonal reefs in Belize

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Abstract

Coral reefs are increasingly threatened by global and local anthropogenic stressors such as rising seawater temperature, nutrient enrichment, sedimentation, and overfishing. Although many studies have investigated the impacts of local and global stressors on coral reefs, we still do not fully understand how these stressors influence coral community structure, particularly across environmental gradients on a reef system. Here, we investigate coral community composition across three different temperature and productivity regimes along a nearshore-offshore gradient on lagoonal reefs of the Belize Mesoamerican Barrier Reef System (MBRS). A novel metric was developed using ultra-high-resolution satellite-derived estimates of sea surface temperatures (SST) to classify reefs as exposed to low (low_{TP}), moderate (mod_{TP}), or high ($high_{TP}$) temperature parameters over 10 years (2003 to 2012). Coral species richness, abundance, diversity, density, and percent cover were lower at $high_{TP}$ sites relative to low_{TP} and mod_{TP} sites, but these coral community traits did not differ significantly between low_{TP} and mod_{TP} sites. Analysis of coral life history strategies revealed that $high_{TP}$ sites were dominated by hardy stress-tolerant and fast-growing weedy coral species, while low_{TP} and mod_{TP} sites consisted of competitive, generalist, weedy, and stress-tolerant coral species. Satellite-derived estimates of *Chlorophyll-a* (*chl-a*) were obtained for 13-years (2003-2015) as a proxy for primary production. *Chl-a* concentrations were highest at $high_{TP}$ sites, medial at mod_{TP} sites, and lowest at low_{TP} sites. Notably, thermal parameters correlated better with coral community traits between site types than productivity, suggesting that temperature (specifically number of days above the thermal bleaching threshold) played a greater role in defining coral community structure than productivity on the MBRS. Dominance of weedy and stress-tolerant genera at $high_{TP}$ sites suggests that corals utilizing these two life history strategies may be better suited to cope with warmer oceans and thus may warrant protective status under climate change.

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Introduction

Coral reefs are threatened locally and globally by anthropogenic stressors such as warming induced by increasing greenhouse gas emissions, excessive nutrients from runoff and sewage effluent, overfishing, and habitat destruction [1,2,3]. Of particular concern are increasing greenhouse gas emissions that continue to cause warming of the global oceans [1,4]. This warming trend is especially troubling in the Caribbean Sea, where rates of warming are higher than in many other tropical basins [5], and where coral cover has declined by up to 80% in recent decades [6]. Elevated sea surface temperature (SST) is the major cause of the breakdown of the essential coral-algal symbiosis, which if widespread results in mass coral bleaching [7,8]. In Belize, the 1998 El Niño bleaching event was the most significant bleaching induced mass coral mortality event on lagoonal reefs over the last 3000 years [9]. These large-scale coral bleaching events are projected to increase in frequency and severity as the climate continues to warm [4,10]. In fact, if ocean warming persists, corals in the Caribbean Sea are predicted to bleach biannually within the next 20-30 years [11], with annual bleaching events occurring as soon as 2040 [12]. Caribbean-wide and global-scale bleaching events are predicted to continue unless corals can increase their thermal tolerance at a rate of 0.2-1.0°C per decade [4].

Annual and daily thermal variability have recently been identified as important factors influencing coral thermal tolerance [13,14,15]. Indeed, previous exposure to thermally variable environments increases a coral's tolerance to future temperature stress [14,16,17,18], and research suggests that Pacific and Red Sea corals living in areas with high summer maximum SST are less susceptible to bleaching [19,20]. Along the Belize Mesoamerican Barrier Reef System (MBRS) and on Pacific Atolls, corals historically exposed to less thermal variability exhibited slower growth rates and/or greater susceptibility to bleaching in response to SST increases [17,18]. In the

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Florida Keys, coral growth rates and coral cover were higher in nearshore environments exposed to more variable seawater temperatures than on deeper reefs experiencing more stable temperatures [21]. In contrast, while many studies suggest that high temperature variability leads to higher coral resilience [14,15,16], there is also evidence that corals experiencing moderate long term temperature variability (either annual or daily variation) are better able to cope with stress [13]. Collectively, these studies emphasize the importance of thermal variability on the response of corals to environmental stress, and highlight its capacity to shape coral community composition across a reef system.

Multi-species coral assemblages have recently been proposed to comprise four major life history guilds: competitive (large, fast growing, broadcast spawning, e.g., Caribbean *Acropora spp.*), weedy (small, opportunistic colonizers of recently disturbed habitat, e.g., Caribbean *Porites spp.*), stress-tolerant (massive, slow growing, broadcast spawning, e.g., *Siderastrea siderea*), and generalist (share traits characteristic of all three other groups, e.g., *Orbicella spp.*) [22]. Grouping species by life history strategy allows for prediction of responses to disturbance (e.g., temperature stress) as life history strategies are trait based [23]. Additionally, each guild is expected to be differentially impacted by stressors and life histories predict coral community response to multiple stressors [24]. Therefore, life history strategies offer a more elegant and predictive alternative to traditional genus or species level analysis.

Competitive corals are by definition not very stress tolerant [22]. As such, region-wide decline of these species would be expected as the impact of anthropogenic stressors increase (including coral disease). This decline has already occurred in the Caribbean [6]. Generalist corals became dominant on Caribbean reefs in the late 1970s following mass die off of competitive corals. Generalists are more stress tolerant than competitive species but bleaching and other stressors have

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led to high mortality of *Orbicella spp.* in the Caribbean [25] and continued decline is expected as temperature stress increases [6,26,27], leading to a decline in reef complexity [28]

Weedy and stress tolerant corals have been shown to be more resilient than competitive and generalist species [22,24], and are hypothesized to dominate warmer and more impacted reefs (e.g., reefs closer to the shore). A shift from dominance of competitive and generalist species to weedy and stress tolerant species occurred on Okinawan reefs following the 1998 El Niño bleaching event [29,30] and an overall decline in coral cover and abundance currently occurring in the Caribbean has been coupled with an increase in abundance of weedy species [27,31]. Interestingly, fossil assemblages from excavated pits on reefs in Panama reveal that mortality and changes in reef communities caused by anthropogenic impact (such as land clearing and overfishing) predate mass bleaching events, indicating that other sub-lethal stressors can impact coral community structure [32,33,34]. Collectively, evidence suggests that differential responses between coral species to increasing anthropogenic stressors may lead to community scale shifts in reef composition from dominance of competitive and generalist species to dominance of stress tolerant and weedy species.

The purpose of the current study was to investigate the impact of thermal regimes on present day coral community composition (coral abundance, species richness, diversity, percent cover, density, and life history strategies) of lagoonal reefs (i.e., region extending from the barrier reef's crest to the mainland) across the Belize MBRS. A novel GIS-based metric was developed to characterize lagoonal reefs across this reef system into three thermally distinct regimes. Within these three regimes, thirteen reef sites were identified and benthic surveys were conducted to quantify coral community composition. These thermal regimes exist along a nearshore-offshore productivity gradient, which may also influence coral community structure. Quantifying coral

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community differences among these thermally distinct reefs will help us better predict how coral community structure may be impacted by climate change. Identifying which areas and species are best able to cope with environmental stress (and which are least able) may allow for more targeted management strategies, as it is important to protect both high-risk and low-risk reef sites to improve our chances of conservation success [35].

