

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

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

41 **Location** Belize, Central America

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

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

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

62

63

64 INTRODUCTION

65 Coral reefs are threatened globally due to interactions of anthropogenic impacts such as
66 warming from increasing greenhouse gas emission, excessive agricultural runoff, overfishing,
67 and habitat destruction (Hughes *et al.*, 2003; Hoegh-Guldberg *et al.*, 2007; Frieler *et al.*, 2013).
68 Of particular concern are increasing greenhouse gas emissions that are leading to significant
69 warming of the oceans (Hughes *et al.*, 2003; Donner *et al.*, 2005). This warming trend is
70 especially troubling in the Caribbean, where rates of warming are higher than in many other
71 tropical basins (Chollett *et al.*, 2012), and where coral cover has declined up to 80% in recent
72 decades (Gardner *et al.*, 2003). Elevated sea surface temperature (SST) is the major cause of the
73 breakdown of essential coral-algal symbiosis, which can ultimately lead to mass coral bleaching
74 (Jokiel & Coles, 1990; D'Croz *et al.*, 2001) and these bleaching events are projected to increase
75 in frequency and severity as the climate continues to warm (Donner *et al.*, 2005; Wooldridge *et al.*,
76 2005). The Caribbean Sea is expected to be severely affected by warming as corals are
77 extremely sensitive to even small temperature increases of less than 1°C (McWilliams *et al.*,
78 2005). In fact, the Caribbean is predicted to suffer bleaching events biannually within the next
79 20-30 years (Donner *et al.*, 2007) with predicted annual bleaching events occurring as soon as
80 2040 (van Hooidonk *et al.*, 2015). Caribbean-wide and global scale bleaching events are
81 predicted to continue through the end of the century unless corals can increase their thermal
82 tolerance at a rate of 0.2-1.0 °C per decade (Donner *et al.*, 2005).

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

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

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

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

112 Although much is known about the influence of temperature and nutrient enrichment on
113 coral health, it is unclear exactly how these stressors interact to affect coral community structure.
114 Community differences induced by anthropogenic stressors may lead to circumstances where
115 reef calcification does not sufficiently counter reef erosion, leading to an overall flattening of
116 reef structure, decline of coral reefs, and shifts from one dominant coral group to another, or
117 from coral to algal dominance (Loya *et al.*, 2001; McManus & Polsenberg, 2004; Alvarez-Filip
118 *et al.*, 2009; Alvarez-Filip *et al.*, 2013). Due to the variety of coral life history strategies and
119 differential response to stress, an overall decline in coral cover and abundance can also be
120 coupled with an increase in abundance of certain coral species (Loya *et al.*, 2001; Darling *et al.*,
121 2012), as seen in the Caribbean with the recent increase in abundance of ‘weedy’ species,
122 including *Porites astreoides* (Green *et al.*, 2008). Brooding, small, opportunistic corals (weedy)
123 and fast growing (competitive) corals recover faster from stress events, but are more impacted by
124 bleaching events than more stress-tolerant, slower growing species (Darling *et al.*, 2012; Darling
125 *et al.*, 2013). Taken together, this evidence suggests that differential responses between coral
126 species to temperature and nutrient stressors may lead to community scale shifts in composition.

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

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

137 **MATERIALS AND METHODS**

138 **Novel Site Identification**

139 *SST Data Assembly*

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

155

156 *Site Classification*

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

179 **Benthic surveys**

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

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

192 **Nutrient analysis**

193 *Chlorophyll a*

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

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

208

209 *In-situ nutrient sampling*

210 125ml water samples (n=3-10) were filtered and collected in acid washed bottles from each
211 survey site (n=13), flash frozen on dry ice, and transported to UNC for analysis. Fine-scale
212 nutrient dynamics were quantified from dissolved inorganic nitrogen [(DIN) = nitrate plus nitrite
213 (NO_x) and ammonium (NH₄)] and dissolved organic carbon (DOC). See Appendix 2 of the
214 supplementary information for measurement and instrumentation details.

