Spatial Changes in Fish Functional Diversity in the U.S. Caribbean

Cambios Espaciales de la Diversidad Funcional Íctica en el Caribe Estadounidense

Changement de la Distribution Spatiale de la Diversité Fonctionnelle des Poissons dans les Caraïbes (U.S.)

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ABSTRACT

Studies on fish functional diversity have rarely considered the ecological roles of reef fishes during different life stages, which are influenced by ontogenic shifts in diet, habitat use, and distribution. Here, we investigate functional diversity as an ecological response metric to understand spatiotemporal patterns and processes that influence the functional organization of fish assemblages on U.S Caribbean coral reefs. Functional diversity quantifies the relative magnitude of similarities and differences among species based on the value and range of their functional, morphological and behavioral traits. This metric allows us to identify the niche space for each species by considering both trait redundancy and relative species abundance. Functional diversity does not clump species within a guild, as species richness of trophic groups do, but instead captures the variability in species traits. We consider the spatial ontogenic shifts of both juvenile and adult fishes and their traits related to use of habitat-specific food resources. We evaluate changes in fish functional diversity inside the MPA Buck Island Reef National Monument in the U.S. Virgin Islands. We provide insights about the variability in functional diversity analysis by considering fish life stages and quality of functional trait information. Our approach is transferable and can be applied to similar assessments elsewhere in the Caribbean.

KEY WORDS: Functional diversity, fish assemblages, spatiotemporal variation, Marine Protected Areas

INTRODUCTION

Traditional metrics to evaluate effects of habitat protection on fish communities include spatial and temporal changes in species richness and trophic group' richness and biomass, but few studies have considered the consequences for fish functional diversity (FD). Likewise, the impacts of protection by considering the spatial ontogenetic shifts of fishes and the trophic roles of fish juveniles and adults have yet to be considered. FD is an ecological metric that quantifies the relative magnitude of similarities and differences among species based on the value and range of their functional, morphological and behavioral traits related to an ecosystem function (Cadotte et al. 2011, Diaz and Cabido 2001, Petchey and Gaston 2006). This metric provides an idea of the niche space used by each species by considering both traits redundancy and species abundance (Cadotte et al. 2011, Diaz and Cabido 2001, Petchey and Gaston 2006). This metric does not clump species within a guild, as species richness of trophic groups do, but instead captures the variability in species traits.

FD in reef fish communities is influenced by changes in the ecological roles that species have due to ontogenetic shifts in diet, habitat use, and distribution during their fish life stages. It can provide insights on the effects of fisheries and protection levels on functionality of habitats and resiliency of fish communities to disturbances. However, the use of this metric to understand resilience of marine fish communities still needs to be tested. This study investigates FD as an ecological response metric to understand spatiotemporal patterns and processes that influence the functional organization of fish assemblages on U.S Caribbean coral reefs, and identifies traits that are important to explain variation in FD. We worked on the hypothesis that fish FD varies by habitat type and fish life stages due to different diet and habitat requirements that fish species exhibit during their ontogeny. We focused on the different roles that fishes play as juveniles and adults. Our approach is transferable and it can be applied to similar assessments elsewhere in the Caribbean.

METHODS

Study Sites

We focused on eleven databases of fish community surveys that covered the Marine Protected Area (MPA) Buck Island Coral Reef National Monument located in St. Croix, U.S. Virgin Islands (USVI) (Figure 1). This is a permanent No-Take Zone established in 1961 (NOAA, NOS 2009). Habitat composition of the studied sites included primarily coral reef and colonized hard bottoms, with secondary cover including seagrasses, macroalgae, and unconsolidated bottoms. The presence of a variety of habitat types in studied sites assured broad representation of local coastal fish communities and important benthic habitats used during fish ontogenetic shifts.