Materials and Methods

Site identification

SST Estimate Assembly

Daily 1-km horizontal resolution SST estimates were acquired from the Jet Propulsion Laboratory's Multi-Scale High Resolution SST (JPL MUR SST) records via the Physical Oceanography Distributed Active Archive Center (PO.DAAC) at the NASA JPL, Pasadena, CA (http://podaac.jpl.nasa.gov). Conventional 1-km resolution satellite-derived 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) [36]. MUR combines these two datasets to present a more comprehensive and complete SST product. It employs multi-resolution variational analysis (MRBA) as an interpolation method to combine high resolution datasets with more conventional datasets, generating a product that contains no cloud contamination [36]. MUR reports estimates of 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), MUR, and other SST products revealed that MUR outperforms other products in estimating in-situ temperature, although it also underestimates the temperature corals experience at depth (S1 Fig). However, due to its temporal coverage and temporal resolution, high

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spatial resolution, lack of cloud contamination, and smaller method error compared to similar products such as Group for High Resolution SST (GHRSST), MUR was determined to be the ideal SST product for use in the current study.

Site Classification

Multiple thermal parameters were calculated at different temporal resolutions and examined across thirteen lagoonal reef sites (S1 Table). Lagoonal reefs are located between the barrier reef's crest and the mainland, and therefore do not include the seaward facing fore-reef. Instead, lagoonal reefs include nearshore reefs, patch reefs, and the back reef. Four thermal parameters produced distinct environments for the reef sites across the Belize MBRS: average annual maximum temperature (S2A Fig), average annual temperature range (S2B Fig), average annual number of days above the regional bleaching threshold of 29.7°C [9] (S2C Fig), and average annual consecutive days above the regional bleaching threshold (i.e., longest potential thermal stress events) (S2D Fig). A metric that combined all four thermal parameters was generated using ArcGIS© in order to assess thermal environments across the Belize MBRS. Data from each of the four parameters in the metric (Table 1) were divided into 8-10 bins (0.5 standard deviations (SD) of the mean) and overlaid on a map of the Belize MBRS. 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 2003-2012). For all four parameters, areas that were classified in bins ≥1 SD above the mean were designated high temperature parameter ($high_{TP}$) sites (Fig 1). 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 the average annual maximum temperature, and within 1 SD of the average annual consecutive days and the average annual number of days above the regional bleaching threshold (Fig 1). Low temperature parameter (low_{TP}) sites were classified as bins that

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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 1). Using the metric presented in Fig 1, fifteen sites were identified, thirteen of which were visited and surveyed in November 2014 (the two northernmost high$_{TP}$ sites were not surveyed as corals were not located within the marked geographic area) (Table 1, Fig 1).

Fig 1. Thermal Regimes and Site Locations

The Belize Mesoamerican Barrier Reef System (MBRS) classified by site type based on four thermal parameters. Blue, green and red regions represent low$_{TP}$, mod$_{TP}$, and high$_{TP}$ areas across the reef system. Stars indicate surveyed sampling sites.

Table 1. Thermal Parameters Used For Site Classification

Factor	Min	Mean	Max	SD	low$_{TP}$ Sites	mod$_{TP}$ Sites	high$_{TP}$ Sites
Mean Annual Max Temp	30.2°C	30.6°C	31.3°C	0.27°C	30.2-30.8°C	30.8-30.9°C	30.9-31.3°C
Mean Annual Temp Range	4.4°C	5.2°C	7.1°C	0.69°C	4.4-5.5°C	5.5-5.9°C	5.9-7.1°C
Mean Annual Days Above Bleaching Threshold	20.0 days	40.1 days	78.4 days	14.3 days	20.0-40.1 days	40.1-54.4 days	54.4-78.4 days
Mean Consecutive Days Above Bleaching Threshold	3.0 days	4.8 days	7.5 days	0.92 days	3.0-4.8 days	4.8-5.7 days	5.7-7.5 days

Values for the four thermal parameters included in site selection metrics. Values are all averages from 2003-2012 and include measurements for minimum, mean, maximum, and standard deviation (SD) for each thermal parameter. The range at which each factor was classified as low$_{TP}$, mod$_{TP}$, or high$_{TP}$ site is also shown.

Benthic surveys

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In November 2014, benthic surveys were performed at the thirteen reef sites. Depth of each reef site was standardized to 3-5m. Reef types surveyed included back reefs, patch reefs, and nearshore reefs. A team of three divers surveyed six belt transects (dimension 6 x 10 m) at each site following Atlantic and Gulf Rapid Reef Assessment (AGRRA) methodology [37]. Briefly, a diver classified the genus and species of every coral >6cm^2 within 1m of the transect line along a 10m transect. The number and size (length, width, and height) of individual colonies of each coral species were recorded on underwater data sheets. The collected data were used to calculate coral species diversity, abundance, richness, and coral life history (following Darling *et al.* [22]) for each site.

Additionally, six video belt transects (1 x 20m) were also performed at each site using GoPro® cameras attached to PVC stabilizing apparatuses allowing each diver to stabilize the camera while surveying transects. Video transects were analyzed at the University of North Carolina at Chapel Hill (UNC-Chapel Hill) in a manner similar to the AGRRA method used in the field, except two additional parameters (percent coral cover and coral density) were calculated. Results of the diver and video transect surveys were not significantly different (p=0.300). As a result diver and video survey data were pooled at each site when possible. Full details and a comparison of the methods employed are available in S1 Appendix.

Coral life history

Coral species were grouped into four life history strategies as previously described by Darling *et al.* 2012 [22]. In their study, Darling *et al*. 2012 identified four life history guilds for corals based on multivariate trait analysis: competitive, weedy, stress-tolerant, and generalist [22]. The four guilds are primarily separated by colony morphology, growth rate, and reproductive rate. The classification was based on a thorough sampling of global Scleractinian coral diversity. Each

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coral that is included in a guild in Darling *et al.* 2012 [22] was classified into the appropriate guild for this study and comparisons of life history strategies between sites and site types were made.

Chlorophyll-a

Eight-day composite 4-km horizontal resolution *chlorophyll-a* (*chl-a*) estimates over the interval 2003-2015 were obtained from NASA's Moderate Resolution Imaging Spectroradiometer (AQUA MODIS) via NOAA's Environmental Research Division's Data Access Program (ERDDAP) [38]. 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 (S2E Fig). *Chl-a* is a widely used proxy for primary productivity and nutrient delivery in seawater [39,40], 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 [41]. Here, *chl-a* data are used as a proxy for primary production across the Belize MBRS.

