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Functional diversity metrics detect spatio-temporal changes in the fish communities of a Caribbean marine protected area

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Citation: Rincón-Díaz, M. P., S. J. Pittman, I. Arismendi, and S. S. Heppell. 2018. Functional diversity metrics detect spatio-temporal changes in the fish communities of a Caribbean marine protected area. Ecosphere 9(10):e02433. 10.1002/ecs2.2433

Abstract. Functional diversity (FD) metrics quantify the trait diversity in biological assemblages and act as a proxy for the diverse ecological functions performed in the community. Analyses of FD offer a potentially useful tool to identify functional changes in diverse, complex, and disturbed marine ecosystems such as coral reefs, yet this metric is rarely applied to evaluate community change. Here, we documented spatio-temporal variability in the trophic function of fish assemblages to identify changes in coral reef communities inside the Buck Island Reef National Monument (BIRNM) in the U.S. Virgin Islands between 2002 and 2010, which included an intense coral bleaching event in 2005. We combined six trait categories related to the trophic function of 95 fish species together with species biomass estimated from underwater surveys to calculate assemblage-level descriptors of functional richness (FRic), dispersion (FDis), and evenness. We tested the effects of habitat type, time, and their interaction on fish FD using a non−parametric permutational multivariate analysis of variance. We found statistically significant differences for FRic and FDis between habitat types and survey years. Coral reef and other hard bottom areas supported highest levels of trophic functional richness and variation, but low functional redundancy. Fish species exhibited high functional uniqueness within the functional trait space suggesting that a significant decline in fish diversity in the BIRNM would likely result in loss of trophic functions from the fish community. Detection of temporal variations in functional trait composition subsequent to the mass coral bleaching event in 2005 indicates that FD descriptors are sensitive enough to track shifts in the emergent trophic organization of fish communities. In the BIRNM, the trophic organization in fish assemblages did not return to the pre-bleaching state even after five years of monitoring. We demonstrate a novel way to monitor resilience to disturbance by plotting and tracking the centroid of the functional trait space through time. Our findings demonstrate the utility of FD descriptors to evaluate changes to the functional integrity of diverse and spatially heterogeneous habitat structure across the seascape.

Key words: Caribbean reefs; fish assemblages; functional diversity; resilience; spatio-temporal variation; trophic traits.

Received 11 January 2018; revised 13 July 2018; accepted 27 August 2018. Corresponding Editor: Hunter Lenihan.

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INTRODUCTION

Understanding the spatial and temporal patterns and processes that influence the functional organization of species assemblages is an essential step in understanding ecosystem structure and function (Oliveira et al. 2012). Traditional descriptors of spatio-temporal changes in species diversity, including species richness, and trophic group richness and biomass (Gotelli and Colwell 2001, Colwell 2009, Maurer 2009, Loiseau and Gaertner 2015, Vallès and Oxenford 2015), are often insensitive to interspecific variability in species traits because they either ignore species-specific functional roles completely or clump species within guilds or trophic groups without sufficient knowledge of trait differences (Villéger et al. 2010, Mouillot et al. 2013*b*, Boersma et al. 2014, 2016, Micheli et al. 2014, Dee et al. 2016). Diversity in the ecological roles of species in complex trophic communities may be a more important indicator of change for monitoring programs to track than a simple number of species when implementing an ecosystem-based management approach (Cadotte et al. 2011).

Functional diversity (FD) metrics have emerged as alternative descriptors of spatio-temporal patterns in community organization that respond to changes in environmental gradients (Villéger et al. 2010, Boersma et al. 2014, Piacenza et al. 2015, Dee et al. 2016). Based on species abundance and their functional traits, these descriptors provide a way to characterize the niche space used by each species. A functional trait is a measurable feature that describes the ecosystem role of an individual or species, and can be morphological, behavioral, and physiological (Diaz and Cabido 2001, Petchey and Gaston 2006, Cadotte et al. 2011). These traits are highly related to environmental tolerance of organisms, which in turn shapes community composition and organization (Boersma et al. 2014, Piacenza et al. 2015, Dee et al. 2016, Silva-Júnior et al. 2016), allowing us to understand the changes in the emergent functional properties of biotic communities and their resilience to perturbations.

For assemblages of organisms, descriptors of trait diversity allow for the inclusion of rare species commonly excluded from community analysis and which can perform unique functional roles (Mouillot et al. 2013*a*, Jain et al. 2014, Leitão et al. 2016). Trait diversity descriptors are sensitive tools to capture interspecific variability in functional roles of species because they capture the variability and redundancy in species traits (Villéger et al. 2010, Mouillot et al. 2013*b*, Boersma et al. 2014, 2016, Micheli et al. 2014, Dee et al. 2016). Trait redundancy, a measure of overlap in ecological function, can be used to estimate how biodiversity loss can influence ecosystem function and services provided by biotic communities (Peterson et al. 1998, Elmqvist et al. 2003, Folke et al. 2004, Cadotte et al. 2011). For instance, high functional redundancy implies high ecosystem resilience, that is, the capacity of a disturbed system to maintain (resist) or recover its functions and ecosystem services (Holling 1973, 1996, Folke et al. 2004, Hodgson et al. 2015, Mora 2015, Oliver et al. 2015). In terrestrial systems, it has been found that high functional redundancy of drought resistance and trophic traits in invertebrate communities buffer against functional changes in their arid-land streams communities even during habitat contraction and fragmentation induced by severe drying (Boersma et al. 2014). By contrast, nearshore marine ecosystems, including high-diversity coral reef fish communities, have relatively low functional redundancy (Bellwood et al. 2003, Micheli and Halpern 2005, Mouillot et al. 2014).

In application, FD descriptors are considered to be simple, logical, and repeatable metrics that can be compared across multiple spatial scales (Carmona et al. 2016) to evaluate the performance of functional organization of communities and ecosystems. Measures of FD offer great potential as an effective tool to monitor and evaluate shifts in the trophic function of fishes and to predict subsequent changes in ecosystem function. However, these metrics need further evaluation to determine whether they are ecologically meaningful in complex, high-diversity systems such as coral reef ecosystems. In Caribbean coral reefs, a low functional redundancy in the trophic role of fish assemblages suggests that small decreases in species richness could lead to loss of ecosystem functions and fish biomass production (Halpern and Floeter 2008, Micheli et al. 2014, Mouillot et al. 2014). Functional redundancy in the trophic function of reef fish communities is highly influenced by species composition and the specific life stages that affect their ontogenetic shifts in diets (Nakazawa 2015), habitat use, and migrations (Helfman et al. 2009, White 2015).

The use of descriptors of FD and redundancy has great potential to evaluate the resilience of communities to perturbations and management interventions such as marine reserves where extractive activities are prohibited. Monitoring and measuring the status and trends in the FD of coral reef fish communities are central to ecosystem-based management because FD is linked to ecosystem-level functions and the provisioning of economically important ecosystem services attributed to coral reefs (Micheli et al. 2014). These metrics are useful to evaluate the resilience of coral reefs following trophic cascades caused by disturbances, such as overfishing of high trophic guilds including sharks, groupers, or snappers (Heithaus et al. 2008, Ruttenberg et al. 2011, Tyler et al. 2011, Valdivia et al. 2017), the effects of changes in species presence and richness in trophic groups (Nyström 2006, Bremner 2008, Estes et al. 2011, Mumby et al. 2012), and the availability of food for fish species of commercial importance and human consumption (Smith et al. 2011, Dee et al. 2016). However, to be a useful metric for monitoring systems, functional redundancy must be measurable and sensitive enough to detect change across the seascape (i.e., multiple habitat types) and timescales to understand the resilience of systems. Furthermore, gaps in the knowledge of the functional traits of reef fishes, especially of juvenile life stages which may have a different ecological role in the community, have hindered advances in the application of trait-based metrics (Rincón-Díaz et al. 2015).

