



# Caribbean Near-Shore Coral Reef Benthic Community Response to Changes on Sedimentation Dynamics and Environmental Conditions

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Coral reefs are facing unprecedented global, regional and local threats that continue to degrade near-shore habitats. Water quality degradation, due to unsustainable development practices at coastal watersheds, is one of the greatest stressors across multiple spatial scales. The goal of this study was to assess near-shore coral reef benthic community spatio-temporal response to sedimentation patterns, weather, and oceanographic dynamics at Bahía Tamarindo and Punta Soldado in Culebra Island, Puerto Rico. Benthic data were collected across a distance gradient from the shore through high-resolution images at marked belt transects. Environmental data were assessed and contrasted with benthic assemblages using multivariate correlations and multiple linear regression. Coral colony abundance and coral recruit assemblages showed significant variation among seasons, sites and distance zones (PERMANOVA,  $p < 0.01$ ). Species diversity ( $H'$ ) increased at both study sites with distance from shore, and the most conspicuous coral recruit species were stress-tolerant *Porites astreoides*, *P. porites*, and *Siderastrea radians*. Difference in coral abundance and coral recruits per site had a strong significant negative relationship with sediment characteristics and depth ( $p < 0.05$ ). Near-shore coral reef benthic community structure was significantly different between sites and distance zones from shore, with depth having an important role in shaping reef zonation. Changes in benthic community structure were associated with local sediment distribution patterns emerging from human alteration of coastal watersheds and natural events that cause terrigenous sediment deposition and sand resuspension across the reef. Coral cover was significantly lower at zones more exposed to recurrent sedimentation stress ( $p < 0.01$ ). It was also correlated with sediment texture ( $p = 0.006$ ) and terrigenous sediment deposition ( $p = 0.016$ ). Scleractinian coral

cover had an inverse relationship with gorgonian and macroalgae cover. In a short-term period, a pattern of increased dominance of encrusting calcareous algae *Ramificrusta textilis* and invasive sponge *Dictyonella funicularis* were documented. Changing land use and increased frequency of extreme weather events, as a consequence of global patterns of climate change, may play an important role shaping near-shore coral reefs benthic communities and could threaten the resilience of coastal regions. Therefore, collaborative and trans-disciplinary ecosystem-based management efforts are urgently needed to effectively reduce land-based stressors and foster near-shore coral reef recovery.

**Keywords:** benthic cover, coral abundance, coral diversity, coral recruit, coral reef community structure, environmental stressors, near-shore coral reefs, sedimentation dynamics

## INTRODUCTION

Coral reefs are affected by a wide array of global, regional, and local stressors that have led to habitat degradation worldwide during recent decades (Hughes, 1994; Gardner et al., 2003; Wilkinson and Souter, 2008). Global and regional trends of coral decline are associated to anthropogenic stressors combined with climate change-related impacts and natural disturbances (Eakin et al., 2010; Wild et al., 2011; Bozec and Mumby, 2015; Hernández-Delgado, 2015). At a local scale, land-based stressors represent a major threat to near-shore coral reefs in the Caribbean region. These land-based stressors are mostly related to increasing trends of land-use changes, coastal urban sprawl and tourism-based activities with direct effects on sediment-laden runoff and sediment distribution along coastal waters (Rogers, 1990; Larsen and Webb, 2009; Hernández-Delgado et al., 2012; Ramos-Scharrón et al., 2012, 2015; Bégin et al., 2013). This is particularly true for small tropical semi-arid islands, where an alteration of sediment delivery and distribution dynamics along near-shore reef ecosystem has been documented as a result of watershed alteration combined with changes in local weather patterns (Otaño-Cruz et al., 2017). Increased terrigenous sediment influx to coastal waters increases coral reef vulnerability and susceptibility to experience phase-shift toward alternate states, often dominated by non-reef building taxa and macroalgal assemblages (Acevedo et al., 1989; Fabricius, 2005, 2011; Bellwood and Fulton, 2008; Dudgeon et al., 2010; Hughes et al., 2010). This combination of factors can have profound permanent effects on reef ecosystem functions and services (Acevedo et al., 1989; Bellwood et al., 2004; Hughes et al., 2010). Therefore, there is a major concern regarding the potential effects of elevated terrestrial sediment input to coastal waters and changes in environmental conditions, especially on coral reef habitats historically adapted to low sedimentation levels.

The coral reef response to local human-induced disturbances depends on the frequency, duration, and distance from the source of the environmental stressor (Fabricius, 2005; Smith et al., 2008; Edmunds and Gray, 2014). Recurrent environmental disturbances have adverse implications for coral reef benthic communities by producing shifts in ecological dynamics and in the population of endangered coral species (Díaz-Ortega and Hernández-Delgado, 2014). Sedimentation stress has been

associated with localized partial coral mortality, reduced coral growth rate, inhibited larval settlement, and reduced fish grazing (Loya, 1976; Nugues and Roberts, 2003a,b; Fabricius, 2005; Bellwood and Fulton, 2008). Impacted coral reefs can have losses of sensitive species, thus reinforcing phase shifts toward sediment-resistant species, and dominance by algae and other non-reef building taxa (Acevedo et al., 1989; Bellwood et al., 2004; Fabricius, 2005, 2011; Hughes et al., 2010). Changes in species composition can produce significant changes in structural complexity and functioning by reducing reef accretion and rugosity (Alvarez-Filip et al., 2013). Coral reefs exposed to recurrent sediment pulses and high turbidity levels also have limited ability to recover after chronic disturbances [e.g., bleaching caused by high sea surface temperature (SST)] and increased prevalence of coral diseases (Cróquer et al., 2002; Toledo-Hernández et al., 2007; Pollock et al., 2014; Stubler et al., 2016). Therefore, the understanding of the interactions between land and sea ecosystems and the short-term response of coral reefs community to sedimentation stressors is paramount for the development and implementation of effective and adaptive ecosystem-based management strategies to prevent further decline in live coral cover and enhance coral reef resilience (Rivera-Monroy et al., 2004; Alvarez-Filip et al., 2009; Mumby and Steneck, 2011).

Live coral cover decline across the Caribbean region has been partly attributed to increased sediment delivery to coastal waters after storms and heavy rainfall events, as a consequence of coastal watershed alteration and unsustainable development trends (Ramos-Scharrón and MacDonald, 2007; Hernández-Delgado et al., 2011, 2012, 2014b; Ramos-Scharrón et al., 2012; Sturm et al., 2014). At a broader spatial scale, the combined effects of chronic anthropogenic stressor impacts, such as declining water quality due to increased land-based source of pollution (LBSP), reduction in grazing due to overfishing and changing climate (e.g., change in rainfall patterns), have contributed to near-shore coral reef ecosystem degradation (Miller et al., 2009; Hernández-Pacheco et al., 2011; Edmunds, 2013; Jackson et al., 2014). This phenomenon illustrates the complexity and interconnectedness between the coastal and marine habitats, and thus, represents unfavorable conditions for coral reef recovery (Hughes and Connell, 1999; Rogers and Miller, 2006; Ennis et al., 2016). The implementation of mitigation and restoration

projects at watershed and coral reef scales has become a management priority and the understanding of the existing land-sea and climate interconnectedness becomes critical for the implementation of rapid and effective strategies to contribute to coral reef recovery worldwide.

The goal of this study was to assess whether there was a significant spatio-temporal difference in the short-term response of benthic communities to variations in sedimentation patterns and environmental variables. Therefore, this study aimed to: (i) assess variation in coral reef benthic community structure through coral colony abundance, coral recruit abundance, percent live coral cover, octocoral, sponge and macroalgae cover in a distance gradient from the shore; and (ii) contrast spatio-temporal changes in coral colony abundance, coral recruit abundance, and coral cover with sedimentation patterns, and environmental variable dynamics.

## MATERIALS AND METHODS

### Data Acquisition, Field Sampling, and Laboratory Analyses

Culebra Island is a mid-shelf semi-arid island located 27 km off the eastern coast of Puerto Rico, in the northeastern Caribbean Sea. The study was conducted from February 2014 to April 2015 across two leeward coral reef locations: Bahía Tamarindo (BTA, 18°18' N, 65°19' W) and Punta Soldado (PSO, 18°16' N, 65°17' W) (Figure 1). Both study sites are part of a long-term community-based coral reef rehabilitation effort to support reef functions and services, including the reefs' role as fish nursery grounds (Hernández-Delgado et al., 2018). Transplant of *Acropora* spp. onto the reef was conducted prior to the initiation of this research in 2003. Belt transects of 10 m<sup>2</sup> were marked parallel to the coastline and were assessed with high-resolution replicate photo-quadrat every 1 m<sup>2</sup>. Marked transects were assessed seasonally, from spring to winter, every 3 months, during a 1 year period. Each monitoring station consisted of triplicate fixed transects. Benthic assessment in BTA was conducted across a total of three replicate monitoring stations within distance zone A (<60 m from shore), with a depth range from 1 to 2 m, and three stations in distance zone B (>60 m from shore), with depth range contour from 2 to 4 m. In PSO, there were a total of two monitoring stations within zone A and B and the depth range contour was similar to BTA.

Scleractinian coral, hydrocoral, and octocoral species assemblages were assessed within each transect using photo-quadrats to identify corals to the lowest taxonomic level possible and to calculate the average abundance for each sampling station. This data was used to calculate coral colony abundance, species richness (S), species diversity index (H'<sub>n</sub>) (Shannon and Weaver, 1948), and evenness index (J'<sub>n</sub>) (Pielou, 1966) at each site and distance zone. Scleractinian coral recruit abundance was also assessed, specifically for colonies ≤4 cm in diameter for larger species (i.e., *Pseudodiploria* spp., *Siderastrea siderea*), and ≤2 cm for smaller species (i.e., *Porites astreoides*) (Dueñas et al., 2010). The benthic cover was assessed from high-resolution images by digitally projecting 48 regularly-distributed dots over each

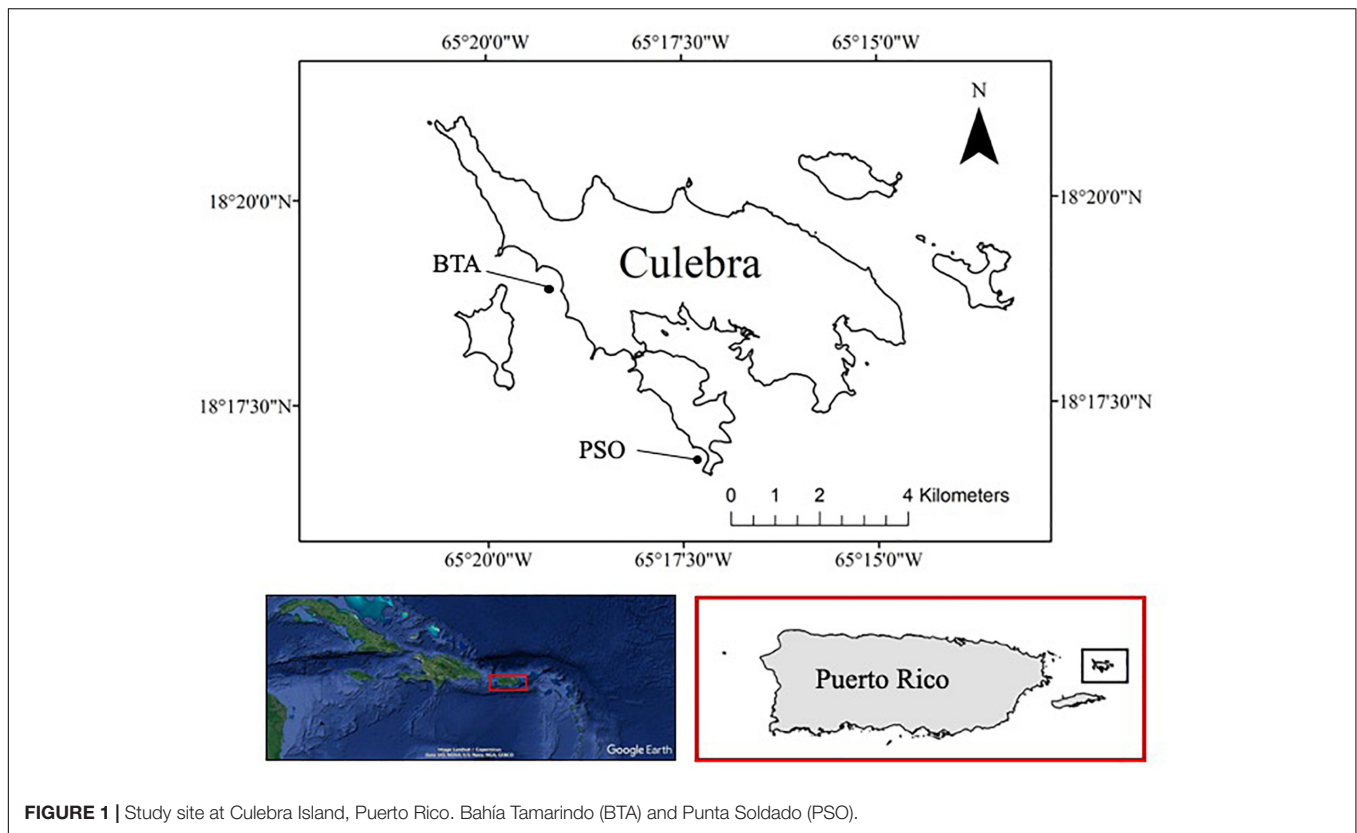
photo-quadrat image. Benthic components under each dot were identified, including scleractinians, hydrocorals, octocorals, sponges, macroalgae, algal turf, coralline algae (CA), and cyanobacteria, among other components (i.e., sand, pavement, rubble). Coral cover as recorded included both Scleractinians and hydrocorals. Algal turf was classified as a mix of short algae (<1 cm) and sediments (NOAA, 2015). Data was used to calculate percent benthic component cover and benthic community structure.