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 [42]. Transect averaged survey data for species richness, abundance, Shannon diversity, coral cover, coral density, 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, and Shannon diversity. Only two fixed factors (site and site type) were included in the ANOVA

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for coral cover and coral density, since only data from video surveys were used to calculate these averages. Two fixed factors (site and site type) were included in the ANOVA for *chl-a* concentrations since they were calculated using satellite estimates and survey type was not a factor.

If factors were significant ($p<0.050$), a post-hoc Tukey's HSD test was used to evaluate the significance of each pair-wise comparison. Spatial autocorrelation was evaluated using Moran's I [43]. Significant *p-values* for Moran's I ($p<0.050$) indicate an effect of spatial autocorrelation. Spatial autocorrelation was only a factor for coral cover ($p=0.040$). To correct for the effect of spatial autocorrelation, the cut-off value for significance within the ANOVA for coral cover was decreased to $p<0.010$, following Dale and Fortin [44].

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 [45]. 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 [45].

Linear models tested for the influence of temperature parameters and *chl-a* on the variation observed along NMDS1 and NMDS2 (within and between site type community variations). Linear models were run 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 (S2 Table). For NMDS1, data were also divided by site type in order to assess within site type variation (S3 Table).

Ethics statement

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All research related to this projected was completed under official permit from the Belize Fisheries Department (#000045-14).

Results

Coral community composition

Combined results of AGRRA diver surveys and GoPro® video surveys for all thirteen sites revealed that coral species richness varied as a function of site location ($p<0.001$) as well as site type ($p=0.002$). Coral abundance was significantly lower at $high_{TP}$ sites compared to low_{TP} ($p=0.005$) and mod_{TP} ($p=0.020$) sites, but was not significantly different between low_{TP} and mod_{TP} sites (Fig 2A). Coral cover, Shannon diversity, coral density, and species richness also followed these same patterns ($p\leq0.020$; Fig 2B-E). NMDS analysis of the ecological parameters showed that community structure was significantly different (stress=0.018, adonis test $p=0.006$) between $high_{TP}$ sites and low_{TP}/mod_{TP} sites along the NMDS2 axis, but was not different between low_{TP} and mod_{TP} sites ($p>0.050$) (Fig 3). The most dominant taxa at low_{TP} and mod_{TP} sites were *Orbicella spp*., *Porites spp*., *Undaria spp*., *S. siderea*, and *Pseudodiploria spp*, while at $high_{TP}$ sites they were *Siderastrea spp*., *P. astreiodes*, and *Pseudodiploria spp*. Variation along the NMDS1 axis represents within site type differences while variation along the NMDS2 axis represent between site type differences (Fig 3).

Fig 2. Differences in coral community structure across site type

Average coral abundance (A), percent coral cover (B), coral species diversity (C), coral density (D), and coral species richness (E) at each site type. Statistically significant differences ($p<0.05$) are marked with an *. Blue, green, and red bars (± 1 SE) represent low_{TP}, mod_{TP}, and $high_{TP}$, respectively.

Fig 3. NMDS of coral community variables by site type.

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Nonmetric multidimensional scaling (NMDS) plot of coral community differences clustered by site type. Blue circles, green triangles, and red squares represent low_{TP}, mod_{TP}, and $high_{TP}$ site types, respectively.

Linear modeling of temperature and productivity parameters against NMDS1 and NMDS2 revealed that average annual maximum temperature, average annual temperature range, average annual days above the bleaching threshold, and average annual consecutive days above the bleaching threshold all had significant effects on the NMDS1 variation. All four temperature parameters, as well as *chl-a*, also had significant effects on NMDS2 variation (S2 Table; S3 Fig). Average annual consecutive days above the bleaching threshold explained the most variation for NMDS1 and NMDS2 (R^2=0.1026, 0.604 respectively; p <0.001 for both; S2 Table; S3 Fig).

Linear regressions of temperature parameters and *chl-a* within site types along NMDS1 revealed significant effects (p<0.050) of average annual maximum temperature, average annual days above the bleaching threshold, and average annual consecutive days above the bleaching threshold for all site types, average annual temperature range for mod_{TP} and $high_{TP}$ sites, and *chl-a* for $high_{TP}$ sites only (S3 Table; S3 Fig). 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 $high_{TP}$ sites (S3 Table; S3 Fig).

Coral life history

Site exhibited a significant effect on the number of corals in each of the four coral life history guilds [22] (p<0.001). The distribution of coral life history strategies differed significantly between low_{TP} and $high_{TP}$ site types (p=0.049; Fig 4), while mod_{TP} sites did not differ from low_{TP} or $high_{TP}$ sites (Fig 4). Overall, there appears to be a pattern of lower abundances of all life history

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guilds at high$_{TP}$ sites compared to low$_{TP}$ sites. Competitive species were not present and generalist species were only present in very small number at high$_{TP}$ sites.

Fig4. Coral life history strategy by site type

Abundance (count) of corals (±1 SE) grouped by life history (from Darling *et al*. 2012). Letters 'a' and 'b' show significant differences between site types (p<0.050) acquired from post hoc Tukey tests.

Chlorophyll-a

Annual average *chl-a* concentrations varied over time and differed by site type (p<0.001), but were consistently lowest at low$_{TP}$ sites and highest at high$_{TP}$ sites regardless of year (Fig 5A). *Chl-a* concentrations averaged over 2003-2015 were significantly different across all three site types (p<0.001 in all cases). Low$_{TP}$ sites exhibited the lowest average 13-year *chl-a* concentrations. Mod$_{TP}$ sites exhibited average 13-year *chl-a* concentrations that were significantly higher than low$_{TP}$ sites, but significantly lower than high$_{TP}$ sites. High$_{TP}$ sites exhibited significantly higher average 13-year *chl-a* values than both low$_{TP}$ and mod$_{TP}$ sites (p<0.001 in all cases, Fig 5B). The pattern seen in *chl-a* concentrations is positively correlated with the patterns seen in all temperature parameters (*chl-a* and temperature parameters are lowest at low$_{TP}$ sites and highest at high$_{TP}$ sites) (Fig 1, S2 Fig).

Fig 5. Average *chl-a* by site type

Chl-a concentration by site type (±SE) Annual average *chl-a* for low$_{TP}$ (blue), mod$_{TP}$ (green), high$_{TP}$ (red) site types over the interval 2003-2013 (A). *Chl-a* concentrations averaged over the 13-year interval (B). Letters x, y, and z indicate results of post hoc Tukey tests showing significant differences in 13-year *chl-a* concentrations across site types (p<0.050).