We compile a new database of the best-available data on the functional and behavioral traits related to the trophic function of Caribbean fish species. We then apply the database to the fish assemblages surveyed by a long-term underwater monitoring program at Buck Island Reef National Monument (BIRNM) in the U.S. Caribbean to evaluate spatial and temporal changes in functional richness (FRic), functional dispersion (FDis), and functional evenness (FEve) of fish assemblages (Appendix S1: Fig. S1). These descriptors were selected because they provide insights into different aspects of FD within the community and can incorporate multiple categorical and numerical traits in multidimensional trait space (Villéger et al. 2008, Laliberté and Legendre 2010, Schleuter et al. 2010, Laliberté et al. 2014). We test the hypothesis that variation in fish FD metrics is a function of habitat type and time, owing to changes in trait composition of fish assemblages through time and differences in habitat structure, and shifts in life stage and habitat–prey preferences. In addition, we test the hypothesis that each functional trait contributes differently to the variability of fish FD descriptors. Our study provides information about functional traits for 95 marine fish species known to occur in the BIRNM, and most of which are also commonly found throughout the Caribbean region. We validate descriptors of FD as important tools to be implemented in monitoring programs of marine biotic communities and provide a visual tool to understand temporal changes in their functional organization to identify levels of ecosystem resilience. Providing park managers with scientifically validated evidence of reserve ecological performance, condition, and community vulnerability is essential to informing adaptive resource management strategies and understanding and anticipating the ecological consequences of disturbance events.

METHODS

Study site

We focused our FD study on an extensive set of fish community data collected by the Caribbean Coral Reef Ecosystem Assessment and Monitoring (C-CREAM) project (2002–2012) of the National Oceanic and Atmospheric Administration (NOAA) in shallow areas (<30 m) inside the marine protected area of BIRNM located in northeast St. Croix, U.S. Virgin Islands (USVI; Fig. 1). BIRNM encompasses 7695 hectares of land and marine areas and is managed by the U.S. National Park Service (NPS; Pittman et al. 2008). Habitat composition of the studied sites included coral reef and colonized hard bottoms, seagrasses, macroalgae, and unconsolidated sediments (Kendall et al. 2001, Costa et al. 2012). This National Monument is a permanent No-Take/No-Anchoring Zone established in 1961. Recognizing the need to further protect vulnerable habitat structure and importance of connectivity between habitat types for ecological communities, BIRNM was expanded in 1975 and again in 2001 to protect a more extensive range of fish habitat and coral reef-building species such as Elkhorn coral (*Acropora palmata*; Rothenberger et al. 2008). Despite the high level of protection, coral reef communities in the BIRNM did not escape from several natural disturbances that caused mass coral mortality and disease outbreaks during the survey years examined in this study (Pittman et al. 2014). A mass coral bleaching in 2005 and subsequent disease outbreak in 2006 decreased 53% of reef-building species in this MPA (Rogers et al. 2009). In 2008, Hurricane Omar and an extreme swell event caused structural damages to coral reefs, and in the same

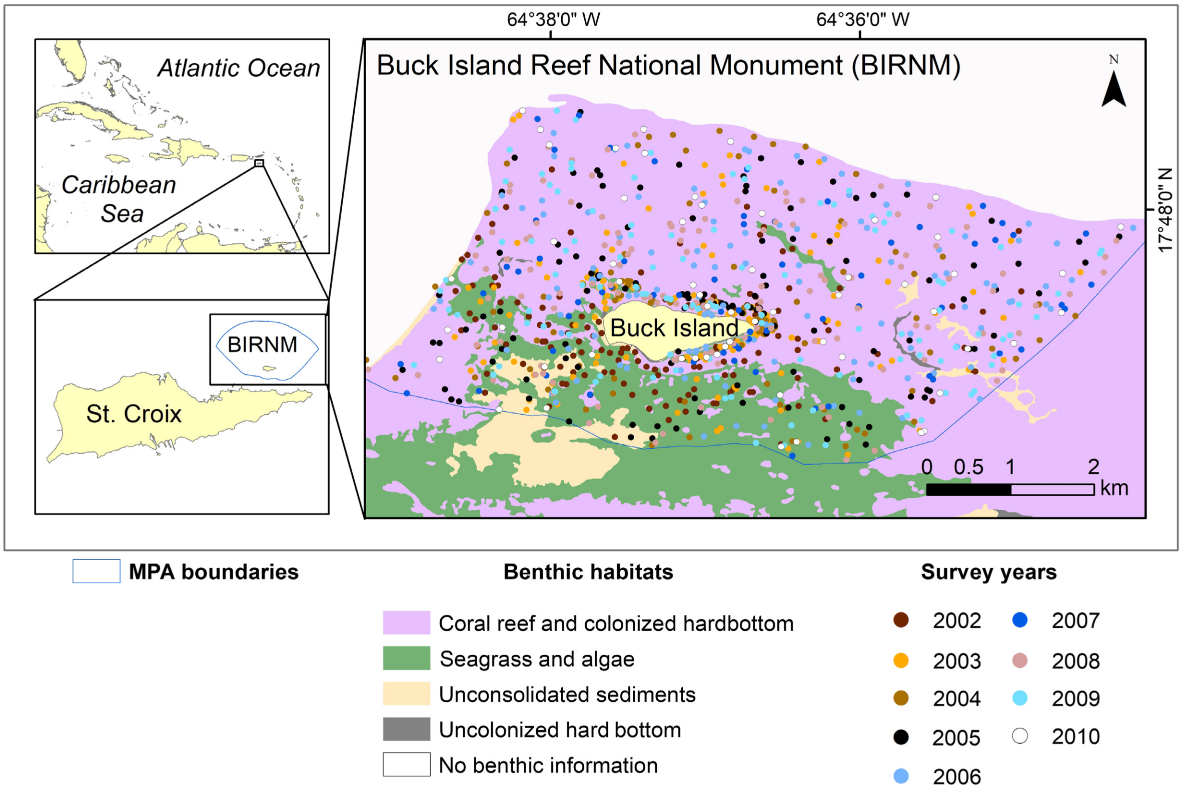

Fig. 1. Survey sites inside the Buck Island Reef National Monument (BIRNM).

year, the ecological invasion of the Indo-Pacific lionfish was first recorded for the USVI (Pittman et al. 2014). In 2010, Hurricane Earl produced high levels of sedimentation on coral reefs from land runoff during heavy rains and resuspension of marine sediments (Pittman et al. 2014).