215

216 **Statistical Analysis**

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

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

227 If factors were significant ($p < 0.05$), a post-hoc Tukey's HSD test was used to evaluate the
228 significance of each pair-wise comparison. To visualize coral community differences between
229 site types non-metric multidimensional scaling (NMDS) ordination was implemented using
230 Bray-Curtis similarity coefficients in the vegan package in R (Oksanen *et al.*, 2013). An optimal
231 stress test was performed to determine the optimal k value ($k=20$). Resulting NMDS scores were
232 visualized in two-dimensional ordination space. A PERMANOVA test was performed to analyze
233 the site type differences using the *adonis* function in the vegan package in R (Oksanen *et al.*,
234 2013).

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

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

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

255

256 **RESULTS**

257 **Coral Community Composition**

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

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

271 threshold, DOC, and DON all had significant effects on the NMDS1 variation and all four
272 temperature parameters, as well as DON and *chl a*, also had significant effects on NMDS2
273 variation (S11; Fig S6). The parameter that explained the most variation for NMDS1 was DON
274 ($R^2=0.3414$, $p \text{ value}=1.18 \times 10^{-15}$) and average annual consecutive days above the bleaching
275 threshold explained the most variation in NMDS2 ($R^2=0.6039$, $p \text{ value}= 2 \times 10^{-16}$, S11; Fig S6).

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

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

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

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

300

301 **Coral Life History**

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

308

309 **Nutrients**

310 *Chlorophyll a*

311 *Chl a* concentrations varied by year and differed by site and site type (Table 2A), but
312 were consistently lowest at low_{TP} sites and highest at ext_{TP} sites regardless of year (Table 2B, Fig
313 2A). 13-year average *chl a* concentrations were significantly different between all three site
314 types. low_{TP} sites had the lowest average *chl a* concentrations, mod_{TP} sites had average *chl a*
315 values significantly higher than low_{TP} sites, but significantly lower than ext_{TP} sites, and ext_{TP}

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

318

319 *In-Situ Nutrient Concentrations*

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

327

328 **DISCUSSION**

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

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

341 Coral species richness, abundance, diversity, coral cover, and coral density were all lower
342 at ext_{TP} sites compared to low_{TP} and mod_{TP} sites, (Fig 3A, S3) suggesting that the coral
343 community at ext_{TP} sites is different from the community at low_{TP} and mod_{TP} sites. This finding
344 was further supported by NMDS and linear mixed effects models (Fig 3B, Table S10B) and is
345 contrary to the results of Soto et al. (2011) which shows that sites with moderate temperature
346 variability (mod_{TP}) have higher coral cover than sites at either extreme and Lirman and Fong
347 (2007) which showed that nearshore reefs (Ext_{TP}) had higher coral cover than offshore reefs in
348 the Florida Keys. Ext_{TP} sites were subjected to higher annual maximum temperatures, more
349 extreme annual temperature variations, a higher number of days above the bleaching threshold
350 per year, more consecutive days above the bleaching threshold per year, and higher *chl a*
351 concentrations than low_{TP} and mod_{TP} sites. As variation between site types occurred along the
352 NMDS2 axis (Fig 4), linear modeling of these parameters against NMDS2 revealed that
353 temperature parameters had a much more significant effect on community differences between
354 site types than did nutrient parameters (Table S11, Fig 3B). The average annual number of days
355 above the bleaching threshold ($R^2=0.5644$) and the average annual consecutive days above the
356 bleaching threshold ($R^2=0.6039$) (S11, Fig S6) were especially important in driving the observed
357 community differences. Interestingly, these same two temperature parameters best explain the
358 trends seen in coral species richness, abundance, diversity, and density between site type (Table
359 S5, S6). This evidence suggests that coral community composition is strongly influenced by time
360 spent above the regional thermal maximum. *Chl a* concentration was also significant, but
361 produced an $R^2=0.0434$ (S11; Fig S6), indicating that while *chl a* may have some impact on
362 coral community differences between site types; it is unlikely to be a primary driver. Taken