Discussion

Coral community composition

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Coral species richness, abundance, diversity, density, and percent cover were all lower at $high_{TP}$ sites compared to low_{TP} and mod_{TP} sites (Fig 2). Differences in coral community composition between $high_{TP}$ sites and low_{TP}/mod_{TP} sites are historically explained by more stressful conditions nearshore and less stressful conditions offshore [46,47]. These nearshore stressors include, but are not limited to temperature, eutrophication, sedimentation, and wave energy [46,47]. Our findings suggest that lower coral species richness, diversity, abundance, percent cover, and density at $high_{TP}$ sites may be driven by high thermal variability, elevated maximum temperatures, and prolonged duration of exposure to temperatures above the bleaching threshold; three variables that have been shown to cause coral community decline [13,29,48,49,50]. These temperature parameters were more strongly correlated with changes in coral community composition between site types than with *chl-a* (S3 Fig), indicating that they likely play a greater role in determining coral community composition than productivity. High weekly thermal variability has also been shown to correlate with low coral cover on nearshore reefs in the Florida Keys [13]. Therefore, differences in thermal variability observed across site types may have influenced coral community composition in Belize.

Our findings are contrary to the results of Soto *et al*. (2011) [13], which showed that reef sites with moderate temperature variability (equivalent to mod_{TP} sites in the current study) in Florida had higher coral cover than sites exposed to low (offshore deep reefs) or high temperature variability. Soto *et al.* (2011) [13] suggests that corals exposed to moderate weekly thermal variation are able acclimatize to a wide range of environmental conditions, making them more resilient than corals that experience less variation. At the same time, corals exposed to extremely high thermal variation generally do not survive[13]. Our results may contrast with that of Soto et al. (2011) because fore reef locations were not included in the present study (i.e.,

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low$_{TP}$ sites are located in the back reef). Our high$_{TP}$ sites follow the same pattern seen in Soto *et al.* (2011) [13] as they have lower coral cover than mod$_{TP}$ sites (Fig 2).

Our results also contrast those of Lirman and Fong (2007) [21], which showed that nearshore reefs (equivalent to our high$_{TP}$ sites) exhibited higher coral cover and growth rates than offshore reefs (equivalent to our low$_{TP}$ sites) in the Florida Keys. Interestingly, these nearshore Florida reefs also experienced lower water quality than the offshore reefs [21]. The authors hypothesized that higher coral cover and growth rates on nearshore reefs were due to the ability of some corals to switch trophic mode under adverse conditions [21], a pattern that has been observed in previous studies, but was not quantified in the current study [51,52]. Differences in coral community composition between the Florida Reef tract and the Belize MBRS may explain our contrasting results in coral cover as nearshore patch reefs in Florida appear to have relatively high numbers of *Orbicella spp*. [21], whereas high$_{TP}$ sites in Belize were almost void of this species.

Life history strategies

In the current study, high$_{TP}$ sites contained no competitive species, few generalists, and were dominated by stress-tolerant and weedy genera, while both 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 roughly equal proportions. Mod$_{TP}$ sites were similar but with fewer competitive species than low$_{TP}$ sites, and high$_{TP}$ 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) [22], and have been recorded in many areas of the world [29,53], including the Caribbean [25,31,54]. Even in the face of region-wide decline in coral cover and decrease in abundance of competitively dominant species [6], some

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weedy species, such as *Porites astreoides*, are actually increasing in prevalence within the Caribbean [31]. This weedy coral species is likely able to succeed in high stress environments due to its ability to brood and mature quickly, which allows it to rapidly colonize a recently disturbed area [22,31].

In contrast, a stress-tolerant species such as *S. siderea* is likely able to survive in high$_{TP}$ environments due to its massive size and long life span, which allows it to sustain a population in the absence of successful recruitment. This can increase the long-term survival potential of this species in harsh conditions [55]. These two contrasting strategies seem most effective in high$_{TP}$ environments (Fig 4), and are likely to be most effective in future conditions as the oceans continue to warm. This prediction is corroborated by Loya *et al.* (2001) [29], who showed that mounding (e.g., *S. siderea*) and encrusting (e.g., *P. astreoides*) species survived a mass bleaching event in 1997-1998 better than corals of other morphologies (e.g., branching). Ten years after the bleaching event these same types of coral continued to dominate. However, some branching species recovered and increased in abundance [56]. In the current study, branching species were almost non-existent in high$_{TP}$ sites, which indicates that these sites have experienced a recent thermal stress event or are exposed to chronic stress (e.g., temperature, eutrophication) that prevents such species from succeeding in these environments. It is also possible that high$_{TP}$ sites are more frequently disturbed than both low$_{TP}$ and mod$_{TP}$ sites. Disturbances such as bleaching events, eutrophication, sedimentation, and overfishing are known to cause declines in coral cover, species richness, and diversity [29,30]. These more disturbed or impacted reefs can then become dominated by stress-tolerant corals and corals that quickly colonize areas after a perturbation (i.e., weedy corals) [13,29,30,57], as observed in the current study (Fig 4). Historical and/or geological investigation of reef assemblages (i.e., through pit excavating or coring of reef framework

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[9,32,34]) would be a useful next step, as it would allow insight into how reef communities within the three thermal regimes have changed after disturbances and over long periods of time.

Influence of primary productivity on coral community composition

Cross-reef *chl-a* concentrations follow the same patterns as temperature (elevated nearshore and decreasing with increasing distance from the Belize coast) (Fig 1, S2 Fig). This means that reefs with higher *chl-a* concentrations have lower coral species richness, abundance, diversity, density, and percent cover. This supports a previous finding that shows a strong negative relationship between *chl-a* and coral cover, species richness, and abundance at nearshore reefs on the Great Barrier Reef (GBR) [58]. However, our results reveal that *chl-a* concentrations are not strongly correlated (R^2=0.040) with changes in coral community structure (e.g., percent cover, abundance, diversity, species richness, and density) across site types (S5H Fig), suggesting that *chl-a* concentrations may not best explain differences in community composition between site types in Belize. This may be due to spatial scale (e.g., we focused on nearshore, patch reef, and back reef sites as opposed to exclusively nearshore sites) [58], or the coarse scale of the *chl-a* dataset (4 km x 4 km grid; each survey site is <1 km). Focusing on variation within nearshore ($high_{TP}$) sites, we do see a correlation between *chl-a* and changes in coral community structure (S4H Fig), which supports results from previous work [58,59].

Other potential factors influencing coral community structure across reef types

Eutrophication

Eutrophication has led to local degradation of reefs [60,61,62]. However, larger scale (regional) reef degradation due to nutrients alone has not been quantitatively shown [63]. Wooldridge (2009) [64] demonstrates that lower water quality (e.g., higher nutrient

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concentrations) are linked to lower bleaching thresholds on nearshore reefs in Australia. If bleaching thresholds are depressed at $high_{TP}$ sites for some species, it may help explain lower diversity measured at these sites, as they experience warmer temperatures and spend more time above the regional bleaching threshold than do mod_{TP} and low_{TP} sites (S2 Fig). While *chl-a* does not correlate well with changes in coral community structure in this study (S3 Fig), it should be noted that *chl-a* is an estimate of nutrient delivery and primary productivity, not a measurement of the concentration of any one nutrient pool. Due to this limitation, manipulative field experiments such as Vega-Thurber et al. (2014)[65] and Zaneveld et al. (2016)[66] are needed to understand the influence of nutrients on coral community structure and bleaching thresholds at local scales.

