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Cole G Easson, Kenan O Matterson, Chris J Freeman, Stephanie K Archer, Robert W Thacker

Recent studies have renewed interest in sponge ecology by emphasizing the functional importance of sponges in a broad array of ecosystem services. Many critically important habitats occupied by sponges face chronic stressors that might lead to alterations in their diversity, relatedness, and functional attributes. We addressed whether proximity to human activity might be a significant factor in structuring sponge community composition, as well as potential functional roles, by monitoring sponge diversity and abundance at two structurally similar sites that vary in distance to areas of high coastal development in Bocas Del Toro, Panama. We surveyed sponge communities at each site using belt transects and differences between two sites were compared using the following variables: (1) sponge species richness, Shannon diversity, and inverse Simpson's diversity; (2) phylogenetic diversity; (3) taxonomic and phylogenetic beta diversity; (4) trait diversity and dissimilarity; and (5) phylogenetic and trait patterns in community structure. We observed significantly higher sponge diversity at Punta Caracol, the site most distant from human development (~ 5km). Although phylogenetic diversity was lower at Saigon Bay, the site adjacent to a large village including many houses, businesses, and an airport, the sites did not exhibit significantly different patterns of phylogenetic relatedness in species composition. However, each site had a distinct taxonomic and phylogenetic composition (beta diversity). In addition, the sponge community at Saigon included a higher relative abundance of sponges with high microbial abundance and high chlorophyll *a* concentration, whereas the community at Punta Caracol had a more even distribution of these traits, yielding a significant difference in functional trait diversity between sites. These results suggest that lower diversity and potentially altered community function might be associated with proximity to human populations. This study highlights the importance of evaluating functional traits and phylogenetic diversity in addition to common diversity metrics when assessing potential environmental impacts on benthic communities.

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Cole G. Easson[1]*, Kenan O. Matterson[1], Christopher J. Freeman[2], Stephanie K. Archer[3], Robert W. Thacker[4]

[1]Department of Biology, University of Alabama at Birmingham, Birmingham, Alabama, 9 USA

[2]Smithsonian Marine Station, Fort Pierce, Florida, USA

[3]Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina, USA

[4]Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York, USA

*Corresponding author is Cole Easson: email: ceasson@nova.edu

Abstract

Recent studies have renewed interest in sponge ecology by emphasizing the functional importance of sponges in a broad array of ecosystem services. Many critically important habitats occupied by sponges face chronic stressors that might lead to alterations in their diversity, relatedness, and functional attributes. We addressed whether proximity to human activity might be a significant factor in structuring sponge community composition, as well as potential functional roles, by monitoring sponge diversity and abundance at two structurally similar sites that vary in distance to areas of high coastal development in Bocas Del Toro, Panama. We surveyed sponge communities at each site using belt transects and differences between two sites were compared using the following variables: (1) sponge species richness, Shannon diversity, and inverse Simpson's diversity; (2) phylogenetic diversity; (3) taxonomic and phylogenetic beta diversity; (4) trait diversity and dissimilarity; and (5) phylogenetic and trait patterns in community structure. We observed significantly higher sponge diversity at Punta Caracol, the site most distant from human development (~ 5km). Although phylogenetic diversity was lower at Saigon Bay, the site adjacent to a large village including many houses, businesses, and an airport, the sites did not exhibit significantly different patterns of phylogenetic relatedness in species composition. However, each site had a distinct taxonomic and phylogenetic composition (beta diversity). In addition, the sponge community at Saigon included a higher relative abundance of sponges with high microbial abundance and high chlorophyll *a* concentration, whereas the community at Punta Caracol had a more even distribution of these traits, yielding a significant difference in functional trait diversity between sites. These results suggest that lower diversity and potentially altered community function might be associated with proximity to human populations. This study highlights the importance of evaluating functional traits and

phylogenetic diversity in addition to common diversity metrics when assessing potential environmental impacts on benthic communities.

Keywords: Porifera, Community Ecology, Anthropogenic influences, Microbial symbionts, Photosynthesis

Introduction

Coral reefs are critical and dynamic habitats that provide a variety of important ecosystem services that support local economies and international industries around the world (Moberg and Folke 1999, Mumby et al. 2008). Historically, scleractinian corals have provided the structural framework for many of these complex reef networks (Aronson et al. 2001). However, in recent decades, reefs worldwide have experienced a marked decline in the abundance of reef-building corals due to multiple stressors including marine pathogens, overfishing of herbivores, and coastal eutrophication (Hughes 1994, Lapointe 1997, Hughes and Connell 1999, Jackson et al. 2001, Harvell et al. 2007). Caribbean reefs exemplify this trend, as many of these reef systems have undergone drastic phase shifts, resulting in the dominance of fleshy macroalgae in place of hard corals (McCook 1999, Maliao, Turingan & Lin, 2008, Dudgeon et al. 2010). Along with altered community composition, structure and function (Norström et al. 2009), these new "stable" states provide fewer ecosystem services (Brock and Carpenter 2006, Carpenter and Brock 2006). Healthy reefs are typically characterized as structurally complex habitats that act as refuges for a variety of species including juvenile fish and invertebrates, effectively increasing the diversity and abundance of the associated community (Graham et al. 2006). In contrast, the reduced habitat complexity of macroalgal

71 communities supports lower species diversity and productivity across numerous trophic levels
72 (McCook 1999, Jones et al. 2004).