Characterization of Fish Communities

Communities were characterized by the Fish Assessment and Monitoring Program and the Biogeography Branch of the National Oceanic and Atmospheric Administration (NOAA) in Puerto Rico, and the U.S. Virgin Islands from 2001 to 2012

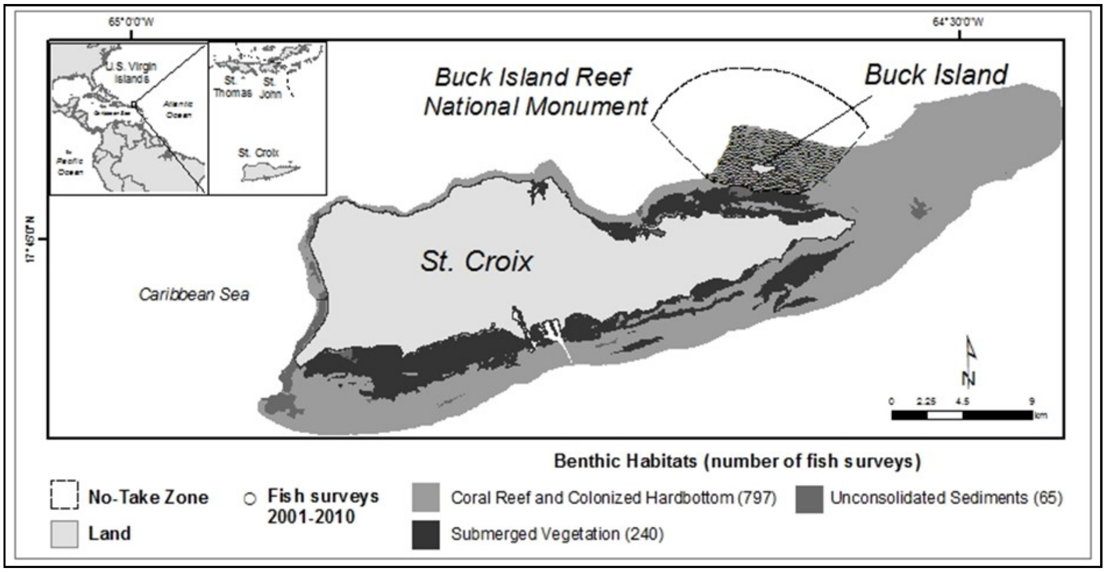

Figure 1. Map of the study sites.

(NOAA et al. 2007a,b,c; http://www8.nos.noaa.gov/biogeo_public/query_main.aspx). Location of surveys were established in a random stratified sample design by habitat type, and conducted by following a standardized technique of 100 m^2 belt transect visual census. Information gathered in each census included identification of fish species, an estimation of the fork length at 5 cm classes up to 35 cm, and number of individuals to calculate fish biomass by life stages (NOAA et al. 2007a, b, c).

Compilation of Fish Functional Traits for the U.S. Caribbean

Fish traits related to the trophic function of marine fish species in the U.S. Caribbean were populated in a database of 166 fish species recorded by NOAA in the MPA. For more details regarding trait justification and compilation please review the extended abstract "Information gaps in the trophic roles of Caribbean reef fishes" by Rincon-Diaz et al. 2016.

Functional Diversity (FD) Metrics per Habitat Type

Calculation of FD metrics was conducted only for adult stages because little information was found for juvenile stages (17% of total listed species). The indexes selected to evaluate temporal and spatial changes in fish FD in the MPA were Functional Richness (FRic), Functional Dispersion (FDis) and Rao Quadratic Entropy (RaoQ). The multidimensional functional diversity indexes were calculated based on traits of listed fish species and their abundances expressed as biomass according to values calculated by NOAA in each surveyed site. These indexes were selected because they can handle categorical traits, are multidimensional (Schleuter et al. 2010), do not correlate with species richness (Laliberté et al. 2015), and give information about functional trait redundancy within the community and between species (Laliberté et al. 2015, Schleuter et al. 2010). FRic estimates the convex hull volume of a trait space to measure how much of the niche space is occupied by species present in a community (Schleuter et al. 2010, Stuart-Smith et al. 2013, Villéger et al. 2008). FDis measures the average distance to the centroid in the trait space of a community (Laliberté et al. 2015). This measure of multivariate dispersion is not correlated to species richness (Laliberté et al. 2015). RaoQ measures the abundance weighted variance of dissimilarities between species pairs in a multi trait space within a community (Laliberté et al. 2015, Schleuter et al. 2010). FD indexes were calculated by using the PAST program and FD package (Laliberté et al. 2015) available for R Project for Statistical Computing, and described for each habitat type.