Sedimentation

Coastal (nearshore) reefs throughout Belize are influenced by runoff from smaller local rivers, and reefs in southern Belize experience additional runoff and river plumes originating from larger watersheds in Honduras and Guatemala [67,68]. It has been previously shown that *Orbicella faveolata* corals on reefs with higher sedimentation rates exhibited suppressed skeletal extension rates for a longer duration than corals on reefs with lower sedimentation rates following the 1998 bleaching event in Belize [69]. In contrast, increased sedimentation did not affect skeletal extension of *S. siderea* or *P. astreoides* corals in Puerto Rico [70]. The results of these two studies suggest that there may be species-specific responses to increased sedimentation rates. In Barbados, reefs with high sedimentation rates were dominated by coral species with high recruitment and high natural mortality (e.g., *P. astreoides*) and reefs with lower sedimentation rates were dominated by coral species with lower recruitment and low natural

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mortality (e.g., boulder corals) [71]. As sedimentation rate was not quantified in this study, the impacts of sedimentation on coral community structure are not clear.

Circulation and wave energy

The Belize MBRS lies west of the Honduras Gyre, a hydraulic feature that recirculates water inside the Cayman basin [72]. The coastal waters of northern Belize are influenced by the Cayman and Yucatan currents, which move water northwest up the coastline toward Mexico [72,73,74,75]. In central and southern Belize, current velocities are lower and dominant circulation patterns are less consistent throughout the year [74]. However, currents appear to bring water and potentially pollution, nutrients, or sediment plumes from coastal Honduras and Guatemala west to southern Belize where they recirculate before slowly moving northward [67,68,74,75,76,77,78]. These circulation patterns have the potential to influence the stress tolerance of corals across sites and latitude in the current study. Our results reveal no spatial autocorrelation between sites for any of our measured variables with the exception of *chl-a* suggesting that the influence of these currents may be minimal. Additionally, wave energy may play a role in shaping coral communities. Wave energy may be elevated at low_{TP} sites as they are located near channels in the fore reef and may not be as sheltered by the reef crest as other mod_{TP}. Similarly, wave energy may be elevated at $high_{TP}$ sites due to the large fetch between the reef crest and nearshore reefs and the prevailing wind direction from offshore to inshore.

Light

Irradiance (light intensity) has been shown to decrease along an offshore-nearshore gradient on the GBR as *chl a* concentrations increase [79]. *Chlorophyll-a* concentrations increase with proximity to shore in Belize (Fig 1), so this pattern of decreasing light intensity towards the

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nearshore likely holds for Belize as well. However, in southern Belize offshore reefs (and nearshore reefs) are subject to seasonal sedimentation and runoff from larger rivers in Honduras and Guatemala [77,78]. Irradiance is a known stressor, proven to cause coral bleaching alone or in consort with elevated temperatures [80]. Although depth was held constant in the present study, it is possible that differing light levels both between site types and between individual sites may influence coral community composition across the site types investigated in the current study.

Proximity to human populations

Declining health of coral reefs worldwide has been linked to land-based stressors including nutrients and human use and exploitation (e.g., overfishing) [60,80,81] as well as proximity to sources of these stressors (e.g., major human population centers) [82]. However, not all reefs that are near to or influenced by land-based stressors are unhealthy [21,83]. Some of the study sites were within close proximity to a major human population center, particularly the $high_{TP}$ sites (populations of major towns and cities in Belize can be seen in S4 Table). Analysis of spatial autocorrelation revealed no significant differences between $high_{TP}$ sites or between $high_{TP}$ sites and sites that were further offshore, suggesting that proximity to human population centers did not have a major impact on coral community composition.

Conclusions

$High_{TP}$ reefs exhibit lower coral diversity, abundance, species richness, and cover than do low_{TP} and mod_{TP} reefs in Belize. These $high_{TP}$ reefs are exposed to higher annual temperatures, greater temperature variability, more time above the regional bleaching threshold, elevated *chl-a* concentrations, and likely increased sedimentation rates and lower flow than low_{TP} and mod_{TP} reefs. Temperature parameters, most notably time spent above the bleaching threshold, correlate

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best with differences in coral community structure. In addition, stress-tolerant and weedy coral life history strategies dominate at high$_{TP}$ reefs. Due to exposure to generally more stressful environmental conditions, high$_{TP}$ reefs may offer a snapshot into the projected future of coral reefs as they become increasingly exposed to local (pollution, runoff, land-use change, and overpopulation) and global (warming and acidification) stressors. Previously, such reefs have been suggested as possible refugia against climate change [84]. Globally, this would mean a shift towards dominance of stress-tolerant and weedy corals [53]. Such a shift would dramatically impact the structure and function of reefs, essentially creating novel ecosystems [85]. High$_{TP}$ reefs should be protected in addition to more pristine reefs in order to improve conservation success [35]. More pristine reefs should be protected as they contain more diversity and provide more ecosystem services than do high$_{TP}$ reefs [86]. However, high$_{TP}$ reefs host coral holobionts that may be best suited to survive in future ocean conditions. To ensure survival and future success of reefs while maintain current diversity both heavily impacted and pristine ecosystems must be protected. The results of the current study highlight the need to better protect and understand impacted nearshore reef systems, including investigations into what conditions allow more sensitive species (e.g., competitive and generalist) to survive and persist on nearshore reefs.

Data Accessibility

All data are archived on PANGAEA at the following DOI:
doi.pangaea.de/10.1594/PANGAEA.859972

Supporting Information

S1 Appendix. Additional detail of AGGRA and video survey methods

S1 Fig. *In situ* temperature versus satellite SST products
A comparison of *in situ* temperature and MUR SST. *In situ* loggers were collected from 6 sites along the BBRS (site numbers are listed in the gray headers above each panel). Each panel shows a month by month comparison of *in situ* logger measurements and SST products. Zero on

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the y-axis represents the average value for the Hobo Pro V2 loggers at each site. Red errors bars the standard deviation over a month for each logger. Gray squares show average values for an additional *in situ* logger that was placed at the site (± 1 standard deviation). Blue, green, and black symbols show monthly average values for various SST products (± 1 standard deviation).

S2 Fig. Temperature parameter and *chl-a* maps

Maps showing the 4 parameters used to calculate site type: yearly maximum temperature (A), Mean annual temperature range (B), Annual mean number of days above the bleaching threshold (C),Annual mean consecutive days above the bleaching threshold (D), and 13 year mean *chl-a* concentration from 2002-2015 (E). Maps generated from means calculated from daily satellite measurements taken from Jan 2003-Dec 2012.