The environmental database included sedimentation rate, sediment texture, and composition. Sediment traps were deployed at both sites across a distance gradient from shore, within a distance of less than 10 m from marked belt transects. Sediment samples were collected on a monthly basis and processed at the laboratory. Sediment samples were oven-dried at 60°C for 24 h and total dry weight was recorded to calculate sediment accumulation rate (Edmunds and Gray, 2014; Otaño-Cruz et al., 2017). Sediment texture (silt-clay <63 μm and sand >63 μm) were analyzed through dry sieving, while loss on ignition techniques were applied to determine the organic matter (3 h oven dry 550°C), carbonate matter (3 h oven dry 950°C) and terrigenous sediment composition (Otaño-Cruz et al., 2017). Rainfall events were documented with HOBO RG3 (Onset Computers, Co.) rain gauges located in coastal watersheds near study sites, while sea surface temperature at both study sites were recorded with HOBO Watertemp Pro V2. Oceanographic hydrodynamics data, such as wave height and wind speed, were acquired from the Caribbean Integrated Coastal Ocean Observing System (CariCOOS) online database<sup>1</sup>, buoy NDBC 41056 located at Vieques sound.

### Statistical Analyses

Benthic components were tested using four-way non-parametric permutational analysis of variance (PERMANOVA) and pairwise comparison for the fixed factors of seasons, time, site and distance from shore (Anderson et al., 2008). Multivariate analyses were performed in Primer v7 + PERMANOVA v1.16 software (Quest Research Ltd., Auckland, New Zealand) to analyze spatio-temporal variation in coral colony abundance, coral recruit abundance, and benthic community structure (Clarke et al., 2014; Clarke and Gorley, 2015). A significant relationship was identified by factors that had  $P < 0.05$ . The rank order of dissimilarities were calculated through Bray-Curtis resemblance from coral abundance, coral recruit abundance, and benthic community matrices. For coral recruitment, a zero-adjusted Bray-Curtis resemblance matrix was calculated, including a “dummy variable” to reduce distortion from absent species by samples (Clarke et al., 2006). Coral colony abundance, coral recruit abundance, and percent benthic community parameters were standardized to balance the contribution of common and rare species, and thus, represented the relative percentage of species for each sample. Species assemblages were also square root-transformed prior to analysis to meet assumptions of normality and homogeneity of variance (Clarke and Warwick, 2001; Gotelli and Ellison, 2013). All multivariate tests were

<sup>1</sup><http://www.caricoos.org/data-download>



**FIGURE 1** | Study site at Culebra Island, Puerto Rico. Bahía Tamarindo (BTA) and Punta Soldado (PSO).

based in 10,000 permutations (Hernández-Delgado et al., 2014a). Sigma Plot v.11 (Systat Software, Inc.) was used for graphical representation of biological data.

Ordination was performed using non-metric multi-dimensional scaling (nMDS) and principal coordinates ordination (PCO), by calculating the distance among centroids, to display the variations in benthic communities in a three-dimensional space and determine which benthic component explained spatio-temporal variation. Cluster and similarity profile test (SIMPROF) were used to identify groups with similarity differences between samples, to test the null hypothesis of no significant spatial and temporal differences on multivariate structure of benthic assemblages. Afterward, a similarity percentage (SIMPER) analysis routine was performed to determine which key taxa contributed most to similarities and spatial variation in the benthic community structure through time, within sites and distance (Clarke et al., 2014).

Environmental variables were correlated with the biological matrices using non-parametric multivariate correlation routine BEST-BIO ENV (Spearman rank correlation) to determine the best environmental variable that explained differences in coral reef benthic community spatio-temporal variation (Clarke et al., 2014). RELATE routine was used to test the relationship between coral recruit abundance and percentage macroalgal cover, with sedimentation and other abiotic variables. DISTLM was performed for multiple linear regression analysis to assess potential effects of environmental variables on coral colony abundance, coral recruit abundance, and benthic

cover with a distance-based redundancy analysis (dbRDA) (Anderson et al., 2008).

## RESULTS

### Coral Colony Abundance, Coral Species Richness, and Diversity

Mean coral colony abundance ( $\pm 95\%$  confidence interval) at Bahía Tamarindo and Punta Soldado near-shore coral reefs was  $13.18 \pm 0.92 \text{ m}^{-2}$ . There were significant differences in coral abundance by season (Pseudo  $F = 2.38$ ,  $p = 0.0002$ ), sites (Pseudo  $F = 36.96$ ,  $p = 0.0001$ ), and distance zones (Pseudo  $F = 9.98$ ,  $p = 0.0001$ ) (**Table 1**). Coral colony abundance was higher at BTA than PSO with a mean of  $13.77 \pm 0.92 \text{ m}^{-2}$ . The highest coral abundance value at BTA was documented a long distance zone B (farther from shore,  $>60 \text{ m}$  from shore), with a mean of  $17.95 \pm 1.27 \text{ m}^{-2}$  (**Figure 2**). The lowest value of coral abundance at BTA was recorded at distance zone A (near to shore,  $<60 \text{ m}$  from shore) with a mean of  $9.59 \pm 0.94 \text{ m}^{-2}$ . Mean coral abundance was lowest at PSO with a mean  $12.29 \pm 1.29 \text{ m}^{-2}$ . The highest coral colony abundance value at PSO was documented near shore, zone A, with a mean of  $12.78 \pm 4.68 \text{ m}^{-2}$ . Coral abundance at both sites experienced significant variation through seasons at offshore zone (**Figure 2**). There were significant interaction effects between site and distance zones (Pseudo  $F = 18.74$ ,  $p = 0.0001$ ), suggesting the influence of the latter on the observed variation between sites. Pairwise analysis indicated that

**TABLE 1** | Results of permutational analysis of variance (PERMANOVA) for coral colony abundance and coral recruit abundance.

Factors	df	Pseudo F	P (perm)
<b>Coral colony abundance</b>			
Season (Se)	3	1.71	<b>0.0112</b>
Site (Si)	1	32.09	<b>0.0001</b>
Distance (Di)	1	10.16	<b>0.0001</b>
Se × Si	3	1.35	0.0933
Se × Di	3	0.77	0.8141
Si × Di	1	18.74	<b>0.0001</b>
Se × Si × Di	3	0.75	0.8338
<b>Coral recruit abundance</b>			
Season (Se)	3	2.72	<b>0.0030</b>
Site (Si)	1	27.30	<b>0.0001</b>
Distance (Di)	1	8.00	<b>0.0001</b>
Se × Si	3	2.25	<b>0.0100</b>
Se × Di	3	1.47	0.1500
Si × Di	1	11.29	<b>0.0001</b>
Se × Si × Di	3	1.60	0.1100

Bold *p*-values represent significance.

coral colony abundance had significant variation in BTA ( $t = 4.02$ ,  $p = 0.0001$ ) and PSO ( $t = 4.02$ ,  $p = 0.0001$ ) by distance zones.

A total of 66 species were documented (34 scleractinians, 2 hydrocorals, and 30 octocorals) in both study sites combined. The scleractinian coral species with highest mean relative abundance at BTA were *Porites astreoides* (24.54%), *P. porites* (11.40%), *Acropora cervicornis* (5.84%), *Siderastrea siderea* (5.76%), *Pseudodiploria strigosa* (5.66%), *Diploria labyrinthiformis* (5.03%), *S. radians* (4.59%), and *Agaricia agaricites* (3.48%), representing a total 66.30% of species contribution (Figure 3). The only species that showed a pattern of increased relative abundance through time at both distance zones was *P. porites*. The hydrocorals *Millepora alcicornis* and *M. complanata* had a higher percentage relative abundance at BTA than PSO, with a mean of 16.54 and 2.35%, respectively. Coral species with the highest mean relative abundance at PSO were *P. astreoides* (31.06%), *P. porites* (10.15%), *O. annularis* (10.14%), *S. siderea* (3.30%), and *P. strigosa* (2.53%), representing a total of 57.18%. Relative abundance *D. labyrinthiformis* and *P. porites* decreased through seasons near to shore and increased farther from shore. The coral species *P. astreoides* and *O. annularis* had higher relative abundance at reef zones farther from shore.

Gorgonians had a higher relative abundance at PSO than BTA, with a mean of 11.87%, mainly composed by *Antilloporgia americana*, *Eunicea flexuosa*, *Gorgonia ventalina*, and *Plexaura homomalla* (Figure 3). In contrast, gorgonians at BTA represented a mean relative abundance of 5.08%. The species that showed patterns of increased relative abundance through time at PSO at both distance zones were *A. cervicornis*, *A. agaricites*, and the octocoral *P. homomalla*. The SIMPER analysis revealed that the species that mostly contributed to differentiate coral colony abundance between sites were *O. annularis* (7.45% contribution), *M. alcicornis* (6.41%), *P. strigosa* (4.86%), and *S. radians* (4.83%), with a total of 23.55%

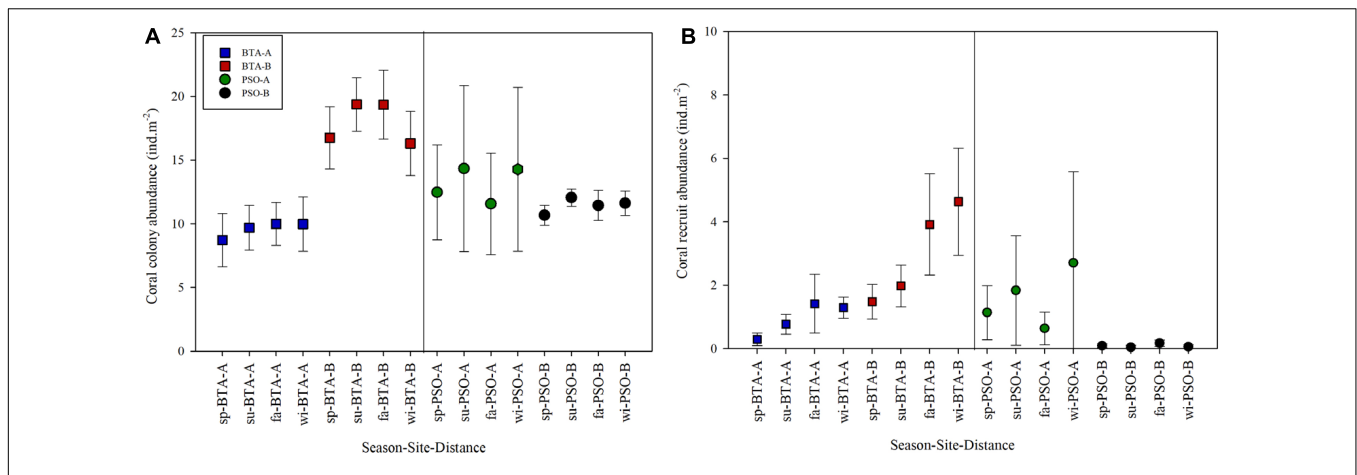
of the observed variation. Differences between distance zones were mostly attributed to *M. alcicornis* (7.31%), *P. porites* (5.82%), *P. astreoides* (5.44%), and *O. annularis* (4.92%), with a total of 23.49% of the observed variation. PCO analysis identified four major groups from the coral abundance structure that represent the interaction between sites and distance zones (Figure 4). The seasonal variation of coral community within distance zone A had higher similarity between BTA and PSO due to the proximity of both clusters. In contrast, the coral community at PSO distance zone B showed a major difference between sites and distances, with clusters farther apart. The proposed PCO explains 74% of the variation between and within groups.