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

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

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

388 Interestingly, and in contrast to our results, coral growth and coral cover were found to be
389 higher in nearshore (ext_{TP}-like) environments in the Florida Keys than cooler and less thermally
390 variable (low_{TP}-like) offshore reefs (Lirman & Fong, 2007). This difference may be due to the
391 fact that corals living in warmer (Williams *et al.*, 2010; van Woosik *et al.*, 2012; Fine *et al.*,
392 2013) or more variable areas (Oliver & Palumbi, 2011; Barshis *et al.*, 2013) are less susceptible
393 to bleaching stress due to adaptation/acclimatization to local conditions. However, here we
394 observe that corals living in ext_{TP} environments were not visibly less healthy than corals at low_{TP}
395 and mod_{TP} sites (data not shown). In fact, *Siderastrea siderea* in nearshore (ext_{TP}) environments
396 have been shown to have higher growth and calcification rates than those on the forereef (low_{TP})
397 (Castillo *et al.*, 2011; Carilli *et al.*, 2012; Castillo *et al.*, 2012), suggesting that this species is
398 locally adapted/acclimatized to more extreme temperature conditions and/or nutrients. These
399 more extreme conditions may not be suitable for other coral species, which can lead to failed
400 recruitment or inability of juveniles from more moderate sites to survive in these more extreme
401 environments due to the influence of thermal history on limiting acclimatization (Howells *et al.*,
402 2013). Lack of differences in community variables between low_{TP} and mod_{TP} sites (Fig 3A, S3)
403 indicates that although reefs subjected to moderate temperature variation have been shown to
404 have higher coral cover (Soto *et al.*, 2011) differences in temperature and nutrient variables
405 between these site types (Table 1) may not have been significant enough to elicit a community
406 level response.

407

408 **Influence of nutrients on coral community composition and life history strategies**

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

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

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

434 **Extreme sites are dominated by weedy and stress tolerant coral species**

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

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

459

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

461 Lower coral community diversity and percent cover at ext_{TP} sites compared to low_{TP} and
462 mod_{TP} sites are likely driven by temperature parameters (particularly the number of days and
463 number of consecutive days above the bleaching threshold per year, as well as average annual
464 temperature range and max temperature). While ecological differences between sites may be
465 mainly driven by temperature parameters, bulk nutrients may still play a role. Lack of
466 community scale differences between low_{TP} and mod_{TP} sites suggests that low magnitude
467 variations in temperature (and nutrient) parameters are less likely to cause measurable,
468 community-wide changes. The change in community structure between ext_{TP} and low_{TP}/mod_{TP}
469 sites was accompanied by a change in the dominant coral genera. Low_{TP} and mod_{TP} sites contain
470 all 4 coral life histories (competitive, generalist, weedy, and stress-tolerant) (Darling *et al.*,
471 2012), but ext_{TP} sites are dominated almost entirely by weedy and stress-tolerant species,
472 suggesting that genera utilizing these two life history strategies may be better suited for survival
473 under more extreme conditions. Future research is needed to examine the relative
474 acclimatization/adaptation potential of corals at each of these site types as well as the relative
475 contributions of thermal and nutrient stressors on coral health. Additionally, ext_{TP} sites may
476 warrant further protection as they potentially harbor the coral genera and individuals that are
477 most likely to thrive as the ocean continues to warm. These sites are not often protected and
478 should be considered in future conservation management decisions.

479

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489

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615 **DATA ACCESSIBILITY**

616 Data will be archived on PANGAEA after acceptance and a DOI will be included here.
617

618 **BIOSKETCH**

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

623

624 **Tables**

625 **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

626 ¹No corals below 30.352

627 ²No corals above 31.169

628 ³No corals below 4.476

629 ⁴No corals above 6.552

630 ⁵No corals below 25.772

631 ⁶No corals above 68.772

632 ⁷No corals below 3.837

633 ⁸No corals above 6.600

634

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

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645 **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	<i>p</i> -value
Site	12	1350	112.75	131.5	<0.0001
Site Type	2	288	144.00	166.7	<0.0001

646 Table 2A: Results of analysis of variance (ANOVA) of the effect of site and site type on *chl a*.

647 Significant effects are in bold ($p < 0.05$). df= degrees of freedom.

648

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

Comparison	<i>p</i> -value
low _{TP} -mod _{TP}	<0.0001
low _{TP} -ext _{TP}	<0.0001
mod _{TP} -ext _{TP}	<0.0001