S3 Fig. Linear regression of Physical Parameters vs. NMDS1 and NMDS2 by site type

Linear regression of average annual max temp (A, F), average annual temp range (B, G), average annual days above the bleaching threshold (C, H), average annual consecutive days above the bleaching threshold (D, I), and *Chl-a* (E, J) vs. NMDS1 and NMDS2 by site type. R^2 values are included for each regression that yielded a significant slope (p <0.05).

S1 Table. Site locations

Summary of survey sites, how they were classified, and where they were located (latitude/ longitude).

S2 Table. *p*-values and R^2 from Linear Regression of Physical Parameters vs. NMDS1 and NMDS2

Summary of p and R^2 values for physical parameters vs. NMDS1 and NMDS 2. Significant p-values are in bold.

S3 Table. *p*-values and R^2 for Linear Regression of Physical Parameters vs. NMDS1 by Site Type

Summary of p and R^2 values for physical parameters vs. NMDS1 by site type. Significant p-values are in bold.

S4 Table. Population of major towns in Belize

Populations of major towns in Belize from 2010-2015. Data source: Statistical Institute of Belize.

Author Contributions

Planned and designed the field surveying: JHB KDC. Identified sites and designed temperature metric: JHB. Downloaded and manipulated the temperature data FPL. Carried out field work and surveys: JHB JET TAC HEA SWD KDC. Analyzed the data: JHB JET TAC SWD FPL. Wrote/ edited the paper: JHB JET TAC HEA SWD FPL KDC.

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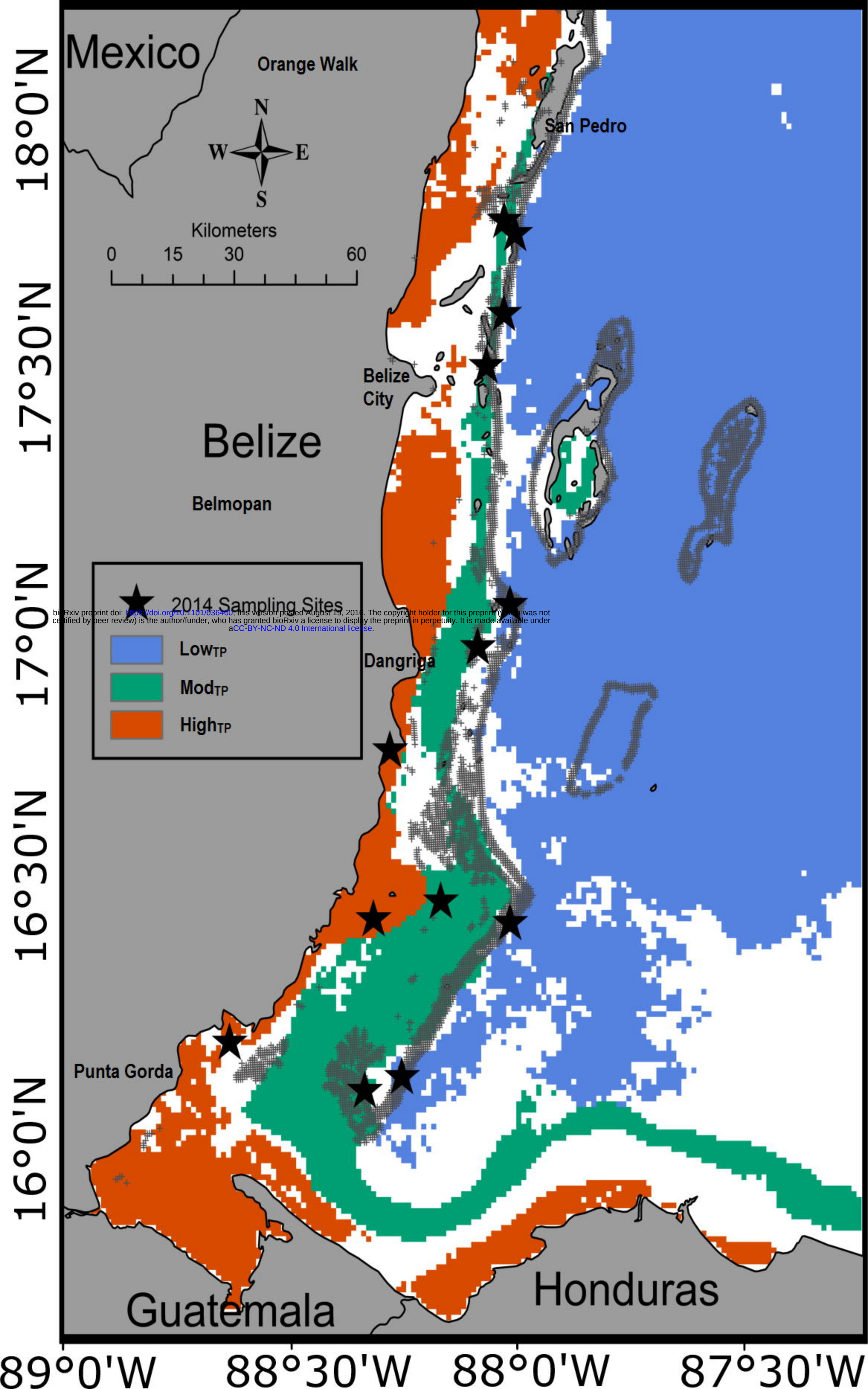