Coral species richness (S) at BTA was highest at distance zone B with a mean of  $18.11 \pm 1.18$  ( $\pm$ CI 95%). Mean S decreased from spring to winter at both distance zones (Figure 5A). Overall, the highest total coral species richness between sites was recorded at PSO distance zone B with a mean of  $18.63 \pm 1.19$ . Species richness at PSO experienced seasonal variation along both distance zones (Figure 5B). Species richness showed significant differences by distance zones (Pseudo  $F = 1.37$ ,  $p = 0.0010$ ), but no difference was recorded between seasons (Pseudo  $F = 1.41$ ,  $p = 0.2300$ ), or sites (Pseudo  $F = 0.91$ ,  $p = 0.3300$ ).

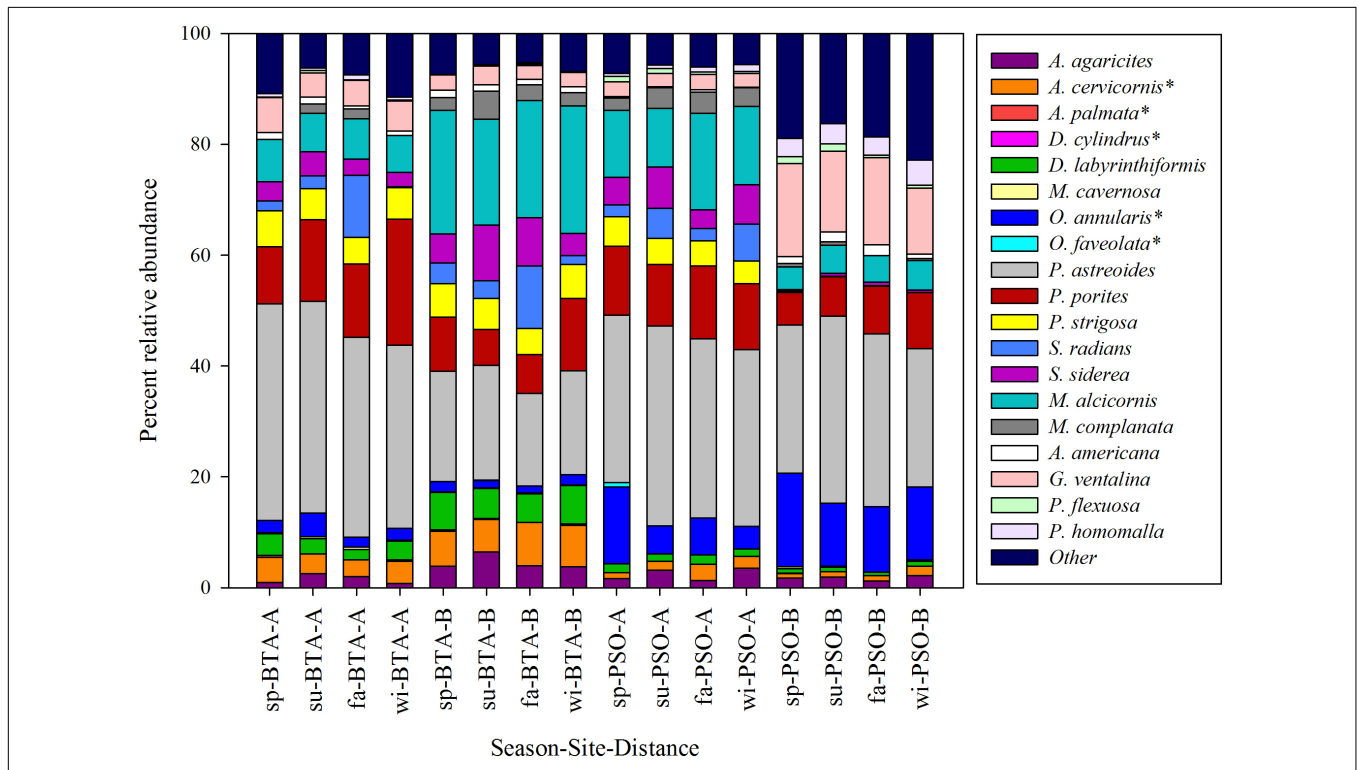
Coral species diversity ( $H'$ ) showed contrasting patterns by sites. In BTA,  $H'$  was higher farther from shore, with the highest values recorded during the summer with a mean of  $2.30 \pm 0.14$  (Figure 5C). At both distance zones,  $H'$  declined gradually from spring to winter season, representing a short-term percent change of -5.98%. The highest  $H'$  between sites was recorded at PSO farther from shore with a mean of  $2.27 \pm 0.07$ . At PSO,  $H'$  increased from spring to winter at both distance zones (Figure 5D). Coral diversity at both sites had lower values at shallower, near-to-shore areas. There were significant differences by distance zones (Pseudo  $F = 32.22$ ,  $p = 0.0010$ ), but no difference was recorded between seasons (Pseudo  $F = 0.44$ ,  $p = 0.7200$ ) or sites (Pseudo  $F = 0.04$ ,  $p = 0.8500$ ). The evenness ( $J'$ ) showed that BTA had a higher difference in species dominance between distance zones, with a higher evenness farther from shore (Figure 5E).  $J'$  at BTA showed a pattern of rapid decline at distance zone A through seasons, reflecting greater changes in species dominance.  $J'$  at PSO had similar patterns of increasing evenness across both distance zones through seasons (Figure 5F). There was a significant difference in  $J'$  by distance zones (Pseudo  $F = 12.24$ ,  $p = 0.0020$ ).

## Coral Recruit Abundance

Coral recruit community structure showed statistically significant differences among seasons (Pseudo  $F = 2.72$ ,  $p = 0.0030$ ), site (Pseudo  $F = 23.30$ ,  $p = 0.0001$ ), and distance (Pseudo  $F = 8.00$ ,  $p = 0.0001$ ) (Table 1). There were also significant differences between the interactions of site and distance (Pseudo  $F = 11.29$ ,  $p = 0.0001$ ). Coral recruit abundance was higher in BTA at areas farther from shore with a mean of  $1.96 \pm 0.46 \text{ m}^{-2}$ . Mean coral recruit abundance at BTA increased from  $0.88 \text{ m}^{-2}$  in spring to  $2.96 \text{ m}^{-2}$  in winter. Coral recruit abundance near to shore increased from 0.28 (spring) to  $1.28 \text{ m}^{-2}$  (winter), while farther from shore increased from 1.47 to  $4.63 \text{ m}^{-2}$  (Figure 2). In contrast, at PSO, coral recruit abundance was higher on reef



**FIGURE 2 |** Mean coral colony abundance (mean ± 95% CI) **(A)** and coral recruit abundance **(B)** by season, site, and distance zone. Coral abundance includes hard corals, hydrozoans and gorgonians. Blue and red squares represent Bahía Tamarindo (BTA); green and black circles represent Punta Soldado (PSO). Seasons are defined as: sp, spring; su, summer; fa, fall; wi, winter.

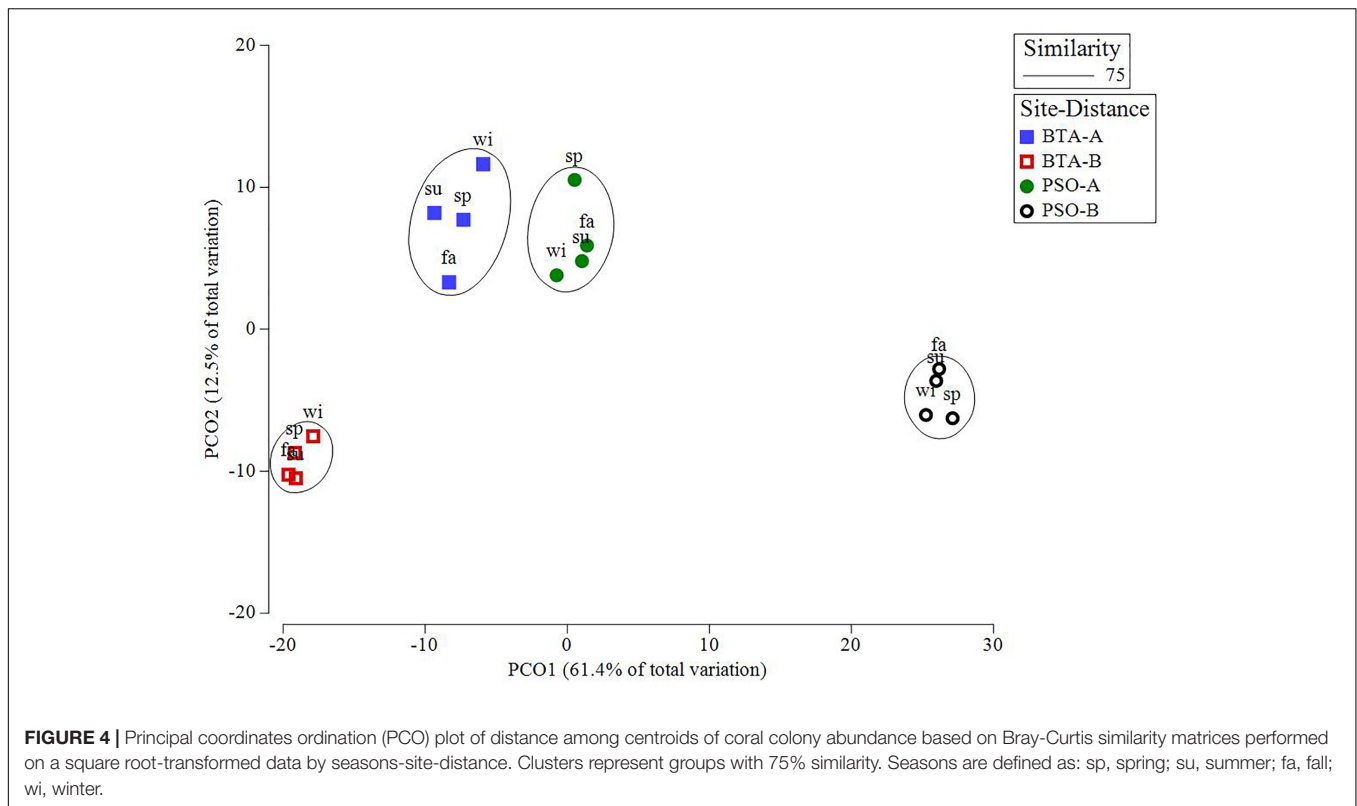


**FIGURE 3 |** Percent relative abundance of scleractinians, octocorals and octocoral species by season, site and distance zones. Colors represent coral species and asterisk identifies coral species listed as threatened under the Endangered Species Act (Federal Register, 2014). Seasons are defined as: sp, spring; su, summer; fa, fall; wi, winter.

areas closer to shore. Mean recruit abundance increased from 0.60 m<sup>-2</sup> in spring to 1.38 m<sup>-2</sup> in winter. Recruit abundance near to shore increased from 1.13 to 2.7 m<sup>-2</sup> and farther from shore decreased gradually from 0.08 to 0.05 m<sup>-2</sup>. A total of 11 coral species recruited at both study sites and the species with highest percentage relative abundance were *Siderastrea radians* (45.1%), *S. siderea* (23.1%), and followed by *P. astreoides* (19.2%)

(Table 2). No coral recruits of large reef-building coral species were documented at BTA through the study period.