Spatial and Temporal Variation of Fish FD by Habitat Type

The spatial and temporal variation of fish FD by habitat type was identified among survey sites within the MPAs boundaries, and accounting for habitat and time effects. A non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008) was used to test for spatial and temporal variations in functional diversity indexes since it allows for interactions among factors. The effects of habitat type, year of survey, and interaction between these factors were tested. Statistical differences were established with the PERMANOVA analysis by p-values < 0.05 (Mateos-Molina et al. 2014). Analyses were conducted using the PAST Program Version 3.08 (Hammer 2015). The identification of functional traits that explain variation in FD was conducted by dropping each trait from the calculations of the three functional indexes, and then indexes values were compared with indexes calculated with the full pool of traits by using linear regressions (Stuart-Smith et al. 2013). Coefficients of determination (R^2) were compared between indexes calculated with all and dropped traits to identify traits that contribute more to explain variation in functional diversity indexes (Stuart-Smith et al. 2013). Low coefficients of determination (R^2) with statistical significance indicated traits that contribute more to functional diversity among other dropped traits with higher coefficients (Stuart-Smith et al. 2013).

RESULTS

Spatiotemporal changes in fish functional diversity (FD): Our results show that the three FD indexes varied over time and habitat, with an interaction between these factors ($p < 0.05$) for the MPA Buck Island Coral Reef National Monument. Statistically significant high values of functional diversity indexes were found for 2006 (Figure 2). We found that coral and colonized hard bottoms were the habitats that supported high functional richness, and variation among the fish community and between species.

Traits that explain variation in fish FD: Our results show that the consumed prey items and feeding habitats are important species traits to explain variation in functional richness (FRic) for evaluated fish communities in the MPA. Significant associations (R^2) for consumed prey items ranged between 0.53 and 0.69, and for feeding habitats between 0.52 and 0.63. The trophic level of fish species and consumed prey items are important traits to explain functional variation in the community (FDis) and between species (RaoQ). Variation of FD is explained by associations (R^2) for species trophic level that ranged between 0.53 and 0.72, and between 0.67 and 0.76 for consumed prey items. Variation in RaoQ is explained by coefficients of determination of species trophic level that varied between 0.35 and 0.60, and between 0.53 and 0.65 for consumed prey items.

DISCUSSION

This study is the first to evaluate functional diversity (FD) as an ecological metric to understand changes in the functional organization of fish communities in MPAs of the U.S. Caribbean. We successfully compiled trait information related to the trophic function of adult stages for 166 fish species recorded in marine habitats of the MPA Coral Reef National Monument located in St. Croix, U.S. Virgin Islands (USVI), and combine these data with species abundances to obtain three important metrics of functional diversity: Function Richness, Dispersion, and Quadratic Entropy between 2001 and 2010.

Spatiotemporal Changes in Fish FD

Our results support the hypothesis that FD in adult fish assemblages varies by habitat. We also found that this variation is correlated with an interaction between habitat type and time. Coral reef areas were found to be the habitat that supports more functional richness and variation within the studied fish assemblages and between fish species overall studied in benthic habitats within the MPA. We found also a large variation in FD metrics, which can be explained by the variety of sub habitat categories included in this main habitat type such as colonized pavements with channels, colonized bedrock and pavement, linear reefs, patch reefs, and scattered coral rock. We did not analyze FD by these sub-habitat categories because the NOAA Fish Monitoring Program selected studied sites based on the three main habitat types, and there was a small sample size of sub-habitat categories to be represented in the functional diversity analysis.

The fact that coral reefs and colonized bottoms supported high fish FD and variation can be explained by their high structural complexity in Buck Island (Pittman et al. 2007). The high structural complexity of reef systems allows for a variety of physical habitats and niches that are occupied by fish species, and provides also refuge for a high number of preys (Hixon and Beets 1993). Our results supports also the assumption that FD covariates with species richness (Schleuter et al. 2010). High species richness was found in coral reef areas that exhibit high mean rugosity indexes (Pittman et al. 2007, 2009), as well as a large adjacency to seagrasses (Grober