73 In addition to increased macroalgal cover, sessile macro-invertebrates, like sponges and
74 gorgonians, are often more abundant on degraded reefs (Maliao, Turningan & Lin, 2008). This
75 increased sponge abundance may have important ecological implications for these communities
76 (Bell et al. 2013), as numerous sponge species are known to perform critical functional roles on
77 shallow reefs. For instance, sponges directly contribute to energy cycling on reefs by efficiently
78 clearing dissolved organic carbon (Yahel et al. 2003, de Goeij et al. 2013), bacteria (Reiswig
79 1971, Pile, Patterson & Witman, 1997) and pathogens from the water column, incorporating
80 these energy sources into the benthic system (Hadas et al. 2006). Moreover, by hosting diverse
81 and often abundant microbial symbionts, sponges contribute to primary productivity
82 (photosynthesis) and nutrient cycling on the reef (Wilkinson and Fay 1979, Wilkinson 1983,
83 1992, Díaz and Ward 1997), even though microbial community composition and, subsequently,
84 functional roles, are highly variable among species (Easson and Thacker 2014, Freeman, Easson
85 & Baker, 2014). Thus, as sponge abundance increases throughout the Caribbean (Nyström, Folke
86 & Moberg, 2000, Norström et al. 2009) and populations of large species such as the giant barrel
87 sponge, *Xestospongia muta,* increase in some regions (increased by 46% from 2000 to 2006 in
88 the Florida Keys; McMurray, Henkel & Pawlik, 2010), it is likely that shifts in nutrient cycling
89 and ecosystem function are also occurring across degraded reef systems (Díaz and Rützler 2001,
90 Wulff 2001, de Goeij et al. 2013).

91 Although overall sponge richness and total biomass may be positively correlated with
92 anthropogenic stressors (Zea 1994), some sponge species may be just as susceptible to alterations
93 in the chemical, biological and physical characteristics of the surrounding environment as corals

(Fang et al. 2014). For example, elevated concentrations of organic pollutants can influence sponge community structure by altering species diversity (Alcolado 2007, Powell et al. 2014). Based on these data, we would predict that sponge community diversity and species composition might change across a gradient of anthropogenic stressors, but the specific response is potentially variable. Recent work has highlighted the need to move beyond simply measuring species diversity, showing that an organism's contribution to a habitat may be more important than its presence or absence (Cadotte 2011, Safi et al. 2011, Stuart-Smith et al. 2013, 2015). This principle is especially relevant in tropical ecosystems characterized by high diversity and often a high degree of functional redundancy (Stuart-Smith et al. 2013). Sponges represent an ideal group on coral reefs to study shifts in organismal contribution to ecosystem function, because they are prolific reef-builders, have a range of functional behaviors, and contribute a variety of crucial services to reef environments (Díaz and Rützler 2001, de Goeij et al. 2013).

The Bocas del Toro archipelago on the Caribbean coast of Panama includes numerous islands, mangrove cays, peninsulas, fringing reefs and seagrass beds that surround shallow bays with historically high coral cover (Collin 2005). The region receives high annual rainfall (3-5m), resulting in variations in temperature, salinity, sedimentation and turbidity (Kaufmann and Thompson 2005). In addition, while the Bocas del Toro region historically was home to several indigenous communities, the areas around Bocas Town and Saigon Village have recently experienced rapid large population growth (Figure 1). This rapid population growth combined with high tourism rates, substandard public infrastructure (e.g. sewers), and deforestation has contributed to increased run-off and pollution of the near shore environment (Aronson et al. 2004). For example, there have been reports of "black water" outflow (sewage, road pollution and solid waste dumping) into Saigon Bay. The concentration of human activities in the Bocas

117 del Toro region implies that some local reef communities may be negatively impacted by chronic
118 fluctuations in water quality, while other reefs more distant from human development may be
119 exposed to these anthropogenic stressors less frequently (D'Croz, Del Rosario, & Gondola, 2005,
120 Gochfeld, Schloder & Thacker, 2007).

121 The goal of our study was to build on the research of Gochfeld, Schloder & Thacker,
122 (2007), who reported signs of sponge community variation that included lower diversity and
123 higher disease prevalence near human settlement. Additionally, because measurements of alpha
124 diversity can overlook important genetic and/or functional variability among species in the
125 community, we also assessed potential variation in phylogenetic diversity, taxonomic and
126 phylogenetic composition (beta diversity), and functional traits between sites, with the goal of
127 forming testable hypotheses for how sponge community variation may translate to meaningful
128 functional variation in communities of these increasingly dominant benthic organisms.

129 **Methods**

130 *Field sites.* To assess potential sponge assemblage differences related to proximity to human
131 development, we conducted belt transects adjacent to concentrated human settlement around
132 Saigon Bay, an area where about 150 houses, an airport and several businesses are in close
133 proximity to shore (n=9, Saigon), and ~5 km away from town where only a few houses are
134 located (n=10, Punta Caracol, Figure 1). Surveys conducted near Saigon Bay were not in the
135 exact same location as Gochfeld, Schloder & Thacker, (2007), whose site was located within the
136 bay, likely subjecting it to naturally different environmental conditions. In the current study we
137 conducted surveys at the mouth of Saigon Bay to better standardize reef structure between sites.
138 Surveys were conducted at these sites in August 2012 and April 2014. Survey sites were similar
139 in depth, exposure direction, and distance from shore. All transect data were collected on

SCUBA at a depth of 5-7 m along the general axis of the reef with a minimum distance of 10 m between each transect. All specimen collection for this study was performed in accordance with a collection permit from the government of Panama, issued to Robert W. Thacker (resolution DGOMI-PICFC No. 36 issued on July 4, 2012).

Sponge richness and diversity Sponge diversity and abundance were characterized by counting individuals that fell within 1 m of the transect line (i.e., creating 10 m x 2 m belt transects). A total area of 200 m^2 and 180 m^2 was surveyed at Punta Caracol and Saigon, respectively. Each sponge was identified to the lowest possible taxonomic level. For sponges that were unidentifiable *in situ*, voucher specimens were collected and identified in the laboratory following spicule and fiber preparations. Using the R package vegan (Oksanen et al. 2007), we calculated three univariate measures of sponge diversity for each transect at each survey site: species richness (*S*), the Shannon index (*H'*), and the inverse Simpson's index (*D*). We compared each of these metrics between the two sites using a two-sample t-test.