Spatio-temporal characterization of fish abundance and size

Community species composition, abundance, and size of fishes by habitat type were characterized at 835 survey sites by the Caribbean Coral Reef Ecosystem Assessment and Monitoring (C-CREAM) project led by the Biogeography Branch of the NOAA in partnership with the NPS. Only surveys within the BIRNM from 2002 to 2010 (NOAA et al. 2007; https://coastalscience.noaa.gov/project/caribbean-coral-reef-ecosystem-monitoring-project/) contributed to analyses. Surveys were conducted during winter and spring (January–April) and fall (August–November) each year to account for seasonal variation (Appendix S1: Table S1). Survey locations were selected with a random-stratified sample design, whereby survey start points were randomly allocated to hard and soft bottom strata on the NOAA benthic habitat map (Kendall et al. 2001) using a Geographical Information System. Trained scientific divers surveyed fish assemblages during daylight hours along a standardized 25 m long and 4 m wide (100 m^2) belt transect during a 15-min swim at a constant speed. Fishes in holes, under ledges, and in the water column were recorded without changing the habitat structure of the survey site (NOAA et al. 2007). Mapped survey locations showed that each survey was conducted at a spatially discrete location with no geographical overlap (Fig. 1). Information gathered in each census included the identification of fish species, number of individuals, and an estimation of the fork length at 5 cm size class bins up to 35 cm to calculate fish biomass by life stages (NOAA et al. 2007, Pittman et al. 2008). Surveys of unconsolidated sediments were omitted from our analysis because of low sample size during the surveyed years.

Compilation of fish functional traits

Traits related to the trophic function of 165 marine fish species, recorded by NOAA in the BIRNM, were extracted from a database created from an extensive literature review of studies conducted in Puerto Rico and the USVI (Table 1). Where trait information was inadequate in the U.S. Caribbean, studies from elsewhere in the Caribbean Sea were used to complete the information about the trophic function of fishes (M. P. Rincon-Diaz et al., *public communication*). Six trait categories were selected to include knowledge of ontogenetic diet shifts through the life cycle that typically coincide with changes in movement patterns (e.g., relocations from seagrass to coral reefs), social foraging behavior, feeding time, trophic location in the food web, and diet plasticity (Stuart-Smith et al. 2013, Oliveira et al. 2012, Micheli et al. 2014; M. P. Rincon-Diaz et al., *public communication*). Habitat use traits included the water column feeding position (Stuart-Smith et al. 2013, Mouillot et al. 2013*a*, *b*, 2014, Parravicini et al. 2014, D'agata et al. 2016*a*, *b*, Mellin et al. 2016, Loiseau et al. 2017) and the feeding habitat, which describes the sea bottom type used as feeding ground. Feeding habitat is a previously unexamined trait for FD analysis of marine fish communities. We also included the social foraging behavior, which describes species social strategies that minimize predation and energetic costs while feeding, and feeding time, which accounts for diurnal and nocturnal use of feeding habitats by reef fish species (Kulbicki et al. 2005, Belmaker et al. 2013, Mouillot et al. 2013*a*, 2014, Parravicini et al. 2014, Loiseau et al. 2017). Feeding time also describes temporal fish species turnover within the reef fish assemblages (Randall 1967, Collette and Talbot 1972). Diet breadth was also a novel trait included in this study; it describes diet plasticity by considering the number of taxonomic groups consumed by a fish species (Oliveira et al. 2012). The trophic level was included because it describes the trophic position of a species within a community (Oliveira et al. 2012, Stuart-Smith et al. 2013, Micheli et al. 2014). Trophic level was calculated by using the TropLab software (Pauly et al. 2000) based on information from diet content analysis reported in studies conducted primarily in the U.S. Caribbean (Randall 1967, Birkeland and Neudecker 1981, Turingan et al. 1995, White et al. 2006, Clark et al. 2009, Leidke 2013).

Binomial presence/absence of functional traits was recorded for this study because differences in quantitative trait measurements were assumed to vary among studies. The trophic level and diet amplitude of fish species were standardized by their maximum and ranged from 0 to 1. Only species with complete information were included in FD analyses after evaluating the methodological issues with available trait information (Appendix S2). A total of 95 fish species representing 57% of all recorded species in adult stages had complete trait information and therefore were included in the FD analysis (Data S1).

Functional diversity metrics

We calculated FRic, FDis, and FEve for each fish survey site and year following the methods of Laliberté et al. (2014; Appendix S1: Fig. S1). We used all proposed fish functional trait categories because we identified no significant levels of association among traits using the Cramer's V index (Appendix S2). We used fish species trait information and abundances expressed as biomass according to values calculated by NOAA

Table 1. Functional traits used to calculate fish functional diversity.

Functional traits	Traits
Water column feeding position	Benthic (BEN), demersal (DEM), midwater (MID), and surface (SUR)
Social feeding behavior	Species feeding as solitary individuals (SOL), in pairs (PAIR), in intraspecific aggregations (AGR), or in mixed groups with other species (MIX)
Feeding time	Diurnal (DIU), crepuscular (CRE), and nocturnal (NOC)
Feeding ground	Species feeding on the following substrates: coral reefs (COR), rocky reefs (ROC), seagrasses (SEA), algae beds (ALG), mangroves (MAN), sand (SAN), coral rubble (RUB), open water (OPE), water column (COL), out of shelf (SHE), and attached to other vertebrates (VER)
Trophic level (TL)	TL go from 2.0 for herbivores up to 4.5 for piscivores
Diet breadth	The number of prey taxonomic groups included in diet: nekton, zooplankton, zoobenthos, detritus, plants, sand, organic matter, ectoparasites, and unidentified animal material

et al. (2007) in each surveyed site as inputs to calculate FD metrics. A trait distance matrix was calculated by using the Gower (1971) dissimilarity distance based on trait values among fish species because the majority of traits were categorical (Villéger et al. 2008). The trait distance matrix was used to conduct a principal coordinates analysis (PCoA) to build a single functional trait space needed to (1) calculate locations of species in the multidimensional trait space, (2) calculate FD metrics of assemblages, and (3) identify differences in FD between assemblages (Villéger et al. 2008, 2017). We used the first four axes of the PCoA because they improve the quality of the multidimensional trait space through the accurate representation of the Gower distances between species in the trait distance matrix (Villéger et al. 2008, Maire et al. 2015, D'agata et al. 2016*a*, *b*). These axes also explained more than 80% of the variation in the functional trait space for fish assemblages in the BIRNM. The trait distance matrix and PCoA were calculated by using the PAST Program version 3.08 (Hammer 2015). A functional matrix based on the four principal axes and a biomass matrix for fish species was used to calculate FD metrics per survey site using the FD software package in R (Laliberté et al. 2014). We evaluated sample size effects on temporal patterns of FD and combined data by years to simplify patterns of fish FD (Appendix S2).

We also calculated species richness per survey site with the FD package and conducted Spearman rank correlation analyses (rho) among fish diversity metrics to examine the influence of this traditional metric on descriptors of FD. Correlation analysis was conducted with the PAST Program version 3.08 (Hammer 2015).

Spatial and temporal variation of fish functional diversity

A non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) was used to test the hypothesis that FD metrics vary by habitat type and year of survey, allowing for interactions among these two factors. Significance in the PERMANOVA was calculated by the permutation of 9999 replicates of factors established in our study, and statistical differences were established at P-values < 0.05 (Mateos-Molina et al. 2014, Hammer 2015). When statistical significance was found for years of the survey, a Mann–Whitney pairwise post hoc test (Zar 1996) was conducted to find differences between all pairs of years for all habitats. Statistical significant differences were established for the Mann–Whitney pairwise test with Bonferroni-corrected P-values < 0.05 (Hammer 2015). Analyses were conducted using the PAST Program version 3.08, and significant levels were determined by following the default setting of this program (Hammer 2015).