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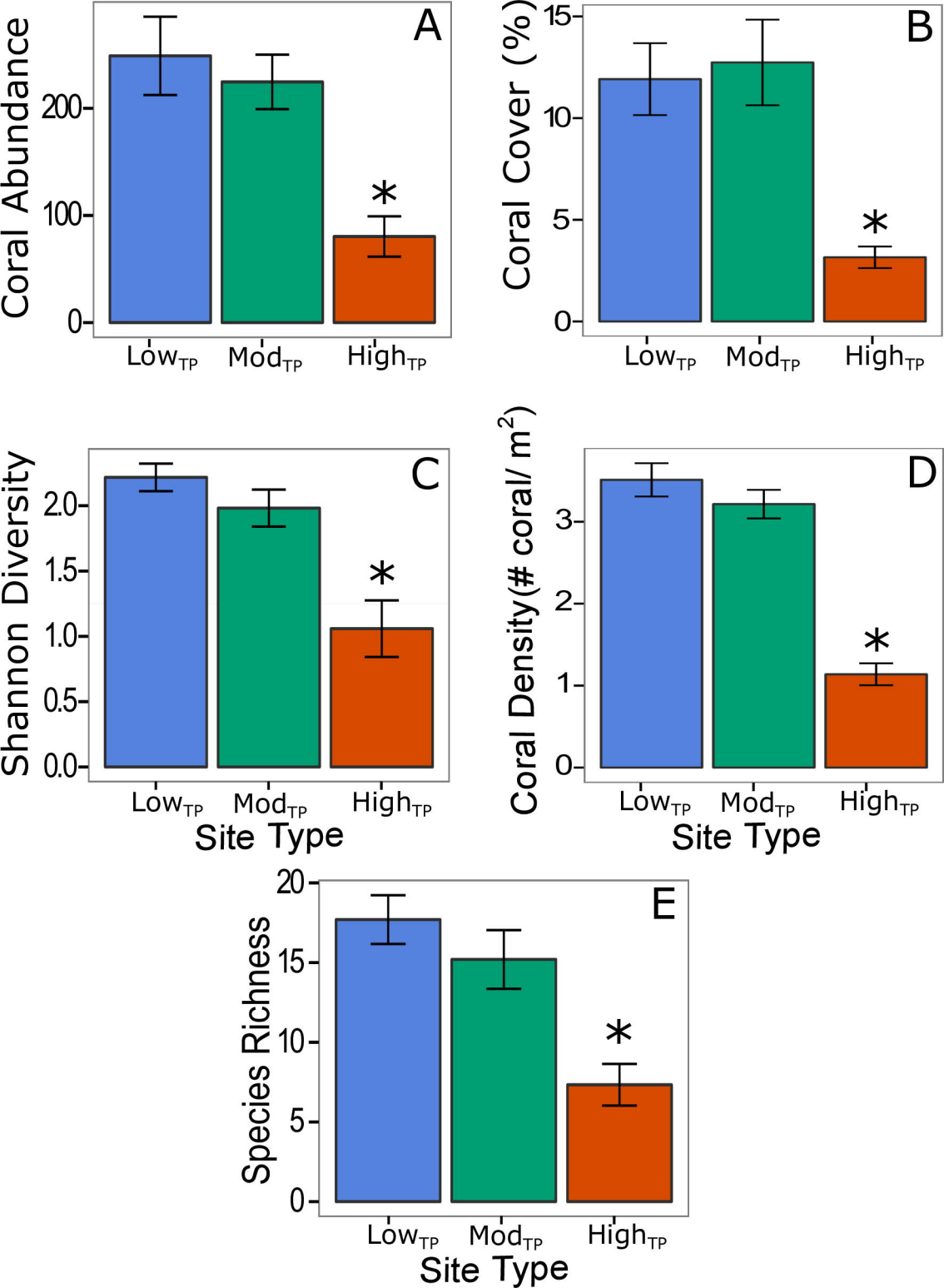
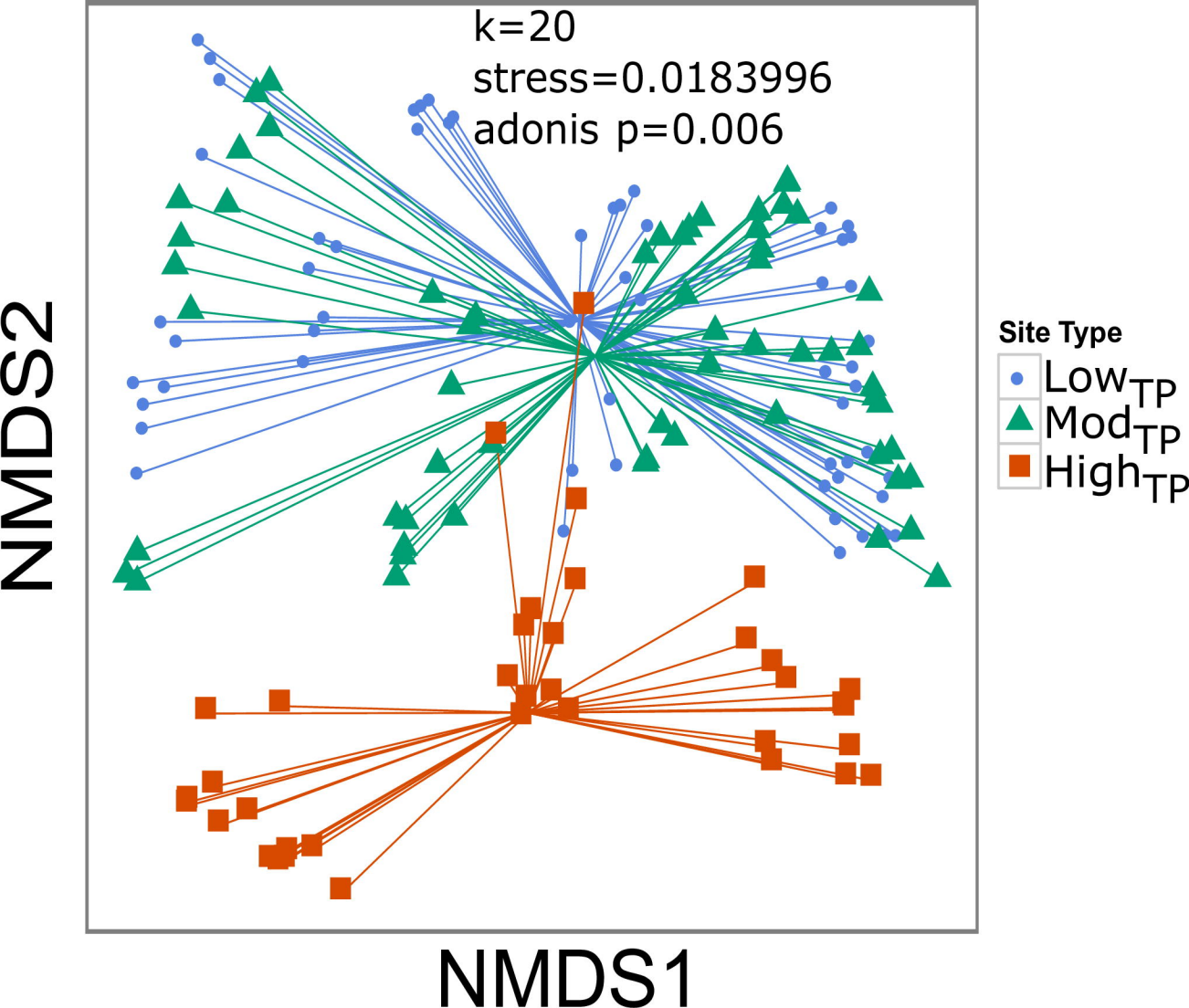