PCO analysis identified two major groups which distinguished different coral recruit abundance patterns of PSO distance zone B from zone A, and from BTA among all seasons (Figure 6). There was also one outlier event identified for PSO zone B during the summer season, particularly due to a



significant reduction recorded with a mean recruit abundance of  $0.4 \text{ m}^{-2}$ . However, SIMPROF analysis only identified two distinct groups for coral recruit abundance. The calculated PCO explains 83.2% of the total variation. Also, SIMPER analysis showed the three species that contributed to explain 79% of the differences of coral recruit abundance patterns between sites were *S. radians* (32.41% individual contribution), *P. astreoides* (23.93%), and *S. siderea* (22.42%). The species that contributed to explain 73% of the differences between distance zones were *P. astreoides* (27.83%), *S. siderea* (24.42%), and *S. radians* (21.21%). The average dissimilarity was 49.69 between sites and 61.01 between distance zones.

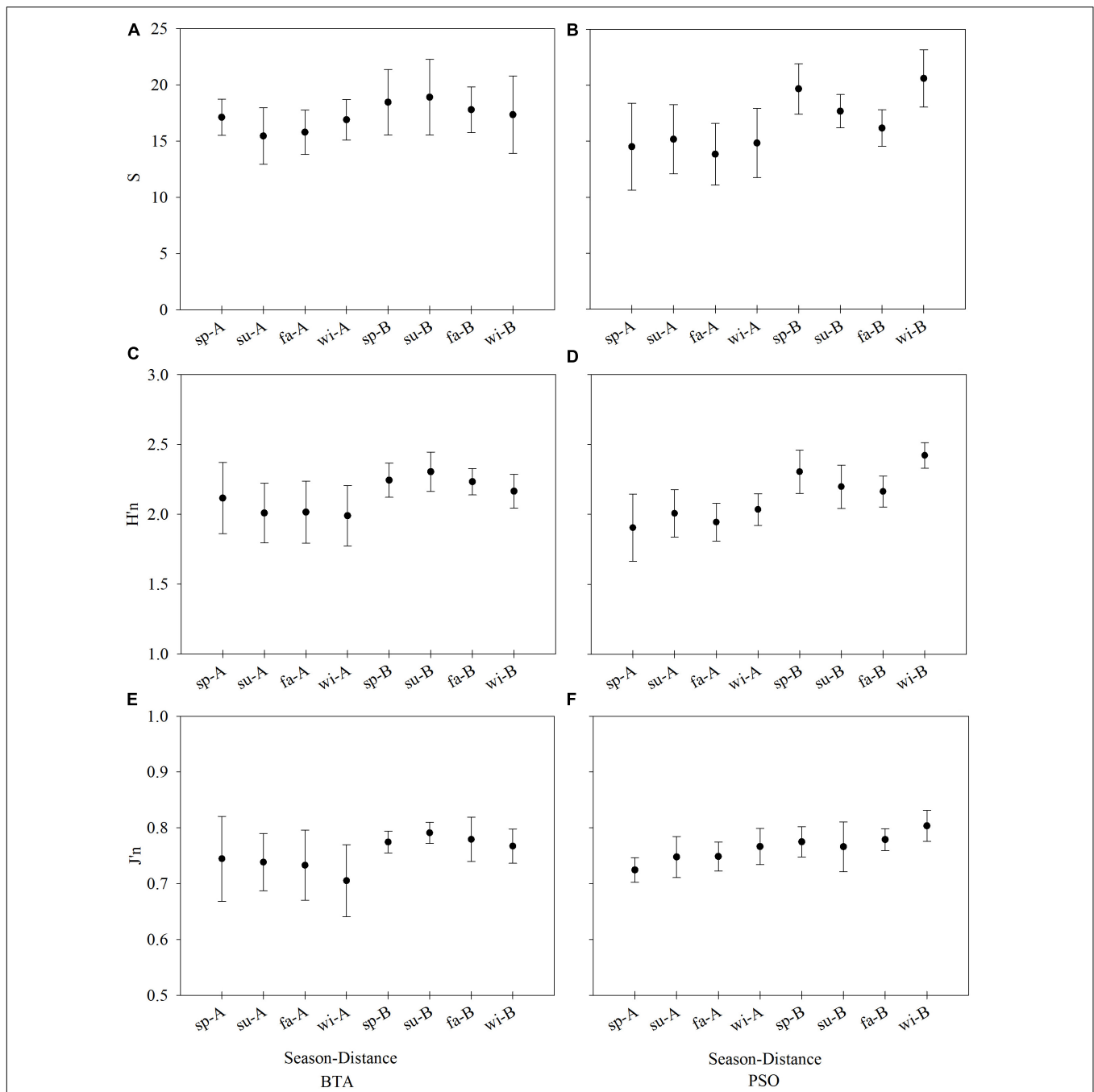
## Benthic Components Percent Cover and Community Structure

Live coral cover was significantly higher on BTA zone B with a mean percent cover of  $17.87 \pm 0.67\%$ , and a gradual reduction was recorded in a short-term period (Figure 7A). Percent coral cover at zone A, near to shore, remained relatively stable through seasons. Coral cover at PSO had the lowest percentage cover farther from shore with a mean of 7.84% and it slightly decreased through time at both distance zones. Percentage coral cover was significantly different between sites (Pseudo  $F = 25.26$ ,  $p = 0.0010$ ), distance (Pseudo  $F = 13.77$ ,  $p = 0.0010$ ), and the interaction site by distance (Pseudo  $F = 18.82$ ,  $p = 0.001$ ) (Table 3).

Stress-tolerant coral species, *P. astreoides* and *P. porites*, had higher percent relative cover in BTA zone A than distance zone

B, and PSO, with a mean of 4.28 and 2.71%, respectively. The hydrocoral *M. alcicornis* had a higher percent cover farther from shore (Figure 8). Percentage cover of *A. cervicornis* was higher in distance zone B with a mean cover of 1.95% and increased from spring 1.56% to winter 2.35%. In PSO, the species with higher percentage cover near to shore was *P. astreoides* with a mean of 2.51% and *O. annularis* farther from shore with a mean of 3.63%. The similarity percentage (SIMPER) analysis revealed that 8 species constituted 75% of the observed variations in percent coral cover between sites and distance zones. The species that had major contributions to variations between sites and distance zones were *M. alcicornis*, *O. annularis*, *P. porites*, and *A. cervicornis*. There was an average dissimilarity between sites of 57.11 and 49.85% between distances zones.

Octocorals mostly dominated benthic cover at PSO farther from shore with a mean of 8.10% (Figure 7B). The octocoral cover near to shore had similar patterns at PSO and BTA with an overall mean cover of 1.80%. Sponges had higher percentage cover at BTA with a mean of 5.77%. Sponges had a pattern of increasing percentage cover at areas farther from shore, reaching benthic cover of up to 12% during the fall and winter season (Figure 7C). The gray encrusting and invading sponge species *Dictyonella funicularis* had a significant contribution at BTA farther from shore, with an increasing benthic cover from spring (0.02%) to fall (7.81%). This species was documented overgrowing dead or diseased *A. cervicornis* colonies, among other benthic components. In contrast, *D. funicularis* had higher percent cover at PSO closer to shore, reef area that experienced an increase in sponge cover from spring to winter.



**FIGURE 5 |** Coral species richness (S, **A,B**), diversity index (H'n, **C,D**) and evenness (J'n, **E,F**) by site, season, and distance zones (mean ± 95% CI). Left column graphs represent Bahía Tamarindo (BTA) and right column Punta Soldado (PSO). Seasons are defined as: sp, spring; su, summer; fa, fall; wi, winter.

Octocoral and sponge cover showed a significant difference among seasons, sites, and distance zones ( $p < 0.05$ ) (**Table 3**). Sponge community also had a significant interaction between site and distance ( $p < 0.05$ ).

Macroalgae and algal turf were important components of the community composition. Macroalgal assemblages had significant differences among season, sites, distance and the interaction site by distance ( $p < 0.05$ ) (**Table 3**). Higher percent macroalgae cover

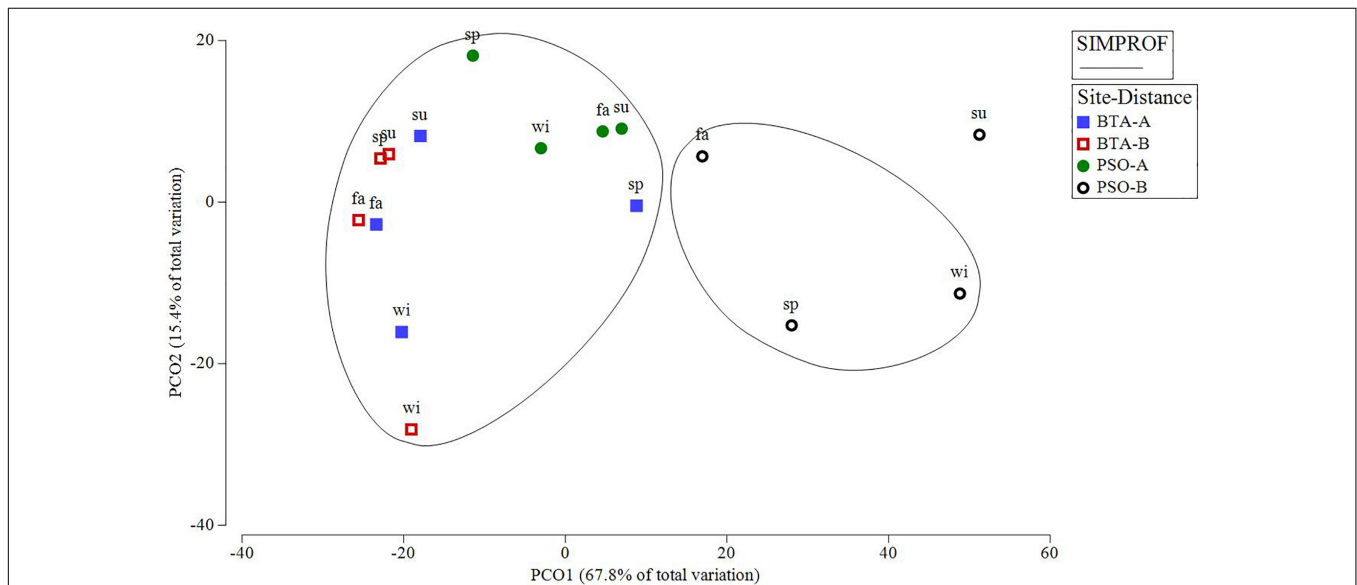
was recorded at PSO, especially at areas farther from shore, where it reached up to 35% (**Figure 9A**). Macroalgae dominance at PSO occurred while the encrusting and invasive red algae *Ramicrosta textilis* overgrew dead skeletons of the *O. annularis* species complex. Reef zones adjacent to the shoreline were dominated by *Dictyota* spp. algae, which reached its highest cover at BTA with 14%. Algae composition at BTA also had a high dominance of turf, which constituted a mean cover of 37.51%, and it was



**TABLE 2** | Results of permutational analysis of variance (PERMANOVA) for benthic components by factors.

Factors	df	Coral		Octocoral		Sponge		Macroalgae		Benthic community structure	
		Pseudo F	P	Pseudo F	P	Pseudo F	P	Pseudo F	P	Pseudo F	P
Season	3	0.59	0.9102	2.24	<b>0.0011</b>	1.53	<b>0.0396</b>	2.69	<b>0.006</b>	1.96	<b>0.0021</b>
Site	1	25.26	<b>0.0001</b>	10.43	<b>0.0001</b>	9.68	<b>0.0001</b>	20.26	<b>0.0001</b>	21.00	<b>0.0001</b>
Distance	1	6.91	<b>0.0001</b>	6.50	<b>0.0001</b>	7.33	<b>0.0001</b>	6.85	<b>0.0007</b>	13.77	<b>0.0001</b>
Se × Si	3	0.76	0.7444	1.03	0.4286	1.02	0.4317	1.27	0.2553	1.95	<b>0.0019</b>
Se × Di	3	0.28	0.9978	0.72	0.8342	1.04	0.3902	1.82	<b>0.0707</b>	0.65	0.9416
Si × Di	1	16.88	<b>0.0001</b>	5.54	<b>0.0001</b>	9.49	<b>0.0001</b>	12.14	<b>0.0001</b>	18.82	<b>0.0001</b>
Se × Si × Di	3	0.68	0.8337	0.68	0.8712	1.80	<b>0.0048</b>	2.54	<b>0.0091</b>	1.84	<b>0.0048</b>

Bold p-values represent significance.