Phylogenetic reconstruction. Phylogenetic relatedness among surveyed sponge species was assessed using a phylogeny constructed from a partitioned alignment of gene sequences from Genbank coding for the small (18S) and large (28S) nuclear ribosomal subunits, which are common markers used for molecular identification of sponge species (Redmond et al. 2013, Thacker et al. 2013, Table S1). One sponge species, *Verongula reiswigi*, was not represented in Genbank, and we obtained sequence from vouchers representing this species as part of the current study (Supplemental methods).

We reconstructed a phylogeny for all sponge species except *Niphates caycedoi*, for which we were unable to obtain sequence information. This species was rare, with only four individuals of this species found at one site. This species was excluded from phylogenetic analysis. For each gene, sequences were aligned using the default options of MAFFT 7.017 (Katoh et al. 2002) in the program Geneious (version 6.1.8, Biomatters Limited). We concatenated the two alignments, treating them as two separate partitions with independent models of sequence evolution. We implemented a relaxed-clock model in MrBayes version 3.2.1 (Ronquist et al. 2012), using the CIPRES computational resources (Miller, Pfeiffer & Schwartz, 2010), and following recommended best practices for implementing partitioned analysis (Wiens and Morrill 2011, Kainer and Lanfear 2015). We constrained sponges in the genus *Plakortis* as an outgroup, using the independent gamma rate relaxed clock model with a birth-death process (Supplemental File 1, Aris-Brosou and Yang 2003). We included three parallel runs of 10 million generations, each using four Markov chains and sampling every 100 generations. A consensus phylogeny of the three parallel runs was summarized following a burn-in of 25% (Supplemental Figure 1).

Phylogenetic relatedness and patterns of diversity. We assessed phylogenetic diversity by calculating Faith's phylogenetic diversity (PD), using the R package picante (Kembel et al. 2010). Faith's PD measures the total branch length spanned by the sub-tree from each community, allowing for a comparison of total branch lengths between communities (Kembel et al. 2010). Additionally, Faith's PD relaxes the diversity measurement assumption that all species are "equally different" by weighting species diversity based on phylogenetic similarity (Gotelli and Chao 2013). Phylogenetic diversity patterns (clustering, dispersion, or random) were assessed by measuring the mean pairwise distance (MPD) and mean nearest taxon distance

(MNTD) scaled to the standard effect size among sponges within each site, accepting the default options in the models. MPD calculates the mean distance between two randomly chosen individuals in the community. Significant clustering measured by MPD implies a higher presence of species related to one another through interior nodes (away from the tips of the phylogeny) belonging to broader phylogenetic groups. MNTD calculates the mean distance separating one individual from its closest relative. MNTD describes clustering at the tips of the tree, and significant clustering by this metric indicates a higher presence of closely related species connected by nodes closer to the tips of the phylogeny. For both MPD and MNTD, we assessed differences in phylogenetic diversity patterns using two t-tests. We used a two-sample t-test to assess differences between sites, and a one-sample t-test to test whether each site differed from a null hypothesis of random phylogenetic relatedness ($\mu = 0$, Kembel et al. 2010, Kembel and Cahill Jr 2011).

Beta-diversity analysis. We assessed taxonomic beta diversity patterns between sites by calculating Bray-Curtis dissimilarity (BCD) among all transects. We also calculated phylogenetic beta diversity among all transects, which compares MPD and MNTD between two individuals selected from different sites as opposed to individuals within the same site as previously measured (Kembel et al. 2010, Kembel and Cahill 2011). To compare taxonomic and phylogenetic dissimilarity between sites, we used the function adonis in the R package vegan (Oksanen et al. 2007). We used similarity percentage analysis (SIMPER) to determine the proportional contribution of each species to BCD.

Functional trait diversity and dissimilarity. We evaluated two traits (1: microbial abundance and 2: chlorophyll *a* concentration) that are often associated with the functional roles of sponges in coral reef communities. Microbial abundance is often linked to water filtration rate. Low

208 microbial abundance sponges (LMA) typically have higher pumping rates and thus filter more
209 particulate organic matter (POM) from the water column. In contrast, high microbial abundance
210 (HMA) sponges often have lower pumping rates but are able to access key inorganic nutrient
211 sources through their symbionts. Photosymbionts represent a unique class of sponge symbionts
212 that provide access to autotrophic nutrition and other key inorganic nutrients. Abundance of
213 photosymbionts is often estimated by measuring chlorophyll *a* concentration within sponge
214 tissue (e.g. Gochfeld et al. 2012, Easson et al. 2014, Freeman, Easson & Baker, 2014). While
215 these two traits are often related, we assessed both traits to tease apart potential differences
216 between HMA and low photosymbiont abundance (e.g. *Agelas conifera, Aiolochroia crassa,*
217 etc.), which might occur in higher abundance at sites with lower irradiance and higher inorganic
218 nutrients. Sponges of different classifications, with respect to these two traits, show distinct
219 biogeochemical cycling in carbon and nitrogen cycling, which might impact the larger reef
220 community (Freeman, Easson & Baker, 2014). We treated microbial abundance as a binary
221 factor, as data for absolute microbial abundance in sponges is limited, categorizing sponges as
222 either high microbial abundance (HMA) or low microbial abundance (LMA) based on their
223 previously published designation (Oksanen et al. 2007, Weisz et al. 2007, Weisz, Lindquist &
224 Martens, 2008, Gloeckner et al. 2014). We treated chlorophyll *a* concentration in sponge tissue
225 as a continuous variable based on values in Erwin and Thacker (2007). The species *Svenzea*
226 *cristinae* was not analyzed in this previous survey, thus vouchers of this sample were collected
227 (n=8) and chlorophyll *a* concentration was measured using the same methodology as Erwin and
228 Thacker (2007) (Supplemental methods). We initially compared differences in these two traits
229 between sites using a two-sample t-test, assessing the proportion of HMA/LMA or High/Low
230 chlorophyll *a* sponges (High/Low chlorophyll *a* defined in Erwin and Thacker 2007) between