Sensitivity of functional diversity metrics to chosen traits

We identified functional traits that explained variation in FD by dropping each trait from the calculations of each functional metric, and then, by using linear regressions, we compared those values with values calculated with the full pool of traits (Stuart-Smith et al. 2013). We compared coefficients of determination (r^2) between indexes calculated with all traits and dropped traits to identify the real contribution of traits to explain variation in FD metrics (Stuart-Smith et al. 2013). Low coefficients of determination (r^2) with statistical significance represented a significant gap in information and indicated traits that contributed more to variation in FD (Stuart-Smith et al. 2013).

Temporal variation in functional organization of fish assemblages

Temporal changes in the fish functional organization were evaluated by describing species functional trait gradients, calculating centroids of convex hulls, and identifying hotspots of functional redundancy in the trait space through time. We created the functional trait space and convex hulls by plotting the first two coordinate's axes of PCoA used to calculate FD metrics (Laliberté et al. 2014) because they explained more than 50% in fish trait variation.

Centroids of convex hulls were plotted in the trait functional space as a proxy to visualize temporal changes in the fish functional organization for the BIRNM. Centroids of convex hulls were calculated by following the concept of center of mass, understood as the weighted relative location where a body is in equilibrium because distributed mass sums to zero (Levi 2009). In our study, a centroid was the location in the trait space in which distances from all species locations, weighted by species annual biomass, were the same (Appendix S1: Fig. S1). These centroids were used as indicators of temporal trajectories in the trophic function of fish assemblages and a potential indicator response of the communities following disturbance.

Temporal hotspots of functional redundancy were identified by plotting kernel density maps calculated from species locations in the functional trait space by years. Density maps were calculated in the PAST Program version 3.08 (Hammer 2015) by using the Gaussian function and locating nearby species within a radius of 0.02 within the trait functional space. Hotspots were formed by species with similar, but not equal functional traits.

RESULTS

Spatio-temporal patterns of fish functional diversity

Our findings supported the hypothesis that FD descriptors varied over time and habitat, with the interaction between them for FDis and FEve values ($P > 0.05$; Table 2). Coral and colonized hard bottom habitats supported highest FRic and variation among fish assemblages, with traits more evenly distributed after 2006 in the multidimensional trait space of fish assemblages (Figs. 2, 3). When data for the different habitats were combined, the largest change in FD was observed in 2006 (Fig. 2). Functional richness values for 2006 were significantly higher than values of 2005 and 2009 (Mann–Whitney test; P-value < 0.05), FDis values for 2006 were higher than values of 2002 and 2004 (Mann–Whitney test; $P < 0.05$), and FEve values for 2004 were lower than values of 2006 and 2008 (Mann–Whitney test; $P < 0.05$).

We observed a significant positive correlation between species richness and FRic (Fig. 4A), as well as a low positive correlation between species richness and FDis, FRic and FDis, and FDis and FEve (Fig. 4B, D, F). There was a low correlation between FEve with species richness and FDis, suggesting that evenness and richness metrics provide an independent evaluation of FD (Fig. 4C, E).

Importance of traits to explain variation in functional diversity metrics

We found that species traits contributed differently to explain variability in fish FD (Table 3). Traits that explain the majority of variance in FD metrics were identified by their lowest coefficient of determination (r^2) obtained when those traits were dropped from the calculation of functional metrics (Stuart-Smith et al. 2013). Two traits, diet breadth and trophic level, were the most important for predicting FD metrics (Table 3). Diet breadth explained the most variation in FRic (49%) and FEve (87%), and species trophic level best explained FDis in the trait space of fish communities (31.5%).

Temporal variation in functional organization of fish assemblages

Although the functional organization in the fish functional trait space was visually similar for most years, the centroids from convex hulls did not always overlap (Fig. 5A, B). This result

Table 2. PERMANOVA on values of functional richness (FRic), dispersion (FDis), and evenness (FEve) for Caribbean fish assemblages (2002–2010).

Source of variation	FRic		FDis		FEve	
	df	*F*	df	*F*	df	*F*
Time of survey (yr)	8	1.236**	8	1.635***	8	1.137**
Habitat type	1	35.89***	1	20.451***	1	6.941***
Time of survey × habitat type	8	−35.299***	8	−33.277***	8	−35.196***
Residual	665		665		665	
Total	682		682		682	

Notes: PERMANOVA, permutational multivariate analysis of variance. From the total of 835 sites, we excluded 153 sites from functional diversity analysis due to their low species richness (<2 species). Convex hull volume for FRic, nor the values of FDis and FEve can be calculated with less than two species per site (Laliberté et al. 2014).