**FIGURE 6** | PCO plot of distance among centroids of coral recruit abundance based on Bray-Curtis similarity matrices performed on square root-transformed data by seasons-site-distance clusters. Clusters represent significant SIMPROF groups (~75% similarity within groups). This model explained 83.2% of the observed spatio-temporal variation in coral recruit abundance by site and distance zone. Blue and red squares represent Bahía Tamarindo (BTA); green and black represent Punta Soldado (PSO). Seasons are defined as: sp, spring; su, summer; fa, fall; wi, winter.

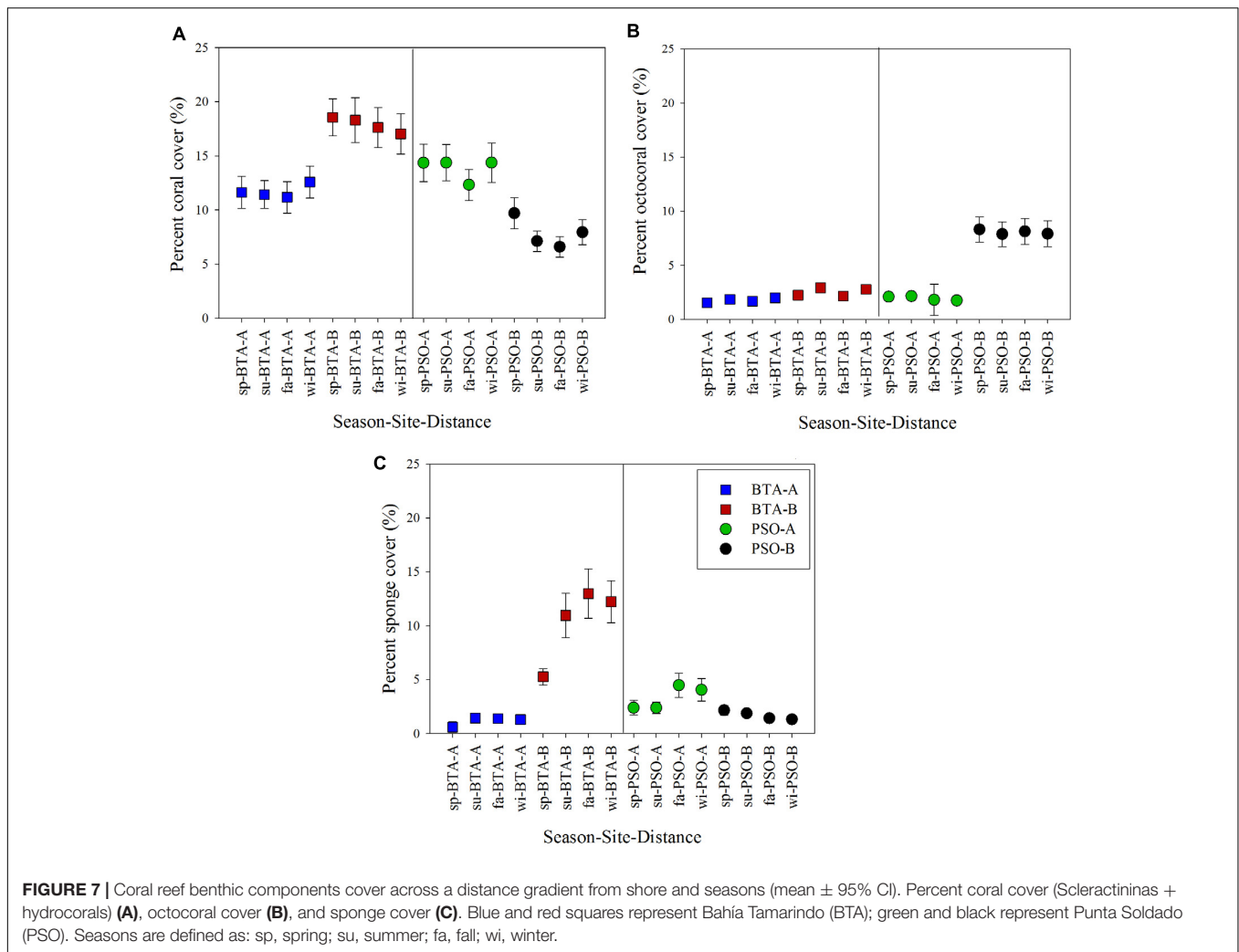
significantly higher at zone A with its highest level recorded during the fall season of 51.67% (Figure 9B). Meanwhile, on distance zone B, the most prominent algae cover were turf and crustose coralline algae (CCA), *Porolithon* spp., since these constituted a mean cover of 28.66 and 9.53%, respectively. The percentage cover of CCA at BTA farther from shore increased through seasons (Figure 9C). Cyanobacterial cover also had an important influence on BTA zone B with increased percentage cover from spring (3.91%) to summer (6.99%) (Figure 9D).

Coral reef benthic community structure presented a statistically significant difference among seasons (Pseudo  $F = 1.96$ ,  $p = 0.0020$ ), sites (Pseudo  $F = 21.00$ ,  $p = 0.0010$ ), distance (Pseudo  $F = 13.07$ ,  $p = 0.0010$ ), and within the interactions season by site (Pseudo  $F = 1.95$ ,  $p = 0.0070$ ), and site by distance (Pseudo  $F = 18.82$ ,  $p = 0.0010$ ) (Table 3). All of the benthic components analyzed in this study showed significant differences in the interaction of site by distance. The PCO analysis identified four major groups

that distinguished benthic community structure between sites and distance zone (Figure 10). Benthic communities were similar between sites at areas near to shore and greater differences between benthic communities were identified farther from shore.

### Benthic Community Structure and Environmental Variables

Among the environmental variables assessed, coral colony abundance had a significant negative correlation with sand (>63 μm) (RELATE,  $Rho = 0.475$ ,  $p = 0.002$ ), silt-clay (<63 μm) ( $Rho = 0.422$ ,  $p = 0.003$ ), carbonate ( $Rho = 0.263$ ,  $p = 0.026$ ), and terrigenous sediment content ( $Rho = 0.328$ ,  $p = 0.009$ ) (Table 3). Coral colony abundance had a significant positive interaction with depth ( $Rho = 0.858$ ,  $p = 0.037$ ) at BTA and a negative interaction at PSO. The nMDS bubble plot showed that sand and terrigenous sediment had a significant negative association with spatial configuration of coral colony abundance at BTA,



while silt-clay had a negative significant association with coral colony abundance at PSO reef (Appendix 1). These patterns suggest that sediment texture differed significantly between sites (PERMANOVA, Pseudo  $F = 31.26$ ,  $p = 0.001$ ) and for the interaction site by distance from shore (Pseudo  $F = 5.52$ ,  $p = 0.030$ ). Multiple linear regressions analyses (visualized in dbDRA diagram) identified sand sediment particle distribution ( $r^2 = 0.33$ ,  $p = 0.0007$ ) as the most significant environmental variable that explained 49% of the total spatial and temporal variation of coral abundance at nearshore reefs (Figure 11A).

Coral recruit abundance had a strongly significant negative relationship with sand (RELATE, Rho = 0.225,  $p = 0.017$ ) silt-clay (Rho = 0.24,  $p = 0.021$ ), and depth (Rho = 0.715,  $p = 0.032$ ) (Table 3). Multiple linear regression analysis showed that silt-clay ( $r^2 = 0.18$ ,  $p = 0.020$ ) had a significant association with coral recruit spatial and temporal array. Furthermore, coral recruit abundance also had a strongly significant relationship with wave height ( $r^2 = 0.52$ ,  $p = 0.0270$ ) and depth ( $r^2 = 0.45$ ,  $p = 0.0250$ ) for season by site interaction (Figure 10B). Vectors superimposed showed that coral recruit abundance was mostly influenced by silt-clay (<63  $\mu\text{m}$ ) and depth at PSO, where higher recruit

abundance was documented at shallower areas closer to shore (Figure 11B). On the other hand, wave height had a stronger correlation to recruit abundance at BTA during the winter season, combined to a lesser extent with total precipitation. These environmental associations explain 87% of the total variation for coral recruit abundance. During the study period, peak SST reached up to 30°C, representing an anomaly of +1.35°C in relation to the mean monthly maximum, and might have also contributed to negatively impact coral abundance through undetected coral tissue loss, as coral decline followed high SST episodes. No bleaching was observed during the study period. However, there was no significant relationship between coral recruit abundance and SST ( $r^2 = 0.71$ ,  $p = 0.37$ ).

The non-parametric correlation BEST BIOENV (Spearman rank) analyses identified two groups of sediment variables that best correlated with coral reef benthic components, composed of sand and carbonate (Rho = 0.42), and sand, organic matter, carbonate, and terrigenous sediment (Rho = 0.412). Changes in percentage coral cover through the study period, 2014 to 2015, correlated with the variation of sand, silt-clay, carbonate, and terrigenous sediment content ( $p < 0.05$ ) (Table 4). Based on our

**TABLE 3** | Summary of RELATE (spearman rank) correlation matrix for coral colony abundance, coral recruit abundance and environmental variables.

	Coral colony abundance	Coral recruit abundance
<b>Season-site-distance</b>		
Sedimentation rate	Rho = 0.031, $p = 0.3280$	Rho = -0.127, $p = 0.7636$
Terrigenous rate	Rho = 0.029, $p = 0.3477$	Rho = -0.070, $p = 0.5928$
Sand	Rho = 0.475, $p = \mathbf{0.0030}$	Rho = 0.225, $p = \mathbf{0.0278}$
Silt-clay	Rho = 0.422, $p = \mathbf{0.0013}$	Rho = 0.240, $p = \mathbf{0.0167}$
Organic matter	Rho = 0.041, $p = 0.2951$	Rho = 0.028, $p = 0.3836$
Carbonate	Rho = 0.263, $p = \mathbf{0.0263}$	Rho = -0.002, $p = 0.4329$
Terrigenous	Rho = 0.328, $p = \mathbf{0.0072}$	Rho = 0.056, $p = 0.2947$
<b>Site-distance</b>		
Sedimentation rate	Rho = -0.086, $p = 0.4950$	Rho = -0.143, $p = 0.6567$
Terrigenous rate	Rho = -0.086, $p = 0.5018$	Rho = -0.143, $p = 0.6714$
Sand	Rho = 0.143, $p = 0.3750$	Rho = -0.029, $p = 0.5023$
Silt-clay	Rho = 0.143, $p = 0.3729$	Rho = -0.029, $p = 0.5001$
Organic matter	Rho = 0.086, $p = 0.4156$	Rho = -0.429, $p = 0.7887$
Carbonate	Rho = 0.543, $p = 0.0834$	Rho = 0.371, $p = 0.2497$
Terrigenous	Rho = 0.086, $p = 0.3767$	Rho = -0.143, $p = 0.6645$
<b>Season-site</b>		
Total precipitation	Rho = -0.157, $p = 0.7964$	Rho = -0.114, $p = 0.7149$
Wind speed	Rho = -0.253, $p = 0.9546$	Rho = -0.249, $p = 0.8867$
Wave height	Rho = -0.278, $p = 0.9659$	Rho = 0.266, $p = 0.1065$
SST	Rho = -0.180, $p = 0.8541$	Rho = -0.192, $p = 0.8831$
SST max	Rho = -0.232, $p = 0.9459$	Rho = 0.026, $p = 0.4539$
SST min	Rho = -0.241, $p = 0.9573$	Rho = 0.181, $p = 0.2380$
Depth	Rho = 0.858, $p = \mathbf{0.0322}$	Rho = 0.715, $p = \mathbf{0.0275}$

Averaged by season, site, distance, site by distance, and season by site. Bold  $p$ -values represent significance.

temporal and spatial analysis, there was a significant negative relationship between coral and macroalgal cover ( $r^2 = 0.70$ ,  $p < 0.0001$ ). A similar pattern was documented between coral and octocoral cover ( $r^2 = 0.462$ ,  $p = 0.003$ ). Spatial and temporal variations of macroalgal cover had a significant relationship with most of the sediment variables ( $p < 0.05$ ), except organic matter (Table 4). Depth gradient across the reefs was correlated with macroalgal cover between seasons by site (Rho = 0.71,  $p = 0.036$ ).