231 sites. We then calculated measurements of trait diversity similarly to phylogenetic diversity by
232 calculating the pairwise distance among species using the values for the measured functional
233 traits (microbial abundance and chlorophyll *a* concentration) to create a distance matrix, which
234 allowed for comparisons of dissimilarity among co-occurring species and between sites (Kembel
235 and Cahill 2011). We compared trait diversity between sites using a two-sample t-test to test for
236 site differences and a one-sample t-test to examine whether either site differed from a null
237 hypothesis for random trait patterns. We assessed functional trait beta diversity similarly to
238 phylogenetic beta diversity (comparing trait distances between two individuals from different
239 sites, Kembel and Cahill 2011), using the function adonis in the R package vegan (Oksanen et al.
240 2007).

241 *Overlap in beta diversity metrics.* To investigate potential overlap among our metrics of
242 community dissimilarity, we used Mantel tests to determine whether BCD, phylogenetic
243 dissimilarity, and trait dissimilarity were correlated.

244 **Results**

245 *Field sites.* Transects at Saigon and Punta Caracol contained an average of 260 and 194
246 individual sponges, representing 17 ± 0.7 and 22 ± 1 (mean ± SE) sponge species per 20 m^2,
247 respectively. Species richness at these two sites combined for a total of 40 sponge species. Two
248 sponges from the genus *Aplysina* were the most abundant members of these sponge communities
249 with 681 and 587 individuals of *A. fulva* and *A. cauliformis*, respectively, pooling data from both
250 sites. These two species accounted for approximately 28% of the total sponge individuals at each
251 site. Other notably abundant species were *Chondrilla caribensis, Mycale laevis, Svenzea*
252 *cristinae, Niphates erecta,* and *Verongula rigida.* Eight species (35% of unique sponge species)

253 were unique to Punta Caracol, while 2 species (11% of unique sponge species) were unique to
254 Saigon. These sponges were present at lower abundances within their respective community,
255 with none of these less common species having more than 12 individuals in the entire dataset.

256 *Sponge richness and diversity.* Species richness of individual transects ranged from 12 to 24
257 species. All three diversity indices were significantly different between the two sites: Species
258 richness (*S)* (mean±SE: 17.3±1.0 and 22.1±0.7 for Saigon and Punta Caracol, respectively; t-test:
259 $t = 3.99$, $df = 14.43$, $P = 0.001$), Shannon Index (*H'*) (mean±SE: 2.2±0.06 and 2.6±0.05 for
260 Saigon and Punta Caracol, respectively; t-test: $t = 4.44$, $df = 16.63$, $P < 0.001$), and inverse
261 Simpson's Index (*D)* (mean±SE: 7.0±0.5 and 10.2±0.7 for Saigon and Punta Caracol,
262 respectively; t-test: $t = 3.64$, $df = 16.42$, $P = 0.002$). Saigon on average had lower species
263 richness and community evenness compared to Punta Caracol

264 *Phylogenetic relatedness and patterns of diversity.* In addition to the lower species diversity at
265 Saigon, we observed significantly lower phylogenetic diversity (Faith's PD; 3.11 ± 0.11 for
266 Saigon and 3.45 ± 0.09 for Punta Caracol; t-test, $t=2.45$, $df =15.39$, $P = 0.027$), indicating
267 differences in the total branch length spanned by the sub-tree from each community. We
268 observed no differences in MPD, between our two sites (t-test, $t = 0.15$, $df = 12.52$, $P = 0.873$).
269 Although Punta Caracol displayed a pattern of random MPD (one-sample t-test, $t = -1.29$, $df = 9$,
270 $P = 0.229$), Saigon showed a pattern of MPD clustering (one-sample t-test, $t = -3.22$, $df = 8$, $P =$
271 0.012). These results imply that Saigon has a slightly higher presence of more closely related
272 species than Punta Caracol. We observed no significant differences in MNTD between our sites
273 (t-test, $t = -1.40$, $df = 12.05$, $P = 0.186$), and each site displayed a random distribution of MNTD
274 (one-sample t-test, $t = -0.99$, $df = 8$, $P = 0.348$ and $t = -1.94$, $df = 9$, $P = 0.084$ for Saigon and
275 Punta Caracol, respectively). These results indicate that while phylogenetic diversity, often

276 correlated with species richness, is lower at Saigon, these two sites do not show significantly
277 different patterns of phylogenetic relatedness in species composition. Given the narrow
278 geographic range of this study (~ 5 km), it is possible that these patterns of phylogenetic
279 diversity may be more indicative of the regional sponge fauna instead of differences between
280 sites.

281 *Beta-diversity analysis.* We observed significant differences in beta diversity for taxonomic
282 (adonis, $F = 8.39$, $df = 1$, $R^2 = 0.33$, $P = 0.001$, Figures 2 and 3a) and MPD phylogenetic
283 dissimilarity (adonis, $F = 1.53$, $df = 1$, $R^2 = 0.083$, $P = 0.001$, Figure 3b), but not for MNTD
284 phylogenetic dissimilarity (adonis, $F = 0.69$, $df = 1$, $R^2 = 0.04$, $P = 0.476$, Figure 3c) between
285 sites. SIMPER analysis revealed that 5 sponge species comprised about 50% of the BCD
286 between the two sites, including: *Svenzea cristinae* (16%), *Aplysina cauliformis* (10%), *Aplysina*
287 *fulva* (9%), *Haliclona walentinae* (8%), and *Chondrilla caribensis* (7%), all of which were found
288 in higher relative abundance at Saigon (Figure 2). Moreover, the SIMPER results demonstrate
289 that the lower species *D* at Saigon was due to the increased abundance of a few sponge species.