A
Coral Abundance
0
100
200
*
Low$_{TP}$
Mod$_{TP}$
High$_{TP}$
B
Coral Cover (%)
0
5
10
15
*
Low$_{TP}$
Mod$_{TP}$
High$_{TP}$
C
Shannon Diversity
0.0
0.5
1.0
1.5
2.0
*
Low$_{TP}$
Mod$_{TP}$
High$_{TP}$
Site Type
D
Coral Density(# coral/ m^2)
0
1
2
3
*
Low$_{TP}$
Mod$_{TP}$
High$_{TP}$
Site Type
E
Species Richness
0
5
10
15
20
*
Low$_{TP}$
Mod$_{TP}$
High$_{TP}$
Site Type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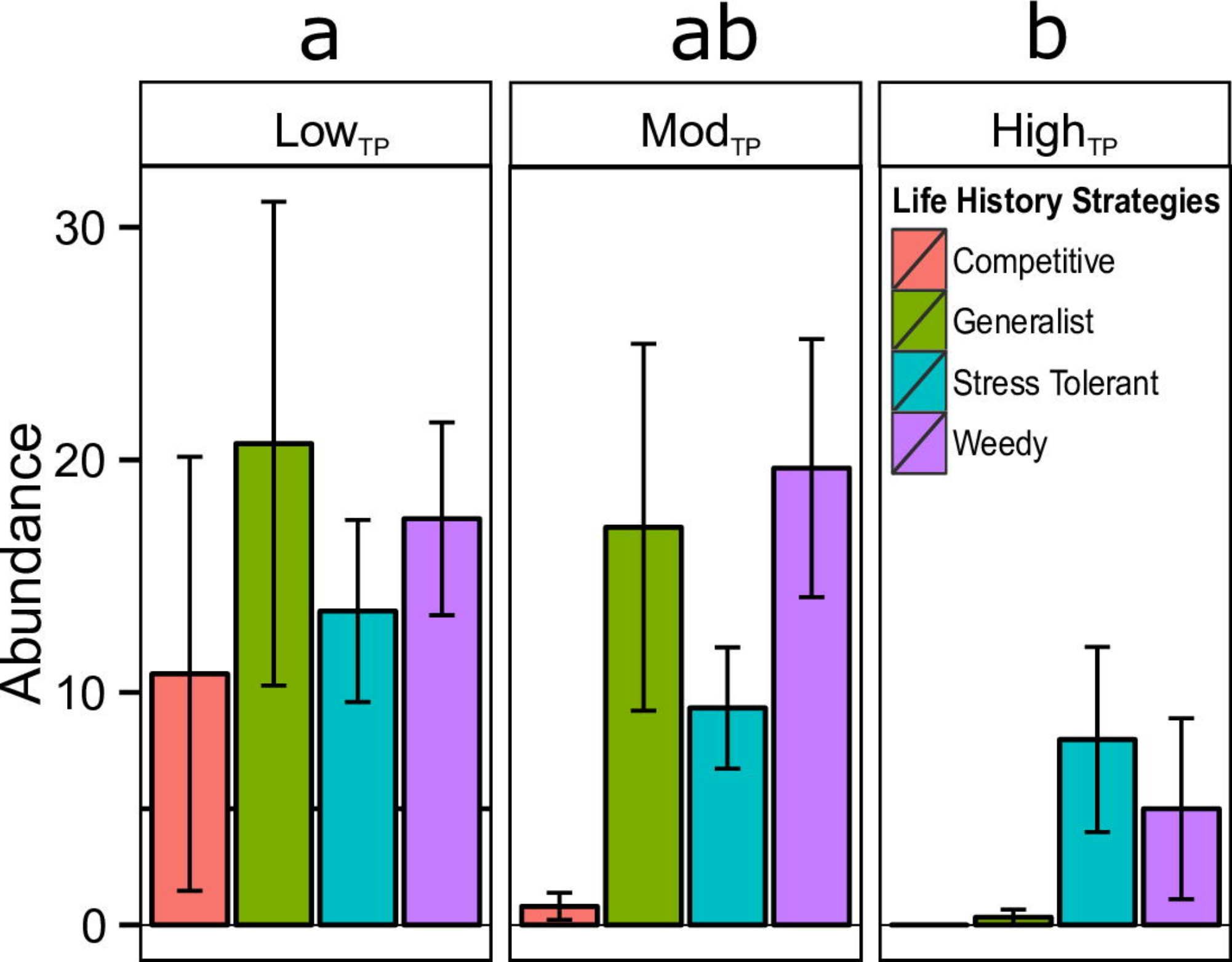
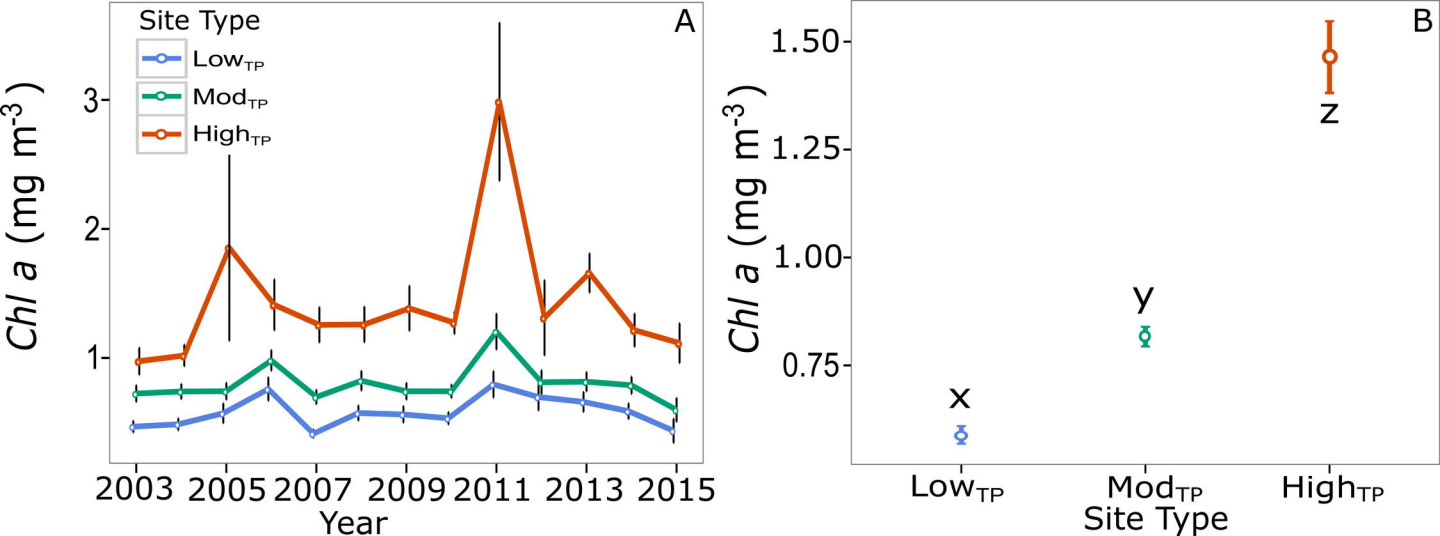
stress=0.0183996
adonis p=0.006
NMDS2
NMDS1
Site Type
Low TP
Mod TP
High TP


a
ab
b
Low$_{TP}$
Mod$_{TP}$
High$_{TP}$
Life History Strategies
Competitive
Generalist
Stress Tolerant
Weedy
Abundance
30
20
10
0


Site Type
Low$_{TP}$
Mod$_{TP}$
High$_{TP}$
A
Chl a (mg m^{-3})
3
2
1
2003
2005
2007
2009
2011
2013
2015
Year
B
1.50
1.25
1.00
0.75
z
y
x
Low$_{TP}$
Mod$_{TP}$
High$_{TP}$
Site Type