** $P < 0.01$, *** $P < 0.001$.

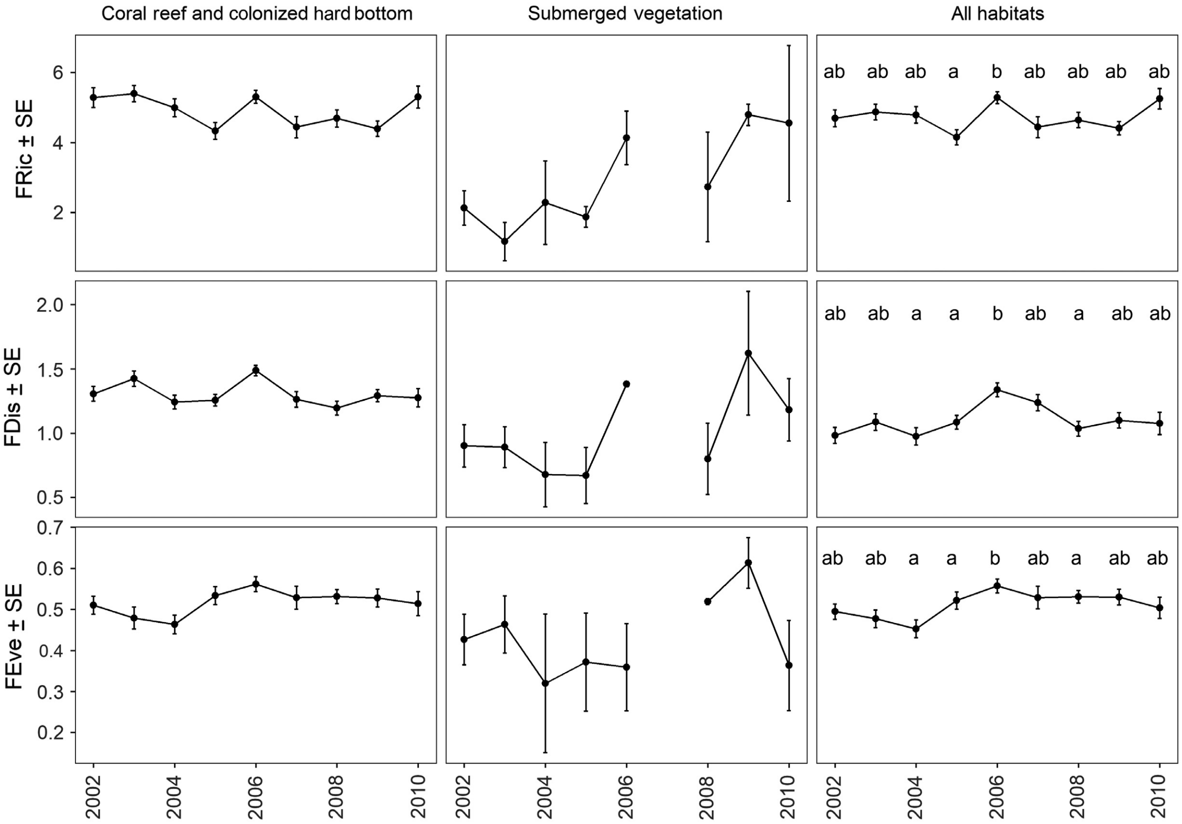

Fig. 2. Spatio-temporal variation in functional diversity (FD) metrics by habitat type and years. Values of FD metrics are express as mean ± standard error (SE). Note that there is a decline in FRic, but an increase in FDis in 2005. Functional diversity metrics were calculated with four coordinate axes that explained 82% of the cumulative total variation of fish species in the functional trait space. Letters above means of FD metrics for all habitats denote multiple pairwise comparisons among years determined with a Mann–Whitney test, $P < 0.05$. FRic, functional richness; FDis, functional dispersion; FEve, functional evenness.

indicated that there were shifts in the trophic organization of fish assemblages during evaluated years. Functional organization of fish assemblages showed a similar distribution of gradients in functional traits among years over (Fig. 5A). Traits associated with the first axis were trophic level, water column feeding position, and feeding habitats. Traits associated with the second axis were diet breadth, social foraging behavior, and time of feeding. Centroids in the functional space had different locations but were mainly concentrated on the right side of the trait space, where species with low trophic levels and specialist diet (herbivorous fishes) were located (Fig. 5B). The exceptions were for years 2008 and 2010 where centroids were pulled by species of higher trophic levels in comparison with previous years.

Fish communities of the BIRNM had low levels of functional redundancy that varied highly through time, as shown by the configuration of the functional trait space in kernel density maps (Fig. 6). Kernel density maps showed that no more than one fish species occupied the same location within the trait space built with our six functional traits, indicating that each fish species had a unique functional role within the fish community. Functional redundancy tended to vary through time as hotspots were reduced after 2005 in the functional trait space and never returned to initial states (Fig. 6). The configuration of functional redundancy was similar for the

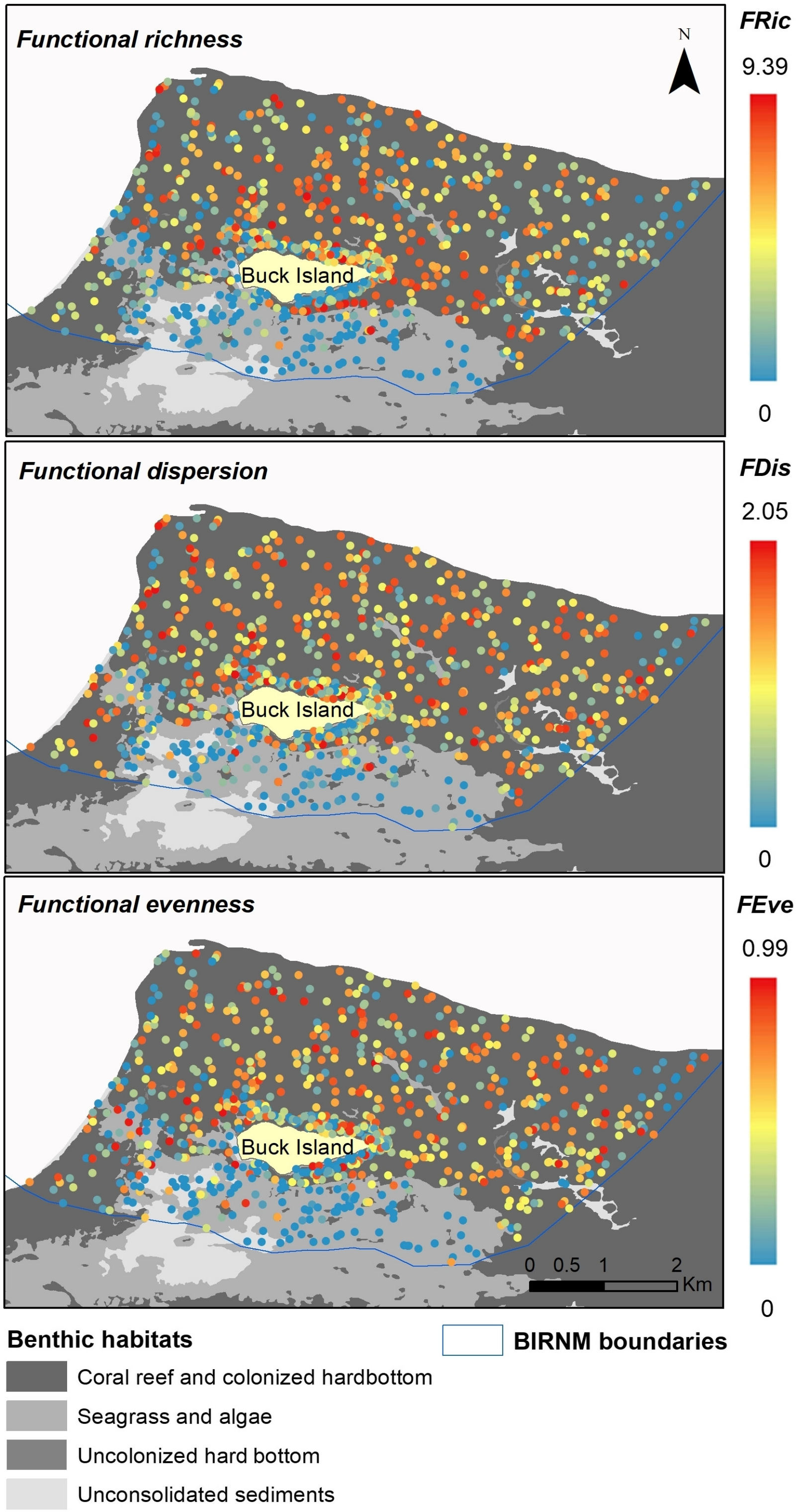

Fig. 3. Spatial distribution of fish functional richness (FRic), dispersion (FDis), and evenness (FEve) values in the Buck Island Reef National Monument (BIRNM).