290 *Functional trait diversity and dissimilarity.* Analysis of trait proportions between sites revealed
291 that Saigon had a higher proportion of HMA (t-test: $t = -2.63$, $df = 16.41$, $P = 0.02$) and high
292 chlorophyll *a* (t-test: $t = -9.00$, $df = 16.50$, $P < 0.001$) sponges, and the proportions of these two
293 traits were correlated (Pearson's correlation, $r = 0.62$, $df = 17$, $P = 0.005$). Trait diversity was
294 significantly different between our two sites (t-test, $t = 3.34$, $df = 10.68$, $P < 0.001$). Traits were
295 significantly more clustered at Saigon (one-sample t-test, $t = -2.49$, $df = 8$, $P = 0.044$), whereas
296 traits were more evenly distributed at Punta Caracol (one-sample t-test, $t = 2.73$, $df = 9$, $P =$
297 0.006, Figure 3d). Species from Punta Caracol had a broad range of chlorophyll *a* concentrations
298 and microbial abundances, while species at Saigon were only represented by a subset of this

299 range. Trait beta diversity between sites was significantly different (adonis, F = 82.264, df = 1,
300 R^2 = 0.83, P = 0.002) and explained approximately 83% of the variation among transects.

301 *Overlap in beta diversity metrics.* Mantel tests indicated that BCD taxonomic dissimilarity was
302 significantly correlated with MPD phylogenetic dissimilarity (Mantel: r = 0.48, P = 0.001),
303 MNTD phylogenetic dissimilarity (Mantel: r = 0.51, P = 0.001, and trait dissimilarity (Mantel: r
304 = 0.24, P = 0.004). Phylogenetic MPD (Mantel: r = 0.22, P = 0.010) and MNTD (Mantel: r =
305 0.27, P = 0.005) dissimilarity were correlated with trait dissimilarity.

306 **Discussion**

307 This study identified clear differences in sponge species diversity and richness between
308 Saigon and Punta Caracol, supporting previous findings from Gochfeld, Schloder & Thacker,
309 (2007), who attributed this variation to chronic anthropogenic influence. Building on these
310 results, we also observed significantly lower phylogenetic diversity at Saigon, and demonstrated
311 that each site had a distinct taxonomic and phylogenetic community structure (Figure 2). This
312 variation in community structure resulted in contrasting trait diversity between sites, with Saigon
313 dominated by sponges with high chlorophyll *a* concentrations and high microbial abundance.

314 The region of Almirante Bay in Bocas del Toro, Panama is characterized by high sponge
315 biodiversity with over 120 species found in reef, seagrass, and mangrove habitats (Diaz 2005),
316 despite episodic heavy rainfall resulting in severe freshwater runoff, sedimentation, and low tidal
317 flushing (D'Croz, Del Rosario, & Gondola, 2005). Much of the development in the area has little
318 or no sewage treatment, and many residences and businesses are built adjacent to or over the
319 water (Figure 1, Collin 2005). Thus, many near-shore environments in this area are heavily
320 influenced by human activity (Aronson et al. 2004), and abundant human debris is often

observed floating and at depth in these areas (Easson personal observation). Although sponges are considered to be sensitive to environmental stressors (Gochfeld, Schloder & Thacker, 2007), including elevated nutrient concentrations (Easson et al. 2014, but see Gochfeld et al. 2012), a factor associated with poor sewage treatment, the Bocas del Toro region maintains high sponge diversity (Diaz 2005). In contrast to the high diversity and abundance of sponges in the region, coral communities have experienced a marked decline associated with changes in water quality, concurrent with increases in human settlement in the region (Guzman 2003, Aronson et al. 2004).

By coupling heterotrophic filter-feeding with microbial metabolic pathways afforded by their symbionts, many sponges are able to utilize a wide range of nutrient sources that likely contribute to their proliferation in a wide range of habitats, even in anthropogenically-stressed areas where corals are in decline (Aronson et al. 2004, Diaz 2005). However, changes in sponge community diversity and composition among sites may indicate chronic environmental stress. Gochfeld, Schloder & Thacker, (2007) found distinct shifts in composition and lower diversity associated with proximity to human development. Likewise, the current study demonstrated that sponge assemblages in close proximity to human populations were less diverse and dominated by a small number of species. When we looked beyond richness and diversity, we observed that the community at Saigon contained lower genetic diversity, selecting for more distantly related species belonging to broader phylogenetic groups. Differences in assemblage composition were driven mainly by the high abundance of *Svenzea cristinae* and *Haliclona walentinae* at Saigon; these species were nearly absent at Punta Caracol. Additionally, Saigon showed a higher abundance of *Aplysina cauliformis*, *Aplysina fulva*, and *Chondrilla caribensis*. Interestingly, these 5 species that comprise the main compositional differences between sites all have high

344 photosymbiont abundance. In contrast to previous surveys in the area (Gochfeld, Schloder &
345 Thacker, 2007), we found that the number of individuals increased at sites in close proximity to
346 human development. This result may be skewed by the occurrence of many small individuals of
347 *Svenzea cristinae* at Saigon (mean = 47 per transect) as compared to Punta Caracol (mean = 5
348 per transect). While estimates of sponge biomass or volume are necessary to definitively
349 measure changes in sponge abundance across sites (Wulff 2001), the number of individuals or
350 species is often related to sponge biomass measurements (Wulff 2006, 2013).