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

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670 **Table 3A: Effects of Survey Method, Site, and Site Type on Species Richness, Abundance,**
 671 **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

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

674

675 **Table 3B: Pair-wise comparisons of effects of Site Type on Species Richness, Abundance,**
 676 **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

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

681

682 **Figure Legends**

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

686

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

690

691 **Figure 3:** Species Richness (# of species present) at each site type (A). Statistically significant
692 differences ($p < 0.05$) are marked with an *. This trend is consistent among other community
693 variables, including: coral abundance (# of corals), percent coral cover, Shannon diversity, and
694 coral density (# of coral/ m²) (Fig S2). B.) Nonmetric multidimensional scaling (NMDS) plot of
695 coral community differences clustered by site type (B).

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

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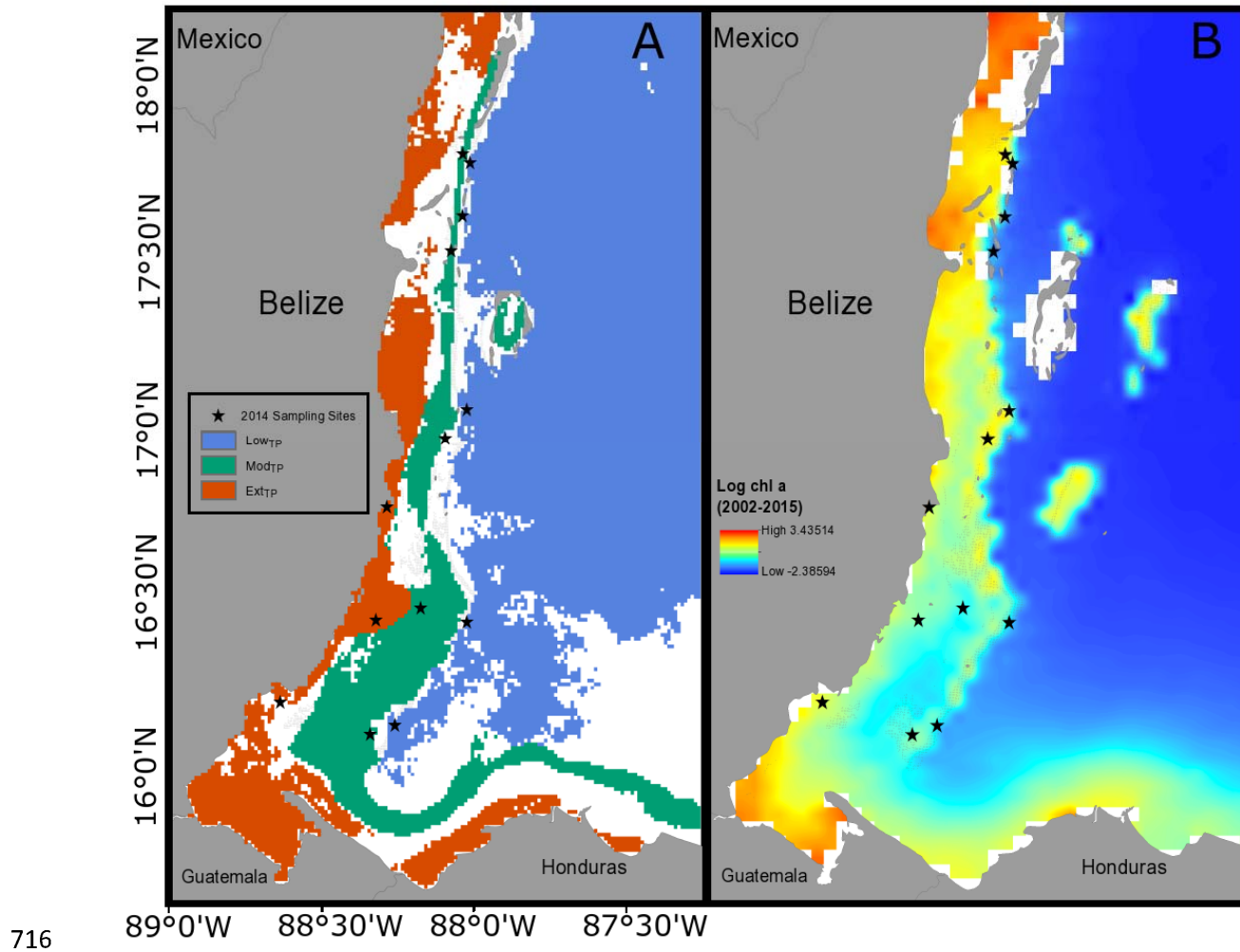
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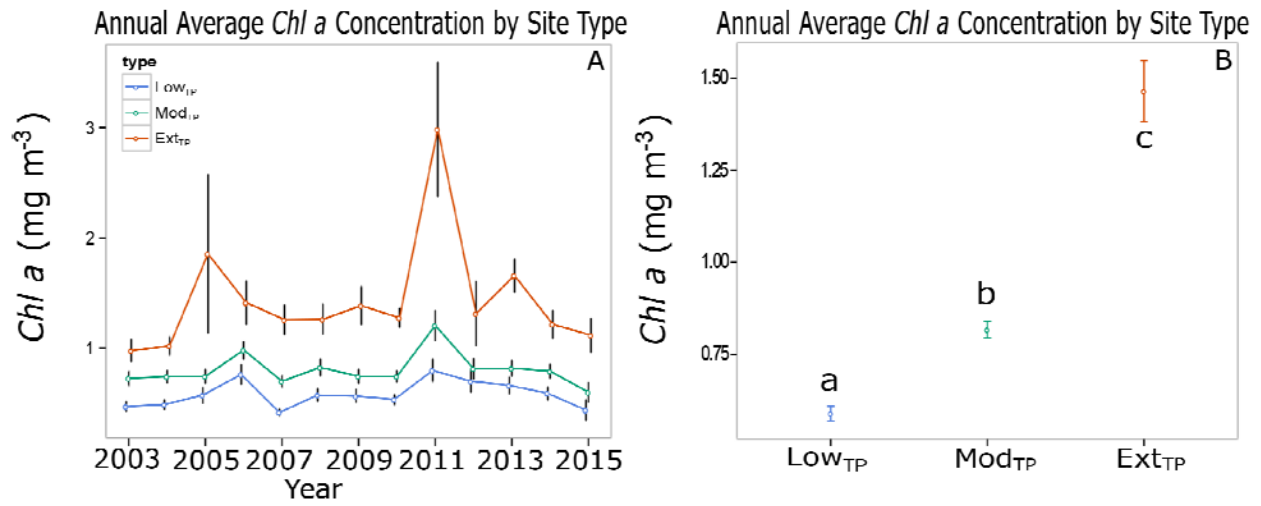
714 **Figures**