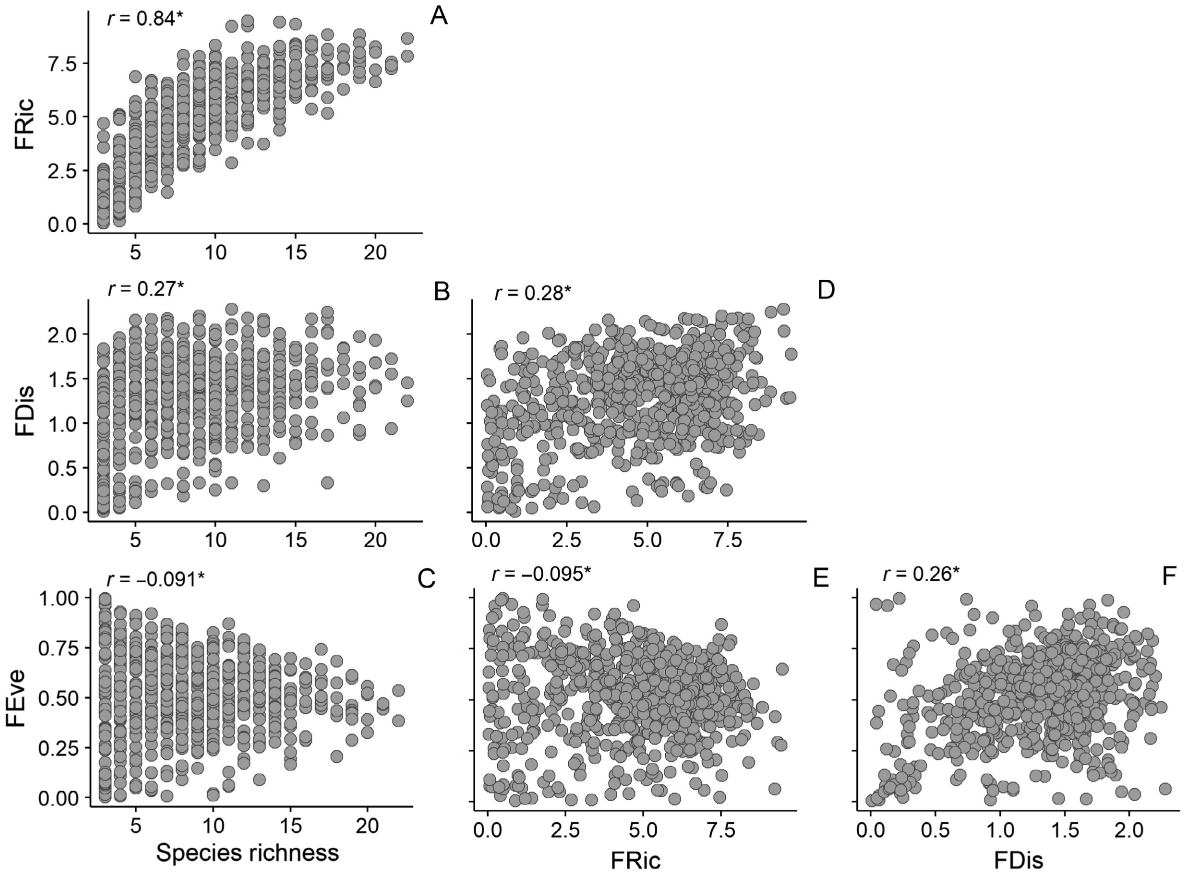

Fig. 4. Spearman rank correlation analysis (rho) between metrics of fish diversity. (A) Species richness vs. functional richness (FRic). (B) Species richness vs. functional dispersion (FDis). (C) Species richness vs. functional evenness (FEve). (D) FRic vs. FDis. (E) FRic vs. FEve. (F) FDis vs. FEve; asterisks denote $P < 0.05$.

Table 3. Real contribution of functional traits to explain variation in functional diversity (FD) metrics for Caribbean reef fishes.

Removed trait from calculation of metrics	FRic		FDis		FEve	
	r^2	Real contribution	r^2	Real contribution	r^2	Real contribution
Diet breadth	0.514***	**0.486**	0.832***	0.168	0.129***	**0.871**
Trophic level	0.649***	0.351	0.685***	**0.315**	0.189***	0.811
Feeding habitat	0.788***	0.212	0.896***	0.104	0.518***	0.482
Social foraging behavior	0.796***	0.204	0.901***	0.099	0.537***	0.463
Water column feeding position	0.843***	0.157	0.899***	0.101	0.477***	0.523
Time of feeding	0.881***	0.119	0.905***	0.095	0.483***	0.517

Notes: FDis, functional dispersion; FEve, functional evenness; FRic, functional richness. Coefficients of determination (r^2) for FD metrics were calculated from sets of functional traits with one trait removed from the pool of traits. Bold values indicate traits that contributed more to variability in FD metrics. The real contribution of a trait to explain variation in FD metrics was identified by subtracting the maximum contribution of the trait (equals to 1) from observed r^2 calculated without the trait in question ($1 - r^2$).