351 While metrics such as diversity and richness have been widely used to estimate
352 community health in many marine systems (e.g. Witman, Etter & Smith, 2004, Schlacher et al.
353 2007, Hewitt, Thrush & Dayton, 2008), these metrics capture only a small part of potential
354 changes and do not consider the functional variability of species are within a habitat (Cadotte
355 2011, Gotelli and Chao 2013, Stuart-Smith et al. 2015). Sponges exhibit a wide range of
356 functional behaviors, and aside from filter feeding, many of the functional roles that sponges fill
357 are tied to the diverse and abundant microbial communities that they host. Both of the traits
358 evaluated in the current study are related to these microbial communities (Taylor et al. 2007a,
359 Taylor et al. 2007b). We observed significant trait diversity differences between sites, partially
360 driven by high trait evenness at Punta Caracol. Further analysis revealed that Saigon contained
361 sponges that were mostly HMA with high chlorophyll *a* concentrations while the community at
362 Punta Caracol included species with a wide range of photosymbiont and overall microbial
363 abundances. The two traits investigated in the current study are correlated because most sponges
364 that have high photosymbiont abundance are considered to be HMA species. However, despite
365 the long-term use of the HMA/LMA classification recent research has made several aspects of
366 this dichotomy less clear by demonstrating that sponge species host a continuum of microbial

367 diversity that is specific to a species and independent of microbial abundance classification
368 (Giles et al. 2013, Easson and Thacker 2014). Moreover, the function of the microbial
369 symbionts is likely more important than abundance and chlorophyll *a* concentration is a better
370 predictor of metabolic differences among sponges than microbial abundance (Freeman, Easson
371 & Baker, 2014).

372 Decreased trait diversity at Saigon compared to Punta Caracol could imply that
373 ecological forces at this site are selecting for a sponge assemblage with particular functional
374 traits. Most sponges that host photosynthetic microorganisms rely on them for nutrition to some
375 degree (Thacker and Freeman 2012), and as a result may rely less on heterotrophic feeding. We
376 originally hypothesized that poor water quality in the region (Collin 2005, D'Croz, Del Rosario,
377 & Gondola, 2005, Gochfeld, Schloder & Thacker, 2007) would lead to increased particulate
378 matter in the water column, potentially benefitting heterotrophic sponge species and selecting
379 against phototrophic sponges (Weisz, Lindquist & Martens, 2008). Instead, a higher abundance
380 of species that host abundant symbionts, specifically, photosymbionts at Saigon may be driven
381 by the ability of these symbionts to utilize diverse inorganic nutrient sources common in areas of
382 anthropogenic input (Freeman et al., 2013; Easson et al. 2014; Zhang et al. 2015).

383 Chlorophyll *a* concentration and microbial abundance are somewhat limited in what they
384 can elucidate about the sponge function, and adding more traits to the analysis would be
385 beneficial. One trait that would provide greater resolution for sponge community function would
386 be nitrogen transformation potential of sponge symbionts. However, data for this trait is limited
387 to a small number of sponge species, and uncertainty surrounding the stability of these symbiont
388 communities, as well as measurement discrepancies within a single species, prevented us from

389 evaluating these traits in the current study (Southwell 2007, Southwell et al. 2008, Hoffman et al.
390 2009, Maldonado, Ribes & van Duyl, 2012, Fiore, Baker & Lesser, 2013).

391 The current study shows that a sponge community in close proximity to human
392 populations consisted of fewer sponge species with higher photosymbiont abundance, as well as,
393 overall microbial abundance. In contrast, the community at a site distant from human
394 development (Punta Caracol) included a more diverse assemblage of species, including those
395 considered to have both high and low microbial abundance and chlorophyll *a*. Although we
396 present no direct evidence of human impact (i.e. nutrient analysis), Gochfeld, Schloder &
397 Thacker, (2007) measured pollutants consistent with anthropogenic inputs in the Saigon area,
398 and thus concluded that reefs in this region likely experience some degree of human impact.
399 This, coupled with the fact that development in the Saigon area has continued (Figure 1), implies
400 that Saigon has been chronically exposed to anthropogenic inputs for at least the last 7 years.
401 Our observations of differences in species and phylogenetic diversity, altered species
402 composition, and functional trait diversity at otherwise similar sites suggest that proximity to
403 human development (and potentially these inputs) may be partially shaping the community
404 composition of these dominant benthic invertebrates. Importantly, our data also suggest that this
405 variation may have important impacts on genetic diversity and ecosystem function. For instance,
406 while species with high photosymbiont abundance may increase local productivity, selection for
407 species with abundant symbiont communities may lead to a reduction in heterotrophic feeding,
408 instead favoring a community capable of diverse nitrogen transformations. Selection favoring
409 HMA species over LMA species, which might rely more on heterotrophic feeding, might further
410 alter the cycling of nutrients and organic matter within reef ecosystems by reducing water
411 filtration rates. Thus, as shifts from coral-dominated systems to sponge-dominated systems are

occurring throughout the Caribbean (Loh and Pawlik 2014), it is important for us to understand how local-scale changes impact the composition of these sponge communities, as well as the functional role of species within these communities.

Acknowledgments

We thank the staff of the Smithsonian Tropical Research Institute Bocas del Toro Research station for their assistance in the field, as well as the participants in the Bocas del Toro Sponge Course in 2012. Specifically we thank the instructors of this course Maria-Cristina Dìaz, Eduardo Hajdu, and Gisele Lôbo-Hajdu for helping the authors with identifying sponge species. We also thank Marc Slattery and Deborah Gochfeld for their support of this research, Julia Korn for help with data visualizations, and Taylor Roberge for manuscript feedback. All R code for statistical analyses was obtained from portions of Steven Kembel's "Biodiversity Analysis in R" workshop (http://kembellab.ca/r-workshop/biodivR/SK_Biodiversity_R.html).

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1

Map of Bocas del Toro Region in Panama

Figure 1: Map of Bocas del Toro region in Panama, where surveys were performed (Punta Caracol and Saigon Bay). The white dot marked STRI represents the Smithsonian Tropical Research Institute. Each yellow dot represents an individual structure (residence) in 2004, and each red dot represents a structure in 2011. Blue dots represent new residences that were built between 2004 and 2011. Approximately 55 new structures were constructed on or adjacent to the shore along Saigon Bay in this 7-year span. Imagery is from 2004 (left map) and 2011 (middle and right maps) and is provided by DigitalGlobe® via Google Earth and ArcGIS® software imagery basemap in ArcMap™ by Esri©.