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



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717 **Figure 2: Average *chl a* by site type**



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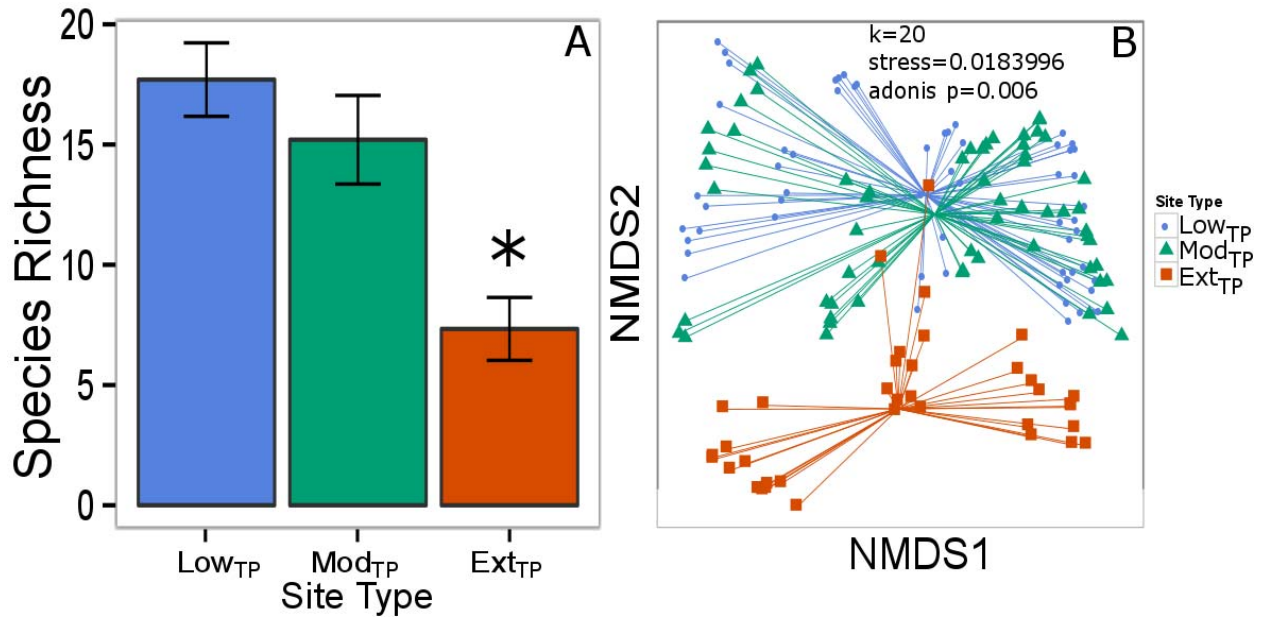
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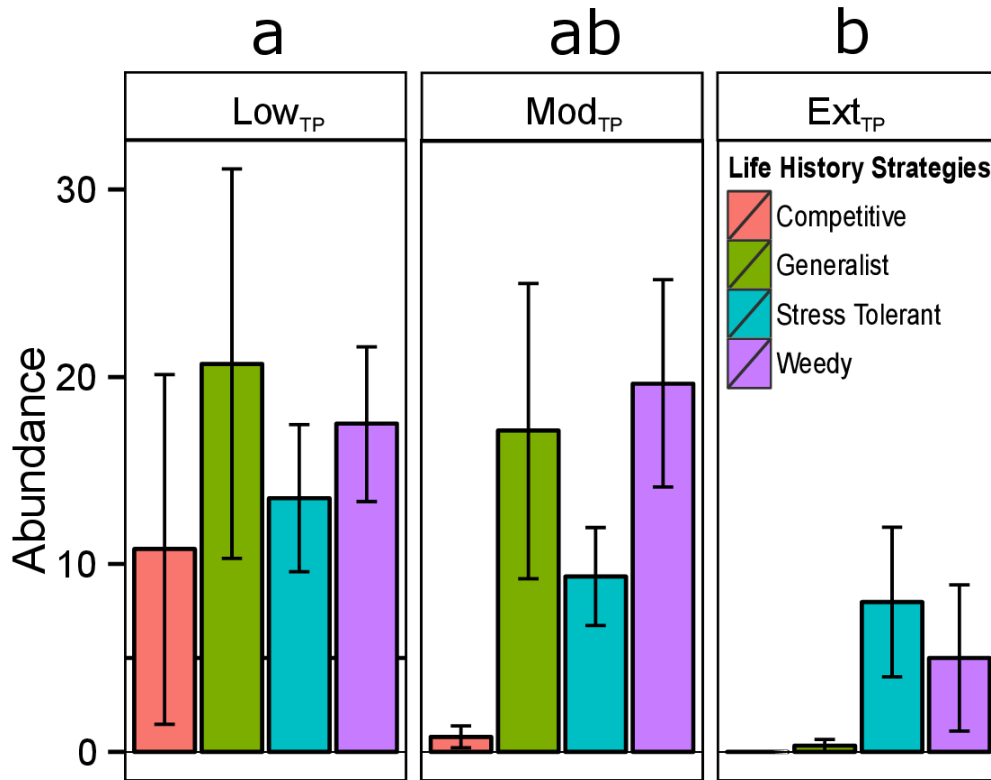
737 **Figure 3: A.) Average coral species richness by site type and B.) NMDS of coral community**
738 **variables by site type**



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741 **Figure 4: Coral life history strategy by site type**



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