*** $P < 0.001$.

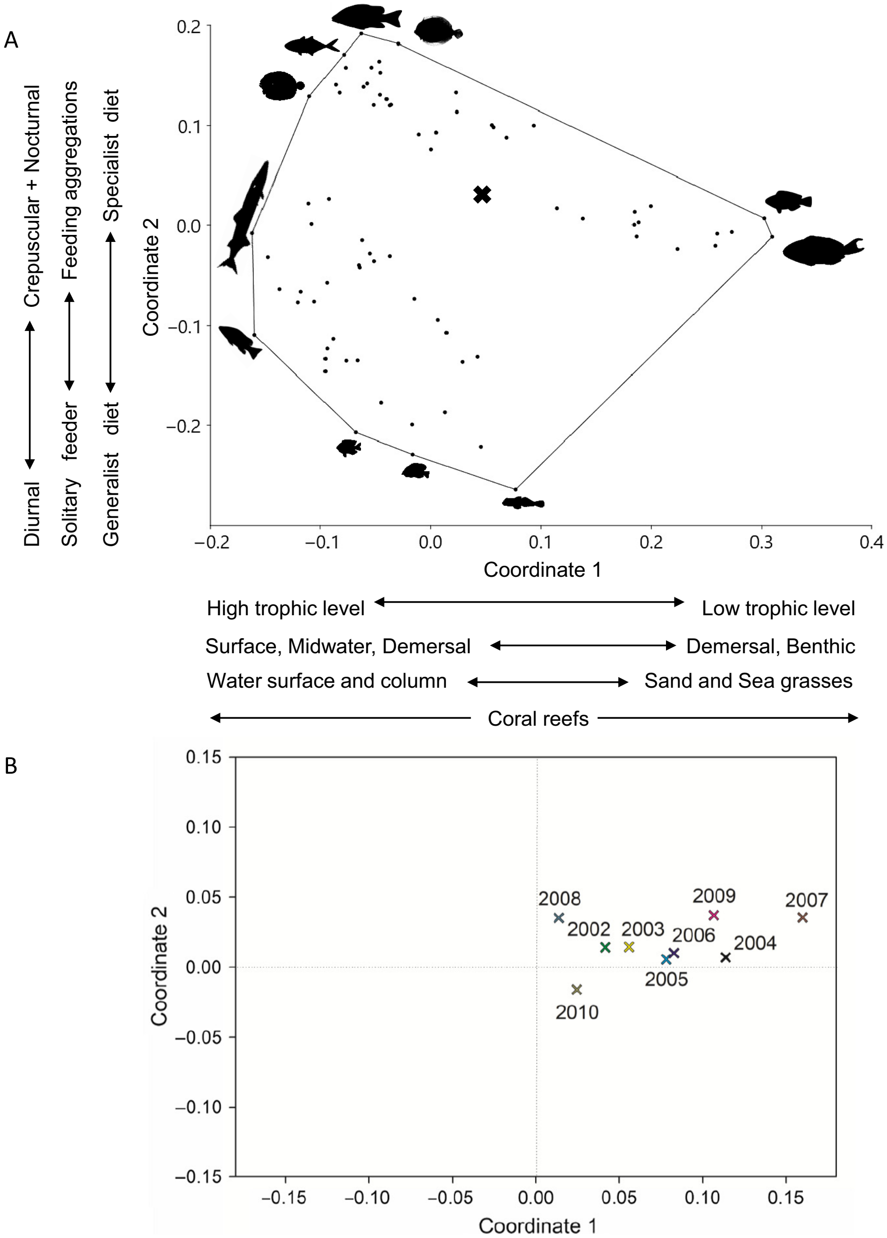

Fig. 5. Temporal changes in the fish functional trait space based on principal coordinates analysis. (A) Functional trait space for 2002 shows the functional organization of fish assemblages in the Buck Island Reef National Monument. Gradients of functional traits are shown for the first and second coordinate axes only for this graphical representation. The first and second axes explain 38% and 27% of the variation in the functional trait space for 2002, respectively. Locations of fish species in the trait space are represented by dots. Fish icons close to dots represent species with extreme trait values that delineate boundaries of the functional trait space in the assemblage for 2002. Centroid of the functional trait space for 2002 is shown as the X symbol. (B) Centroids by years of survey in a two-dimensional functional trait space show trajectories of the functional organization over time. Gradients of functional traits are shown for the first and second coordinate axes only for this graphical representation. Variation in the functional trait space by the first coordinate axis explained between 38% and 44%, followed by the second axis that explained between 25% and 27% of trait variation for all years.

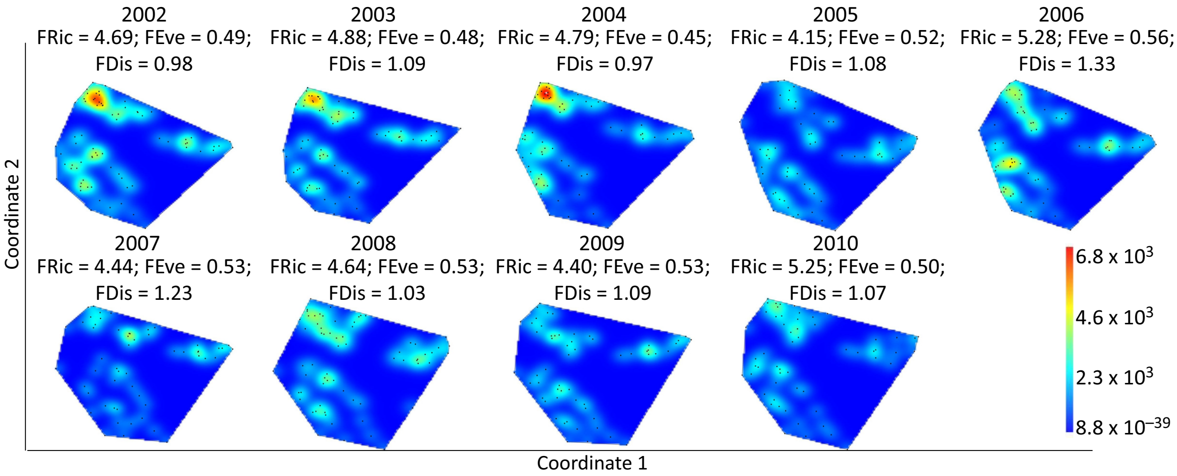

Fig. 6. Temporal variation of functional redundancy in fish assemblages of the Buck Island Reef National Monument. Plots maps show boundaries of the functional trait space, species location in the trait space as dots, and hotspots of species with similar trophic function as reddish regions. Functional trait spaces were plotted with the first two axes of the principal coordinate analysis for graphical representation. Mean values of functional diversity descriptors were detailed in the upper side of the trait space. Functional diversity descriptors were calculated with the first fourth axes of a single functional trait space that explained 82% of the cumulative total variation. The scale bar gives an estimate of the number of species per area based on species distances within a radius of 0.02 within the trait functional space.

four initial years, with hotspots of redundancy concentrated on specialist fishes with high and intermediate trophic levels. In 2005, the density of species with similar traits diminished drastically in the trait space suggesting a reduction in fish functional redundancy. In 2006 and 2008, five hotspots of functional redundancy were observed with a high concentration of species of high and intermediate trophic levels. In 2007 and 2009, redundancy was concentrated in specialist species with intermediate and low trophic levels. Lastly, in 2010, two hotspots of functional redundancy were located on specialist species with high and intermediate trophic levels. However, like the centroid shift shown in Fig. 6, the system failed to return to the state shown in the first four years of surveys by 2010 (Fig. 6). For all years evaluated, size of empty regions in the trait space varied, suggesting that there is a change in species composition which results in a change in trait distribution within the trait space over time. The observed temporal changes in the configuration of functional redundancy confirmed that functional organization of fish communities was highly dynamic.

DISCUSSION

Importance of functional diversity metrics to monitor reef fish assemblages

We have evaluated FD metrics as ecological tools to map spatio-temporal changes in the trophic function of marine fish communities across seascapes of BIRNM, St. Croix in the USVI. Our results show that FD metrics are sensitive enough to capture habitat effects and changes through time in the fish FD of tropical marine systems, supporting the use of FRic, FDis, and FEve as ecological tools to characterize spatial variability in fish communities and monitor spatio-temporal trajectories of functional change and resilience. Our results advocate the use of these metrics to identify sites that support high levels of FD, as well as those with high functional redundancy that are likely to affect ecosystem resilience.

We postulate that FD metrics can be used with traditional biodiversity metrics (Stuart-Smith et al. 2013), such as species richness, to monitor changes in the functional organization and resilience of species assemblages. Functional diversity provides a deeper picture of ecological organization than species richness alone. For example, we found that after 2005, levels of trait redundancy in coral reef fish assemblages never returned to initial states observed during the first four years (pre-bleaching event) of the dataset. Likewise, we found low levels of functional trophic redundancy (high FDis) in fish assemblages that had high species and FRic in BIRNM. This finding suggests that only a small number of fish species inhabiting coral reefs and hard bottoms share a similar trophic niche within the fish community. This weak relationship between FRic and FDis is also documented in studies that use functional variation metrics weighted by fish species abundance at global scales (Stuart-Smith et al. 2013) and support previous evidence of narrow functional redundancy in the trophic organization of fishes in other tropical coral reefs in the Caribbean and the Indo-Pacific (Mora et al. 2016). Fish trophic groups in coral reefs in the Bahamas (Micheli et al. 2014) and in high-biodiversity areas of the Indo-Pacific (Bellwood et al. 2003, Mouillot et al. 2014, D'agata et al. 2016*a*, *b*) also exhibited low functional redundancy, with the majority of functional groups formed by one or two fish species, which represents a threat to multiple functional traits that would likely be lost under declines in species richness (Micheli et al. 2014). Although the study in the Bahamas used a different methodology to characterize FRic and redundancy than did our analysis, both studies showed that Caribbean coral reefs are highly vulnerable to the loss of functional roles in diverse fish assemblages. This low overlap in functional roles in the Caribbean means that coral reef systems experiencing harvesting of fish will have low capacity to replace the loss of key ecosystem functions resulting in greater fragility to stressors. Global studies on functional redundancy in coral reefs by Mouillot et al. (2014) conclude that "the promised benefits of functional insurance from high species diversity may not be as strong as we once hoped."