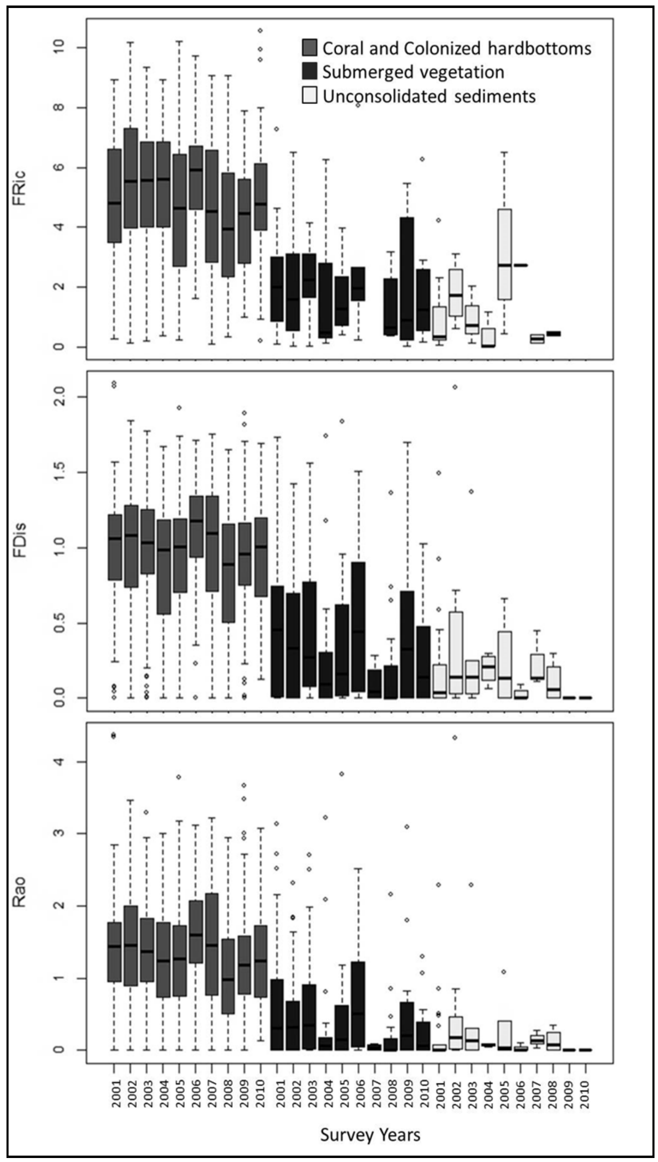

Figure 2. Functional diversity indexes of fish assemblages in adult stage between 2001 and 2010.

-Dunsmore et al. 2007) in Buck Island and other areas of the U.S. Virgin Islands. This fact confirms the strong relationship between species richness and FD richness. The high functional variation showed by FDis and RaoQ indexes in coral reef areas suggest that redundancy of trophic roles in studied fish assemblages is low compared to submerged vegetation and unconsolidated sediments. This finding means that each species in coral reef areas occupies an exclusive niche within the community that cannot be replaced by other fish species. Our results show the importance of protecting coral reefs, adjacent benthic bottoms, and their fish assemblages as a whole to achieve goals of MPAs to protect sites of high functional redundancy and resilience.

High values of FD indexes were found for the year 2006, suggesting a strong reorganization of the functional trait space in comparison with the previous years. We found low values of FD indexes for 2005, which suggests a reduction in trait richness and variation. Low FD values coincide with a large coral bleaching event occurred in the Caribbean in 2005. Although we need further analyses, it is plausible that this disturbance affected the functional organization of fish assemblages as is suggested by changes in the functional trait space and gradients observed between 2005 and 2006 (Figure 3). For example, there is an important turn over in feeding categories of fish species that defines boundaries of the functional trait space, as well as changes in gradients of traits such feeding time and distribution of feeding categories and trophic levels between the two years. Important changes found in the trait space can be supported by traits that explain FD variation in the fish assemblages such as trophic levels of fish species and consumed prey items.

Our analysis gives insights about the important habitat types that drive FD, and traits that drive its variation. Our analysis shows that protection efforts on coral reef areas that support high levels of functional richness and variation are important strategies to manage for ecosystem resilience. This study contributes to the understanding of ecosystem changes in MPAs and impacts on the fish FD, by providing useful methods for application in similar assessments elsewhere in the Caribbean and worldwide.