Sponge cover variation at nearshore reefs had a strong correlation with most of the sediment characteristics assessed, including sedimentation rate (Rho = 0.433,  $p = 0.002$ ) and terrigenous rate (Rho = 0.371,  $p = 0.0001$ ) (Table 4). Crustose coralline algae had similar correlations and had significant relationships to sedimentation rate (Rho = 0.256,  $p = 0.042$ ), terrigenous rate (Rho = 0.295,  $p = 0.042$ ), among other sediment dynamics, and depth ( $p < 0.05$ ) (Table 3). Increased cyanobacteria cover, especially at BTA farther from shore, correlated with increased organic matter content (Rho = 0.262,  $p = 0.012$ ) for the interaction site by distance from shore.

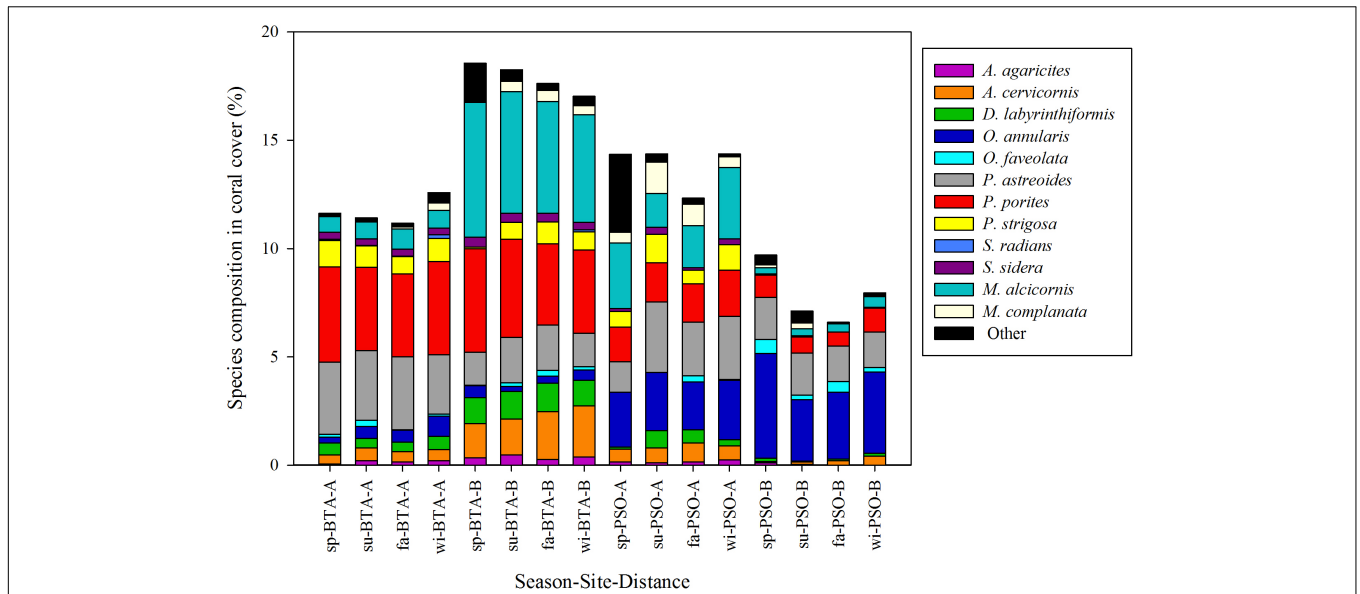
## DISCUSSION

Near-shore coral reefs are experiencing rapid and significant spatial and temporal ecological changes in apparent response to human-induced degradation of coastal watersheds and

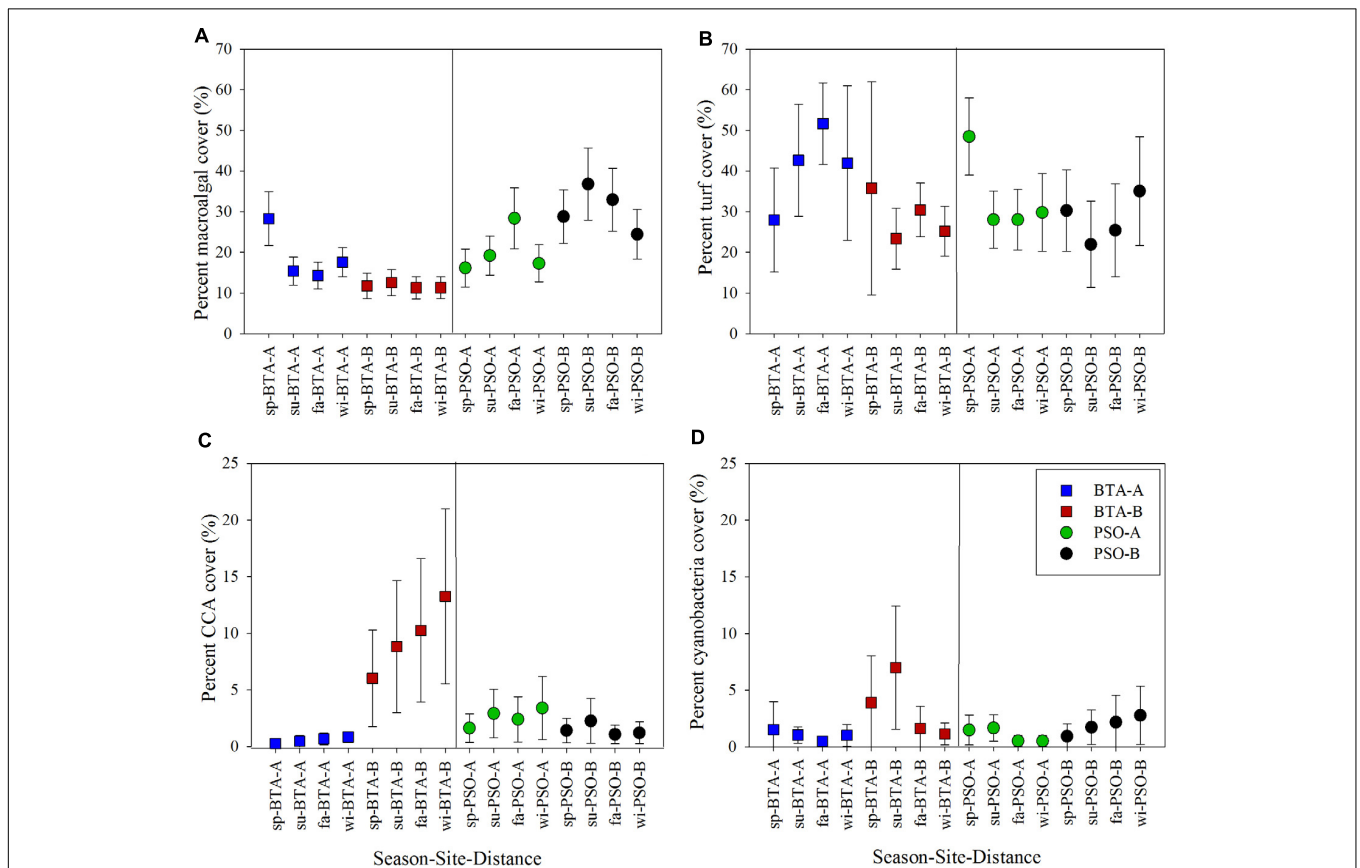
interconnected coastal and marine habitats. In the context of current and forecasted climate change trends, such influences become increasingly significant. This study was primarily correlational and does not prove cause and effect. However, in the absence of other major disturbances during the study period of time (i.e., bleaching, disease outbreaks, hurricanes), documented land-based sediment pulses may have been one of the most important factors causing damaging effects on corals. Documented spatio-temporal patterns of coral reef benthic community structure near shore (<120 m from shore) had associations with sedimentation dynamics and interacting hydrodynamic forces. Sediment characteristics had an important role shaping benthic communities across a distance gradient from shore were sediment texture, categorized as silt-clay (<63  $\mu\text{m}$ ) and sand (>63  $\mu\text{m}$ ), and terrigenous sediments content (Tables 3, 4). Results from this study suggest that significant spatio-temporal differences at near-shore coral reefs were associated with changing environmental conditions, in combination with increasing influences of coastal hydrodynamics.

Coral colony abundance in this study showed significant spatial and temporal differences and it was significantly associated with sand distribution patterns. Abundance decline during fall and winter seasons was related to the occurrence of extreme and acute weather events caused by a tropical trough and tropical storms that impacted the northern Caribbean region from August to November 2014. These atmospheric events produced the combined effect of sediment-laden runoff from disturbed coastal watersheds and increased wave action on shallow reefs (Otaño-Cruz et al., 2017). Coral reef benthic community structure and its ecological response is not only associated with variation in land-derived sediment input and distribution dynamics but is also related to bathymetry, as well as changes in local weather and oceanographic conditions. Weather and oceanographic dynamics that influence wave height and energy are the main drivers of sand sediment resuspension and transport (Hernández-Cruz et al., 2009; Field et al., 2011; Edmunds and Gray, 2014).

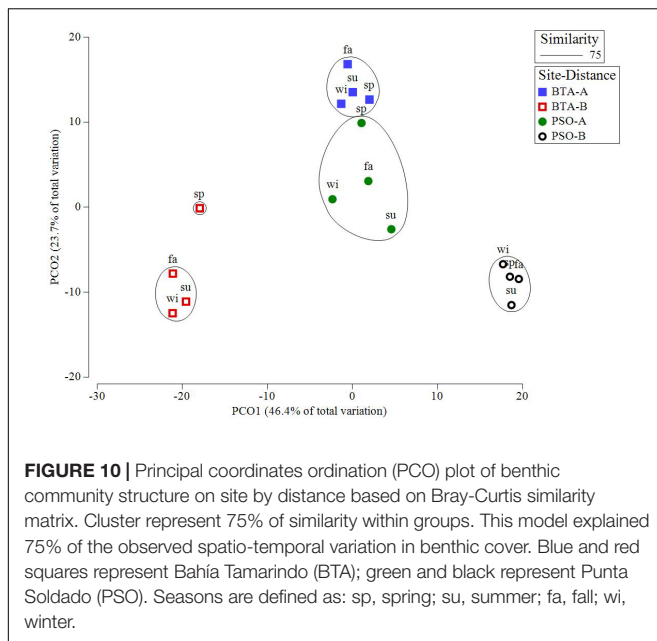
Coral species richness and diversity declined in a short-term period, especially at areas subjected to recurrent runoff and sedimentation stress. Further, seasonal variation was observed in multiple parameters, which also fluctuated between sites and distance zones, suggesting combined effects of natural seasonal variability at the studied spatial scales and terrestrial influences associated with changing land use and human-influenced runoff pulse dynamics. The scleractinian species recorded in BTA and PSO shallow reefs approximately represent two-thirds of the total number of species known for the northeastern region of Puerto Rico (Hernández-Delgado, 2000). The most conspicuous species at reef areas under continual sediment stress were *P. astreoides* and *P. porites*. The *Porites* spp. complex and the *Siderastrea* spp. complex have been recognized as species with high tolerance to sediment due to their ability to effectively reject particles, and they are becoming more abundant on shallow reefs throughout the Caribbean (Loya, 1976; Cortés and Risk, 1985; Torres and Morelock, 2002; Green et al., 2008; Ennis et al., 2016). Other common coral species at both study sites were *A. cervicornis*,



**FIGURE 8 |** Percent species composition of Scleractinian and hydrocoral species. Most dominant species among site, distance zone and seasons identified by colors. Seasons are defined as: sp, spring; su, summer; fa, fall; wi, winter.