The low functional redundancy found in our reef fish assemblages seems to agree with the hypothesis that community-scale properties such as the niche complementarity influence relationships between diversity and ecosystem functioning (Loreau and Hector 2001, Williams et al. 2017). The location of reef fish species in the trait space showed that species were mainly packaged by community diet breadths, but were also dispersed along the gradients of trophic levels and habitat use. Resource partitioning in the microhabitat use and diet by fish species offers niche complementarity in food resource utilization allowing the coexistence among species in fish assemblages (Werner 1977, Ebeling and Hixon 2001). We consider that in areas of high structural complexity such as coral reefs the position of fish species in the food web and their habitat use promotes niche complementary through the low overlap of fish species in the functional trait space to maintain the trophic functions of fish assemblages.

Habitat effects on fish functional diversity

We hypothesize that the high structural complexity and high diversity of trophic niches provided by coral reefs and similar hard bottom substrata drive the strong effect of habitat on levels of fish FRic and FDis observed in our analysis across the seascape. Recognition of the ecological importance of topographic complexity (e.g., rugosity), to coral reef fishes, is not new (Luckhurst and Luckhurst 1978, Gladfelter et al. 1980, Gratwicke and Speight 2005, Graham and Nash 2013), but is now increasingly demonstrated at a range of spatial scales relevant to the movement neighborhoods of fishes using three-dimensional models of the seafloor (Pittman et al. 2007, 2009, Wedding and Friedlander 2008, Agudo-Adriani et al. 2016). For example, high-resolution maps of the seafloor have linked high topographic complexity coral reefs in the USVI and Puerto Rico to fish diversity hotspots (Pittman et al. 2007, 2009, Pittman and Brown 2011, Sekund and Pittman 2017). Thus, coral reefs with high structural heterogeneity support a rich variety of physical habitats and niches occupied by diverse fish species and functional groups (Pittman et al. 2007, 2009, Pittman and Brown 2011), and include prey refuges (Hixon and Beets 1993) which increase functional trait richness and variation in fish assemblages. In the Indo-Pacific too, the structural complexity of coral reefs was the best predictor of the differences in fish FRic and divergence among habitats, with branching coral habitat associated with highest FRic (Richardson et al. 2017).

We believe that high levels of fish FRic in coral reefs can also be explained by the habitat context and connectivity of reefs that increase local species richness through the provision of food to species with different trophic roles. In other areas of the USVI, high fish species richness in coral reefs was explained by their proximity to seagrasses (Grober-Dunsmore et al. 2007*a*, *b*), which serve as nursery and foraging areas for many fishes (Randall 1967, Ogden and Gladfelter 1983, Nagelkerken et al. 2000). In our study, more than one-third of fish species (36% of the 95 species) use seagrasses as their primary and secondary feeding habitat. These fish species represent all trophic levels, as well as specialist and generalist fishes. Seagrass beds offer a great abundance of prey biomass to reef fishes in Caribbean systems (Clark et al. 2009), which highlight the importance of protecting the ecological connectivity between marine habitats to enhance species diversity and abundance of trophic groups at the seascape level (Guillemot et al. 2011, Olds et al. 2012, 2013, 2016). This supports the need for connectivity among evaluated habitats in the BIRNM to maintain fish species trait diversity and biomass, as well as sites with high functional redundancy to avoid disruptions in the trophic function of fish assemblage.

Temporal variation in fish functional diversity

We analyzed annual changes in FD descriptors and configuration of the trait space to understand the trophic organization of reef fish assemblages through time. The temporal variation that we found in fish functional redundancy and evenness in the trait space suggests that FD metrics can be useful tools to track changes in the ecosystem function and trophic organization of fish assemblages. Using centroids of the functional trait space, we captured temporal trajectories of fish FD and changes in redundancy because the function of biotic assemblages is highly sensitive to trait presence, which is a function of temporal dynamics in species presence and abundance (Mouillot et al. 2013*b*, Stuart-Smith et al. 2013). We found significantly higher values of FRic in 2006 compared to 2005 due to an increase in species richness (Fig. 2). However, functional redundancy and evenness for 2006 were low and high, respectively, compared to previous years, which suggests that a strong reorganization in the functional trait space happened between 2004 and 2006.

The reduction in fish trophic traits in 2005 coincided with a regional mass coral bleaching event that resulted in an estimated loss of 53% of reef-building species in the USVI, followed by coral diseases and macroalgal overgrowth during subsequent years (Mayor et al. 2006, Miller et al. 2006, Rothenberger et al. 2008, Rogers et al. 2009). Because the structural complexity of reefs is driven most by corals, changes in coral cover influence coral-associated fish communities (Garpe et al. 2006) by changing body size structure (Wilson et al. 2010), reef fish predator–prey dynamics (Graham et al. 2007), and community composition (Coker et al. 2012). We observed changes in species composition and reduction in the extent of functional redundancy hotspots formed by fish species of high trophic levels and specialist diets, which constitute medium-sized classes in studied fish assemblages (Fig. 6). For example, the midwater piscivore *Scomberomorus regalis*, the pelagic piscivore *Caranx latus*, and the generalist carnivore *Alphestes afer* disappeared from the trait space after the bleaching event in 2005. The structural erosion of coral reefs caused by bleaching events (Garpe et al. 2006) can explain the absence of medium-sized fishes and changes observed in functional redundancy in the trait space. In general, reductions in reef structural complexity cause a progressive reduction in microhabitats for habitat-specialist reef fishes of small size that constitute prey for medium-sized piscivores (Graham et al. 2007). This reduction causes an indirect decline in piscivore numbers and so changes sizes of functional redundancy hotspots for these species. Other evidence of reorganization in the trophic function of fish assemblages after 2005 is observed through the similar concentration of functional redundancy hotspots for 2006 and 2008, which covered a broader area in the trait space in comparison with years prior to the bleaching event. For these two years, FEve was significantly higher in comparison with 2004, which suggests a change in species composition and abundance of functional traits. After 2005, trophic traits were more evenly distributed, and so more niches were exploited by reef fishes in the trait space.

Ecologists and managers have noted the need for metrics of resilience (Standish et al. 2014, Lam et al. 2017), particularly in light of the increasing disturbance regimes associated with climate change (Hughes et al. 2003, Bozec and Mumby 2015, Conversi et al. 2015). In our study, changes in the trait space revealed a signal of destabilization in the trophic function of fish assemblages in the BIRNM and showed that the system did not return in five years to its original functional state (Fig. 6). While this research intended to describe potential mechanisms that explain changes in the trait space, we could not relate changes in FD descriptors to variation in benthic biotic data. Future research should investigate the response of FD metrics to abiotic environment characteristics, disturbances, or levels of habitat protection on the reef community and identify the time lag that the system requires to return to its initial functional state.

ACKNOWLEDGMENTS

This study was supported by the fellowship for doctoral studies abroad of the Colombian Department for Science and Technology COLCIENCIAS and the scholarship from the International Cultural Service Program at Oregon State University. Publication of this paper was supported, in part, by the James R. Sedell Graduate Award in Fisheries and Wildlife from Oregon State University. Database of fish species was provided by the Biogeography Branch of the National Oceanic and Atmospheric Administration (NOAA). Simon J. Pittman was supported by funding from NOAA Coral Reef Conservation Program. We thank Mark Hixon from the University of Hawaii and Matthew Ramirez from Oregon State University, for providing valuable observations to improve this manuscript. Martha Patricia Rincon Diaz conceived and designed the study; conducted the literature review, data compilation, and verification of functional traits; conducted data analysis; and wrote this manuscript. Simon J. Pittman provided data and academic guidance, and Ivan Arismendi and Selina S. Heppell provided guidance on data analysis. All coauthors provided editorial advice.

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