Gaps in Knowledge of Trophic Roles for Juvenile Stages

We found a high lack of knowledge on the trophic ecology of juvenile stages not only in Puerto Rico and the U.S. Virgin Island, but also throughout the Caribbean region. Only 17% of species in juvenile stage were characterized with functional traits that describe their trophic roles. The lack of information for juvenile stages of reef fish species limited our analysis to compare FD among fish life stages and habitats. These gaps in information signify a major threat for ecosystem-based management and conservation efforts for juvenile stages. Gaps can be filled with important collaborations among researches and fish experts from the Caribbean region. We established a side project to join collaborators that want to provide primary and anecdotic information about the functional traits evaluated in this project. Collaborators can provide references (e.g. papers, reports, class projects, and thesis manuscripts), as well as anecdotic information through a survey created for this purpose:

(http://oregonstate.qualtrics.com/SE/?SID=SV_brvBEAO93amWBlH).

Functional trait information gathered through this process will be available for the public in open access journals, the Heppell Lab web page (www.oregonstate.edu/heppell), and the on line repository for PhD thesis of Oregon State University library. Contributors will be acknowledged as sources of information for these products.

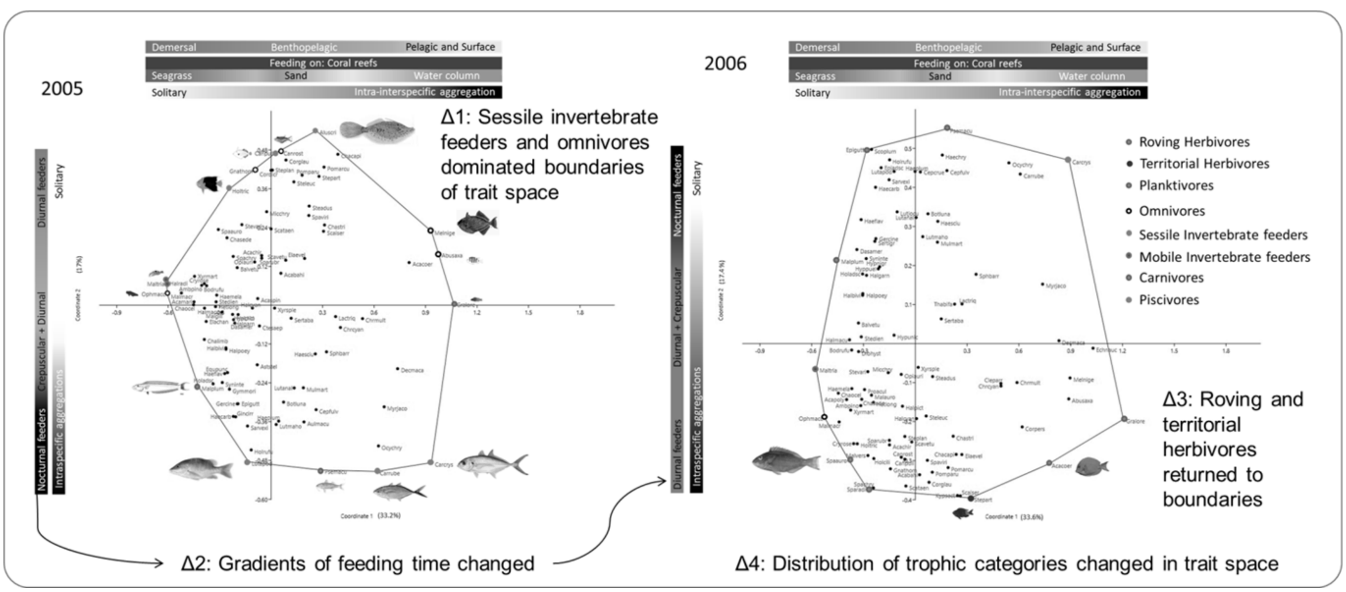

Figure 3. Functional trait space of fish assemblages in 2005 and 2006. Symbols: changes in the trait space (Δ).

ACKNOWLEDGEMENTS

This study was supported by the fellowship for doctoral studies abroad of the Colombian Department for Science and Technology COLCIENCIAS. Database of fish species was provided by the Fish Assessment and Monitoring Program and the Biogeography Branch of the National Oceanic and Atmospheric Agency (NOAA). We thank Patricia Quintero Fajardo for her assistance in the searching of literature for some fish species.

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