**FIGURE 9 |** Coral reef benthic components cover across a distance gradient from shore, site, and seasons (mean  $\pm$  95% CI). Percent macroalgal cover (A), turf (B), crustose coralline algae (CCA) (C), and cyanobacteria cover (D). Blue and red squares represent Bahía Tamarindo (BTA); green and black represent Punta Soldado (PSO). Seasons are defined as: sp, spring; su, summer; fa, fall; wi, winter.



*D. labyrinthiformis*, and *O. annularis*, abundant at reef zones less subjected to sedimentation stress (Figure 3). Transplanting, that was conducted prior to the initiation of this research, produced a high abundance of *Acropora* spp. across the study sites, showing that these species successfully established in areas less exposed to waves and land-based anthropogenic stress (Figures 3, 8).

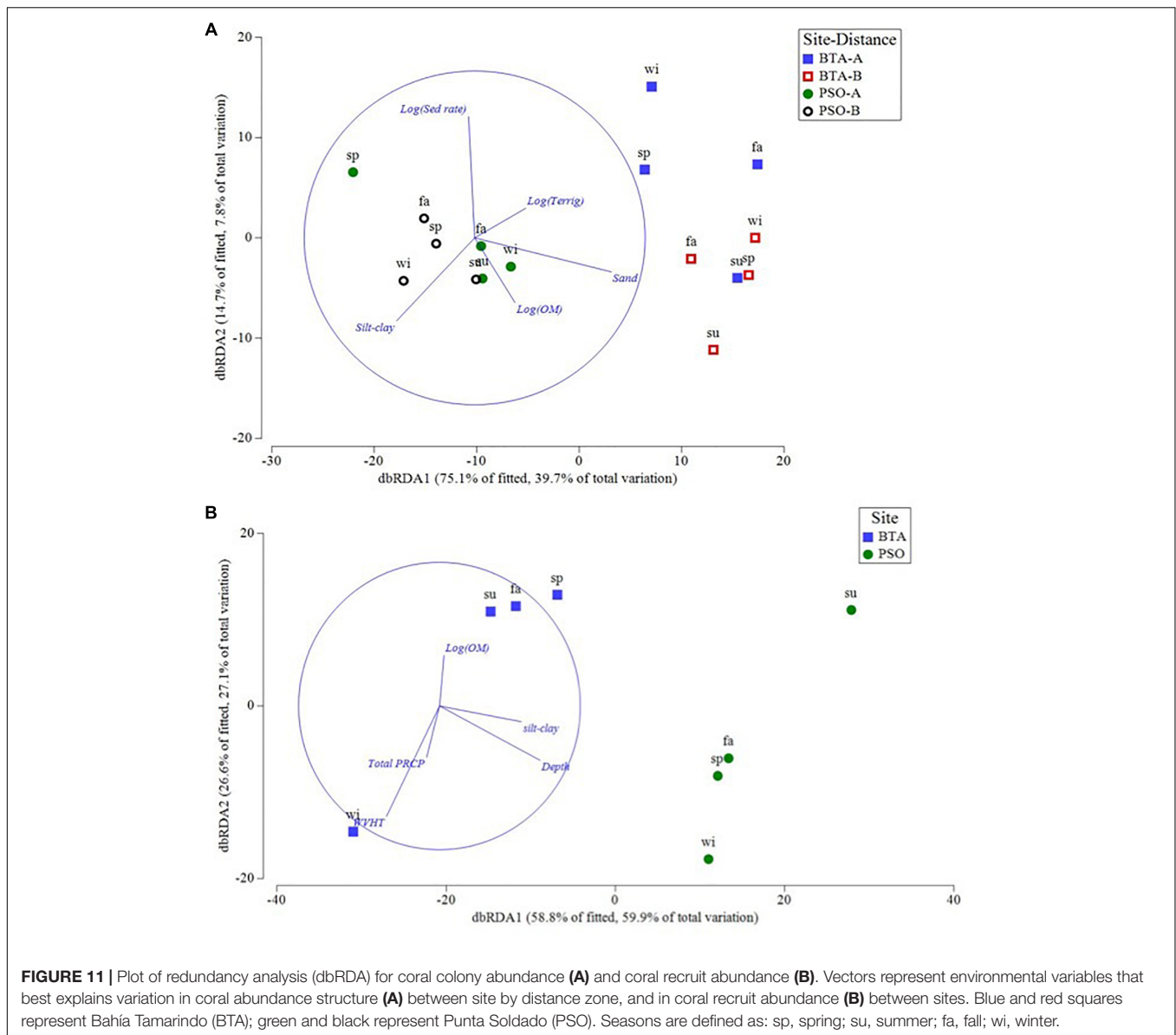
Rare and sensitive coral species have disappeared from locations affected by chronic sedimentation regimes across northeastern Puerto Rico (Hernández-Delgado, 2000). Over the last few decades, multiple Caribbean coral reefs have shown similar trends of declining coral diversity and coral abundance at sites impacted by recurrent pulses of sedimentation and LBSP (Loya, 1976; Cortés and Risk, 1985; Pastorok and Bilyard, 1985; Acevedo et al., 1989; Ennis et al., 2016). LBSP effects on coral reefs do not always reflect a discrete spatial gradient from shore since it mostly depends on the characteristics of marine sediment deposited across the reef (Pastorok and Bilyard, 1985) and on the ecosystem capability to process and adapt to sediment, organic matter and nutrient influxes (Lirman and Fong, 2007; Olds et al., 2018). Such changes might have adverse long-term repercussions due to reduced reef accretion and increased vulnerability to future and extreme climate scenarios (Knowlton, 2001; Edmunds, 2010; Hoegh-Guldberg et al., 2014). Degradation of the reef's structural complexity could further affect social-ecological services provided to coastal communities, including sustaining fish assemblages (Alvarez-Filip et al., 2009; Graham and Nash, 2013; Newman et al., 2015).

Coral recruit abundance of stress-tolerant species, such as *S. radians*, *S. siderea*, and *P. astreoides*, have become dominant in this study, as in many other locations in Puerto Rico. The increasing dominance of brooder species recruits has also been documented across the wider Caribbean (Lirman and Fong, 2007; Green et al., 2008; Edmunds, 2010; Hernández-Delgado et al., 2014a), which could be, not only the result of local environmental

changes, but also the result of large-scale phenomena, such as climate change. This trend might be responsible for the overall shift in species composition as community trajectory is skewed toward ephemeral, fast growing, and stress-tolerant species. Under such regime, coral reefs experience a multiplicity of threats and recurrent changes in environmental conditions, thus limiting the success of reef-building species recruit settlement, such as *O. annularis* and *Acropora* spp. (Hernández-Delgado, 2000; Van Woesik and Jordán-Garza, 2011). In PSO reef, coral recruit abundance declined on the reef zone farthest from shore (> 60 m) and it had a significant relationship with increased the proportion of silt-clay sediment deposition after an extensive deforestation event that disturbed the adjacent coastal watershed. Increased sediment influx and distribution of fine sediments through PSO reef was documented after strong precipitation events that were followed by wind-induced waves and currents that transported fine, land-based sediments until they were deposited in calmer waters (Otaño-Cruz et al., 2017). The effects of cold front events, characteristic of the winter season across the northern Caribbean, can produce strong long-period swells and a significant increase in sedimentation rate by both sediment bedload transport and resuspension (Otaño-Cruz et al., 2017). Previous studies have shown similar patterns of reduced or inhibited recruitment under sediment stress (Pastorok and Bilyard, 1985; Edmunds and Gray, 2014).

Other factors that affect coral recruit abundance are thermal stress (Edmunds, 2004; Van Woesik and Jordán-Garza, 2011), out-competition by fast-growing macroalgae (Nugues et al., 2004), and cyanobacteria (Fong and Paul, 2014). Algal dominance can inhibit coral larval settlement, predominantly when combined with deposited sediments, disturbing long-term coral reef resilience and their ability to recover after disturbance (Birrell et al., 2005; Kuffner et al., 2006; Vermij, 2006; Fong and Paul, 2014; Stubler et al., 2016). Extreme precipitation events have also been identified as a key factor that can trigger land-derived sediment pulses and distribution along near-shore coral reefs (Otaño-Cruz et al., 2017). Increased frequency of extreme rainfall events can have deleterious impacts on local coral populations and on nearshore coral rehabilitation efforts (Hernández-Delgado et al., 2014b). This combination of factors operating at multiple temporal and spatial scales can interact as long-term drivers of coral reef species composition change and should be further addressed.

Trends of live coral cover decline worldwide have often been associated with synergistic and complex local and regional chronic factors (i.e., disease, sedimentation, LBSP, increasing SST). Their combined effects with natural stochastic factors (i.e., hurricanes) have resulted in the long-term loss of primary reef-building species (i.e., *O. annularis* complex) and in shifts in species composition through the last few decades (Pandolfi et al., 2003; Rogers and Miller, 2006; Knowlton and Jackson, 2008; Miller et al., 2009; Hernández-Pacheco et al., 2011). Although the primary cause of coral decline in the Caribbean has been coral disease (Aronson and Precht, 2001a,b; Weil and Rogers, 2011), terrestrial sediment input is one of the main threats to near-shore coral reefs (Ogston et al., 2004; Hernández-Cruz et al., 2009; Ennis et al., 2016; Otaño-Cruz et al., 2017). Documented



differences in percentage coral cover near shore were mostly associated with local sedimentation dynamics, principally with sand and silt-clay sediment distribution patterns. Coral cover decline at reef areas subjected to higher terrigenous sediment accumulation suggests an important relationship between coral reef health and changes in coastal watershed management, weather and local oceanographic dynamics. Documented mean live coral cover of 12.82% positions Culebra Island nearshore reefs below mean coral cover reported for the Caribbean region of 16.80% (Jackson et al., 2014), though this study was limited to shallow fringing reef systems which are often characterized by lower mean percentage live coral cover. However, the observed inverse relationship between live coral and macroalgal cover at nearshore reefs is a strong ecological indicator of degraded water quality conditions resulting from runoff pulse events and other land-derived stressors. Results from this

study validate previous studies conducted across the Caribbean region that have recognized that increased human activities and unsustainable development along coastal watersheds can have major negative consequences on live coral cover and coral reef benthic community structure (Acevedo et al., 1989; Fabricius, 2005; Smith et al., 2008; Risk and Edinger, 2011; Bégin et al., 2013; Oleson et al., 2018).