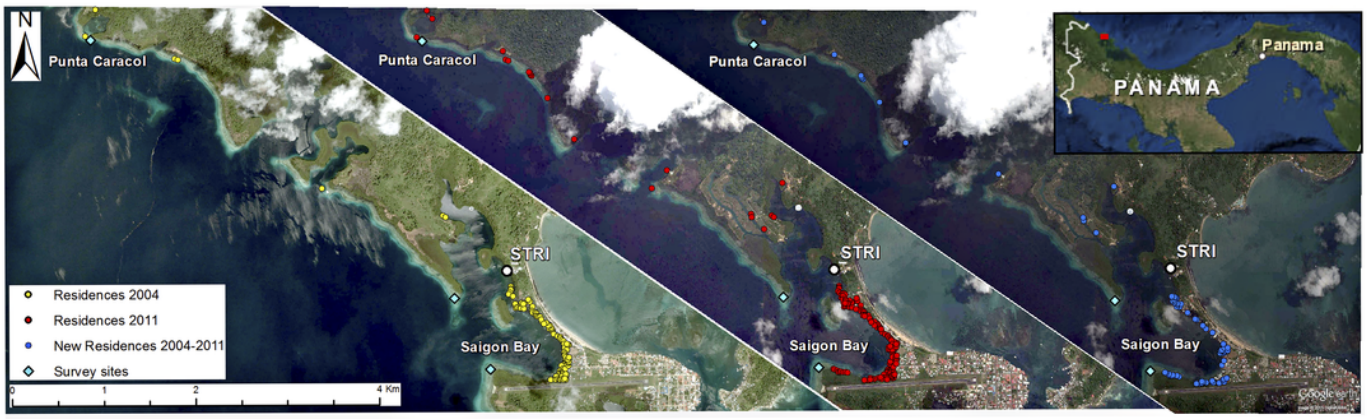
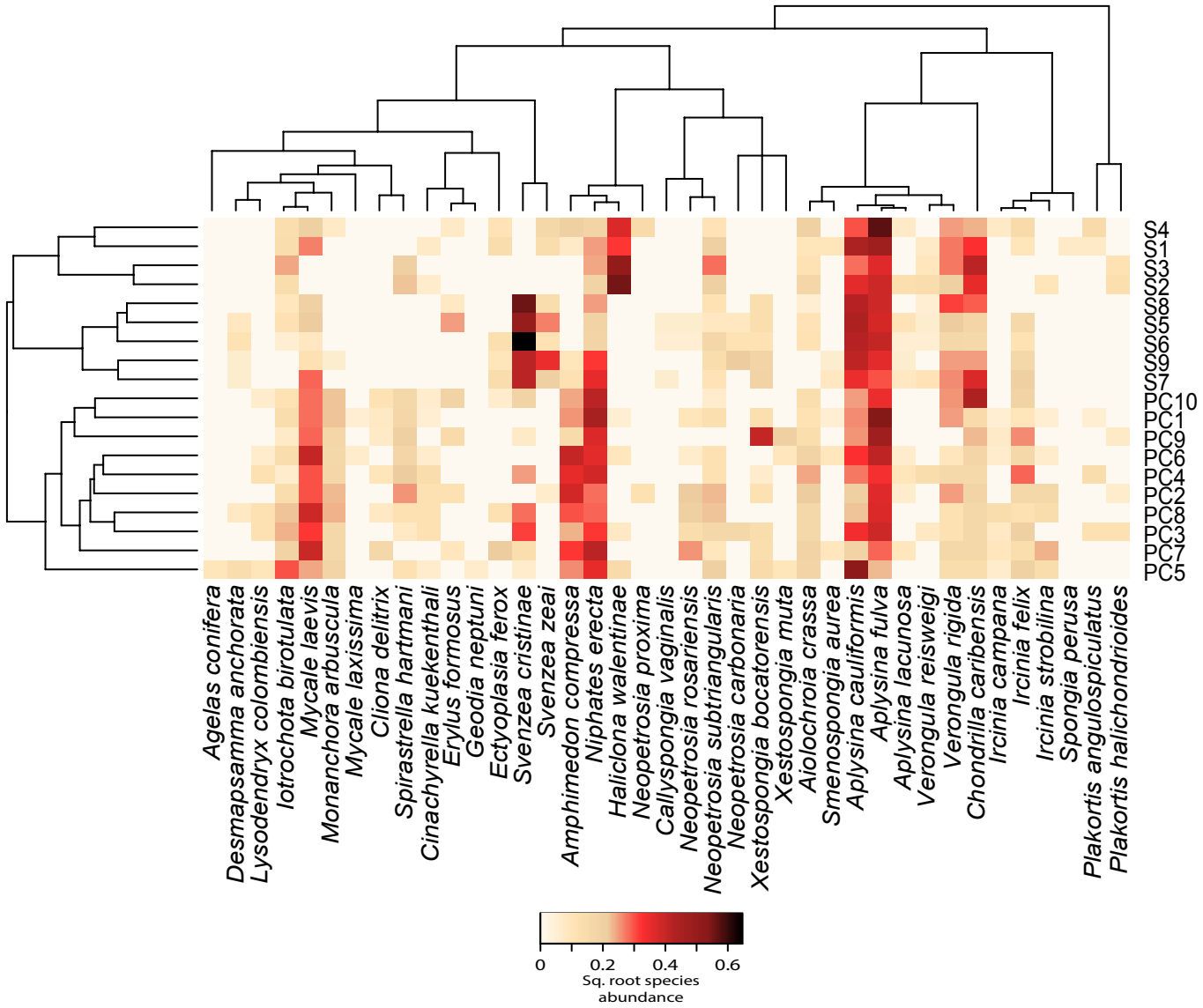


Figure 2(on next page)

Figure 2 Relative abundance heatmap

Figure 2: Relative abundance heatmap of sponge species encountered within each transect. These data are square-root transformed for easier visualization. A Bray-Curtis dissimilarity dendrogram on the left highlights the taxonomic dissimilarity among transects. The reconstructed phylogeny of these sponge species is displayed across the top, and species names are displayed across the bottom. S(1-9) represent transects near Saigon Bay, which are closer to a larger number of residences, while PC(1-10) represent transects at Punta Caracol.