Sediment accumulation on coral surfaces, especially fine sediments, can produce significant adverse physiological responses as a consequence of energy relocation, required to achieve rejection of sediment particles through the production of mucus and ciliary action (Acevedo et al., 1989; Telesnicki and Goldberg, 1995; Woolfe and Lacombe, 1999; Fabricius, 2011). Coral abilities differ between species and coral morphologies, with branching, meandering, and large coral colonies being more tolerant to sediment accumulation (Rogers, 1990;

**TABLE 4 |** Relate (Spearman rank) correlation of benthic components and environmental variables.

Variables	Coral cover	Octocoral	Sponge	Macroalgae	Turf	CCA	Cyanobacteria
<b>Season-site-distance</b>							
Sedimentation rate	Rho = -0.063 $\rho = 0.6698$	Rho = -0.093 $\rho = 0.8067$	Rho = 0.433 $\rho = \mathbf{0.0011}$	Rho = 0.001 $\rho = 0.4821$	Rho = 0.077 $\rho = 0.2319$	Rho = 0.256 $\rho = \mathbf{0.0406}$	Rho = 0.156 $\rho = 0.1038$
Terrigenous rate	Rho = -0.073 $\rho = 0.6801$	Rho = -0.060 $\rho = 0.6763$	Rho = 0.371 $\rho = \mathbf{0.0015}$	Rho = 0.021 $\rho = 0.4340$	Rho = 0.026 $\rho = 0.3702$	Rho = 0.295 $\rho = 0.0380$	Rho = 0.173 $\rho = 0.0862$
Sand	Rho = 0.380 $\rho = \mathbf{0.0014}$	Rho = 0.290 $\rho = \mathbf{0.0069}$	Rho = 0.469 $\rho = \mathbf{0.0003}$	Rho = 0.308 $\rho = 0.0044$	Rho = 0.086 $\rho = 0.1657$	Rho = 0.285 $\rho = 0.0104$	Rho = 0.038 $\rho = 0.2999$
Silt-clay	Rho = 0.293 $\rho = 0.0075$	Rho = -0.264 $\rho = 0.0116$	Rho = 0.421 $\rho = 0.0003$	Rho = 0.260 $\rho = \mathbf{0.0122}$	Rho = 0.082 $\rho = 0.1771$	Rho = 0.241 $\rho = \mathbf{0.0194}$	Rho = 0.002 $\rho = 0.4416$
Organic matter	Rho = 0.096 $\rho = 0.1693$	Rho = -0.147 $\rho = 0.9597$	Rho = -0.013 $\rho = 0.5111$	Rho = -0.07 $\rho = 0.7495$	Rho = -0.012 $\rho = 0.4974$	Rho = 0.16 $\rho = 0.0795$	Rho = 0.262 $\rho = \mathbf{0.0151}$
Carbonate	Rho = 0.255 $\rho = \mathbf{0.0325}$	Rho = 0.272 $\rho = \mathbf{0.0150}$	Rho = 0.467 $\rho = \mathbf{0.0004}$	Rho = 0.425 $\rho = \mathbf{0.0003}$	Rho = 0.065 $\rho = 0.2446$	Rho = 0.303 $\rho = \mathbf{0.0237}$	Rho = 0.065 $\rho = 0.2599$
Terrigenous	Rho = 0.261 $\rho = \mathbf{0.0151}$	Rho = 0.165 $\rho = 0.0559$	Rho = 0.402 $\rho = \mathbf{0.0008}$	Rho = 0.208 $\rho = \mathbf{0.0323}$	Rho = 0.061 $\rho = 0.2348$	Rho = 0.288 $\rho = \mathbf{0.0114}$	Rho = 0.080 $\rho = 0.1887$
<b>Site-distance</b>							
Sedimentation rate	Rho = -0.086 $\rho = 0.4956$	Rho = -0.143 $\rho = 0.6670$	Rho = 0.543 $\rho = 0.2108$	Rho = 0.143 $\rho = 0.4918$	Rho = 0.771 $\rho = 0.2050$	Rho = 0.714 $\rho = 0.1671$	Rho = -0.200 $\rho = 0.6637$
Terrigenous rate	Rho = -0.086 $\rho = 0.5044$	Rho = -0.143 $\rho = 0.6666$	Rho = 0.543 $\rho = 0.2094$	Rho = 0.143 $\rho = 0.4882$	Rho = 0.771 $\rho = 0.2096$	Rho = 0.714 $\rho = 0.1637$	Rho = -0.200 $\rho = 0.6660$
Sand	Rho = 0.143 $\rho = 0.3667$	Rho = -0.029 $\rho = 0.5071$	Rho = 0.257 $\rho = 0.2917$	Rho = 0.257 $\rho = 0.3367$	Rho = 0.314 $\rho = 0.2032$	Rho = 0.371 $\rho = 0.2526$	Rho = -0.371 $\rho = 0.7970$
Silt-clay	Rho = 0.143 $\rho = 0.3846$	Rho = -0.029 $\rho = 0.4981$	Rho = 0.257 $\rho = 0.2950$	Rho = 0.257 $\rho = 0.3311$	Rho = 0.314 $\rho = 0.2056$	Rho = 0.371 $\rho = 0.2464$	Rho = -0.371 $\rho = 0.7888$
Organic matter	Rho = 0.086 $\rho = 0.4142$	Rho = -0.429 $\rho = 0.7911$	Rho = 0.257 $\rho = 0.4460$	Rho = 0.543 $\rho = 0.2073$	Rho = -0.086 $\rho = 0.4546$	Rho = 0.200 $\rho = 0.3299$	Rho = 0.829 $\rho = \mathbf{0.0455}$
Carbonate	Rho = 0.543 $\rho = 0.0855$	Rho = 0.371 $\rho = 0.2452$	Rho = -0.086 $\rho = 0.7077$	Rho = 0.429 $\rho = 0.1297$	Rho = 0.029 $\rho = 0.4965$	Rho = -0.029 $\rho = 0.4926$	Rho = -0.486 $\rho = 0.9178$
Terrigenous	Rho = 0.086 $\rho = 0.3824$	Rho = -0.143 $\rho = 0.6647$	Rho = 0.486 $\rho = 0.1636$	Rho = 0.314 $\rho = 0.3280$	Rho = 0.486 $\rho = 0.2509$	Rho = 0.600 $\rho = 0.1698$	Rho = -0.314 $\rho = 0.7896$
<b>Season-site</b>							
Total precipitation	Rho = -0.062 $\rho = 0.5636$	Rho = 0.048 $\rho = 0.3195$	Rho = 0.313 $\rho = 0.0762$	Rho = -0.005 $\rho = 0.4367$	Rho = -0.259 $\rho = 0.9659$	Rho = -0.083 $\rho = 0.6343$	Rho = 0.032 $\rho = 0.3503$
Wind speed	Rho = -0.197 $\rho = 0.8690$	Rho = -0.194 $\rho = 0.8599$	Rho = -0.152 $\rho = 0.7491$	Rho = -0.067 $\rho = 0.5824$	Rho = 0.126 $\rho = 0.1950$	Rho = -0.178 $\rho = 0.8221$	Rho = 0.039 $\rho = 0.3203$
Wave height	Rho = -0.270 $\rho = 0.9477$	Rho = -0.124 $\rho = 0.7138$	Rho = -0.073 $\rho = 0.6061$	Rho = -0.276 $\rho = 0.9173$	Rho = -0.131 $\rho = 0.6478$	Rho = -0.035 $\rho = 0.5341$	Rho = -0.048 $\rho = 0.5128$
SST	Rho = -0.151 $\rho = 0.7957$	Rho = -0.189 $\rho = 0.8776$	Rho = 0.044 $\rho = 0.3595$	Rho = -0.248 $\rho = 0.9616$	Rho = 0.093 $\rho = 0.2764$	Rho = -0.212 $\rho = 0.9322$	Rho = -0.08 $\rho = 0.5629$
Depth	Rho = 0.858 $\rho = \mathbf{0.0284}$	Rho = 0.759 $\rho = \mathbf{0.0272}$	Rho = 0.456 $\rho = 0.0625$	Rho = 0.706 $\rho = \mathbf{0.0274}$	Rho = -0.009 $\rho = 0.5703$	Rho = 0.759 $\rho = \mathbf{0.0319}$	Rho = -0.17 $\rho = 0.8587$

Bold  $p$ -values represent significance.

Fabricius, 2005; Sanders and Baron-Szabo, 2005). Field studies conducted at Costa Rica (Cortés and Risk, 1985) and southwest Puerto Rico (Torres and Morelock, 2002) documented that the *O. annularis* complex experienced significant reduction of growth rates and live tissue cover with increased terrigenous sediment accumulation. Similar trends were evidenced in this study where massive *O. annularis* composed the lowest live coral cover, and in contrast, *P. astreoides* and *P. porites* had the highest benthic cover. Benthic cover dominance by species that can survive in sub-optimal conditions suggests that these reefs

have already experienced changes due to a chronic, recurrent land-based stressors.

Other benthic components that correlated with terrigenous sediment deposition were macroalgae, calcareous algae, and sponge percentage cover. Macroalgae, turf, and calcareous algae cover experienced variation in benthic cover in a short time period, particularly the fast-growing *Dictyota* spp. and encrusting calcareous algae *Ramicrusta textilis*, which were documented overgrowing dead coral skeleton. In 2011, *R. textilis* was first documented in Puerto Rican coral reefs (Ballantine et al., 2011;

Ballantine and Ruiz, 2013), and continues to outcompete and overgrow multiple coral species (Ballantine et al., 2016). This encrusting species has been documented overgrowing at least 14 species of scleractinian corals, gorgonians, hydrocorals and other algae (Eckrich et al., 2010) and has become a critical factor adversely influencing coral assemblages across the Caribbean region. Its role should be carefully studied. Increased sediment deposition could inhibit fish grazing and promote the growth of macroalgae and filamentous algal turfs (Bellwood and Fulton, 2008). Macroalgae can also proliferate under high nutrient concentration from runoff (Cloern, 2001), under low herbivory pressure due to the slow recovery of *Diadema antillarum* (Ruiz-Ramos et al., 2011; Rodríguez-Barreras et al., 2018), overfishing (Hernández-Delgado et al., 2006), or due to a combination of any of these factors (Littler et al., 2006). This suggests that coral reef trophic condition is also a critical co-factor, in combination with climate change-related impacts, in shaping coral reef benthic assemblages.

Increased frequency and severity of sedimentation stress and LBSP can increase sponge competition for space and could favor benthic cover of resistant species, thus leading to alternate dominant states (López-Victoria et al., 2006; Chadwick and Morrow, 2011; González-Rivero et al., 2011). Even though the increased cover of encrusting sponge *D. funicularis* has been recently reported on Caribbean reefs (García-Sais et al., 2016; Kramer et al., 2016), its distribution and coral out-competition effects are still unknown. High octocoral cover documented in deeper areas at PSO concurs with previous studies that have shown increased dominance of octocorals at deeper reefs (Sánchez et al., 1997). Results from this study show that there was an inverse relationship between coral and octocoral cover.

A possible limitation of the study was the lack of resources to assess benthic community and environmental variables at a larger spatial scale to contrast various land uses and coastal management strategies, and the response of coral reefs. Future research could address larger spatial scales and multiple environmental factors affecting water quality, such as nutrient concentration, to identify which factors exert greater influence in coral abundance, coral recruit patterns, coral cover, and macroalgae cover at local and regional levels. It is also imperative to address potential effects of increased frequency of extreme events, including intense storms and wave action, in the context of changing land use and other localized human-driven influences. Hurricanes can have highly destructive mechanical impacts to coral reefs (Woodley et al., 1981; Fenner, 1991; Toledo-Hernández et al., 2018), and in the context of changing land use, they can magnify sediment delivery and resuspension along coastal coral reefs and associated ecosystems.

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The potential influence of sedimentation in determining coral reef trajectories highlights the need for a broader understanding of sedimentation dynamics and of coral reef social-ecological responses under variable environmental scenarios, in order to inform decisions and policies to reduce local stressors, improve water quality, and effectively conserve and restore threatened coral reefs.

## AUTHOR CONTRIBUTIONS

AO-C, AM-A, EH-D, EC, and JO-Z conceived and designed the study. AO-C, AM-A, NG-R, DD-M, and EB performed the coral reef monitoring, field sampling, and analysis. AO-C, AM-A, EH-D, EC, and JO-Z analyzed the data. AO-C, AM-A, and EH-D wrote the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00551/full#supplementary-material>

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