S4
S1
S3
S2
S8
S5
S6
S9
S7
PC10
PC1
PC9
PC6
PC4
PC2
PC8
PC3
PC7
PC5
Agelas conifera
Desmapsamma anchorata
Lysodendryx colombiensis
Iotrochota birotulata
Mycale laevis
Monanchora arbuscula
Mycale laxissima
Cliona delitrix
Spirastrella hartmani
Cinachyrella kuekenthali
Erylus formosus
Geodia neptuni
Ectyoplasia ferox
Svenzea cristinae
Svenzea zeai
Amphimedon compressa
Niphates erecta
Haliclona walentinae
Neopetrosia proxima
Callyspongia vaginalis
Neopetrosia rosariensis
Neopetrosia subtriangularis
Neopetrosia carbonaria
Xestospongia bocatorensis
Xestospongia muta
Aiolochroia crassa
Smenospongia aurea
Aplysina cauliformis
Aplysina fulva
Aplysina lacunosa
Verongula reisweigi
Verongula rigida
Chondrilla caribensis
Ircinia campana
Ircinia felix
Ircinia strobilina
Spongia perusa
Plakortis angulospiculatus
Plakortis halichondrioides
0
0.2
0.4
0.6
Sq. root species abundance

3

NMDS scaling plots for beta diversity metrics

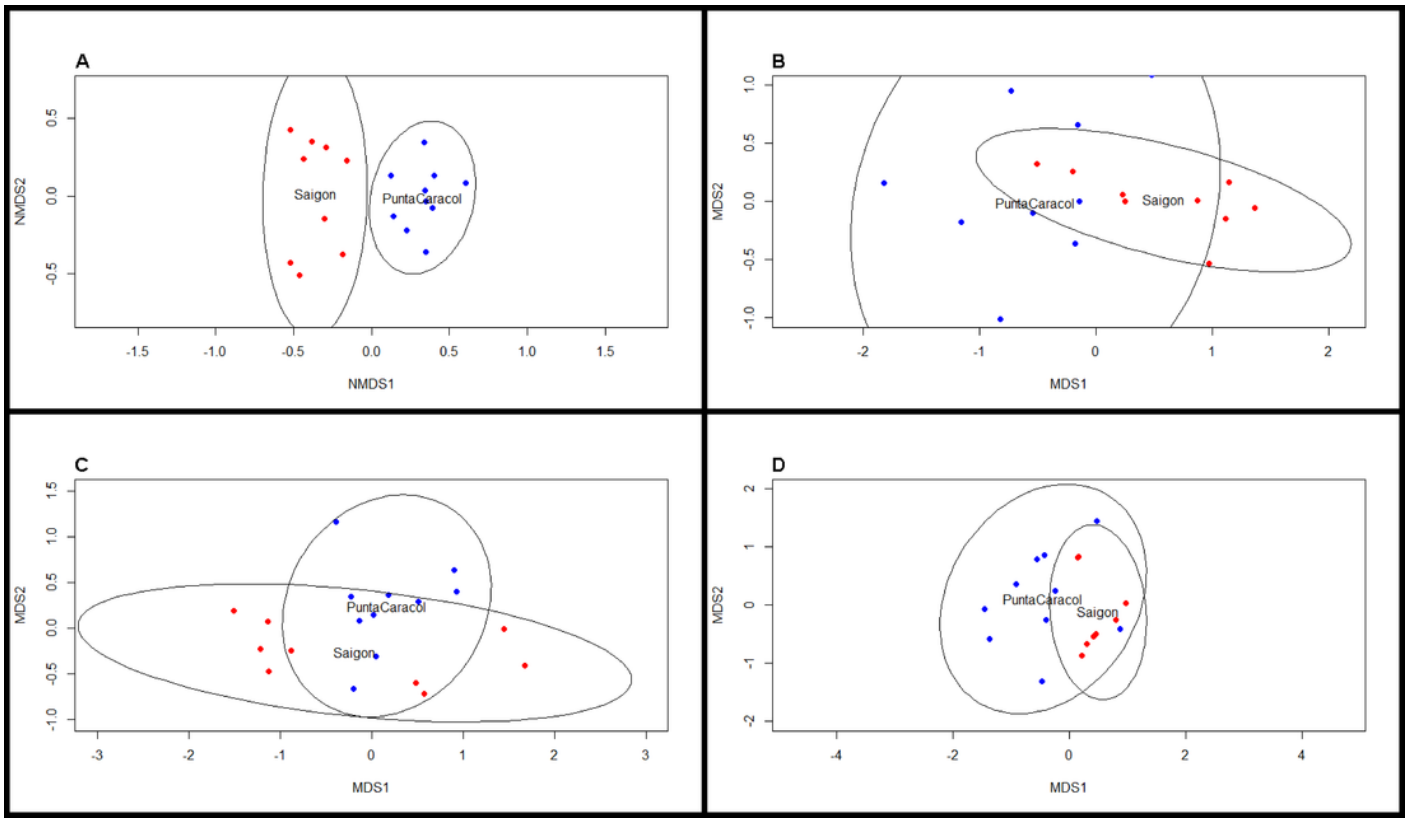



Figure 3: Nonmetric multi-dimensional scaling plots of (A) BCD taxonomic, (B) MPD phylogenetic, (C) MNTD phylogenetic, and (D) trait dissimilarity between sites. Blue dots indicate transects at Saigon, while red dots indicate transects at Punta Caracol.