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Abstract

Increased rates of species extirpation or extinction have often been attributed to the foraging behavior of invasive predators, with drastic effects on native food webs. In the Caribbean, the invasive red lionfish (*Pterois volitans*) is of primary concern, as it reduces the overall recruitment and biomass of reef fishes by as much as 80% and 65%, respectively. Understanding the functional role that this predator plays in the context of entire communities is critical to assessing how it impacts those that have already experienced regime shifts due to disturbance. Here, a trait-based ecospace was employed to characterize the functional role of red lionfish trophic behavior, focusing on a regional pool of reef fishes from Jamaica, Cuba, and the Cayman Islands. A high-resolution model of a Greater Antilles coral reef food web, including micro- and macrobiota, producers and consumers, and invertebrates and vertebrates, was used to assess the impacts of *P. volitans* on community structural parameters such as food chain length, the number of interactions, modularity, and trophic position. Results indicate that lionfish select prey based on specific traits, foraging primarily on those that are diurnal, below a threshold of total length, occur higher in the water column, do not possess a physical defense, and are either herbivorous,

invertivorous, or omnivorous. The functional role of lionfish significantly overlaps with a number of endemic high trophic level predators, such as *Rhizoprionodon porosus*, *Negaprion brevirostris*, and *Scomberomorus regalis*. Lionfish could be fulfilling trophic roles previously vacated by extirpated species, as the prey of the lionfish were found to be functionally indiscriminate relative to those of extirpated predators such as *Sphyrna tiburo*, *Carcharhinus acronotus*, and *Galeocerdo cuvier*. In addition, food web results suggest that lionfish alter the trophic dynamics of the entire reef community by increasing the total number of interactions and changing trophic level structure. Interestingly, the invasive lionfish may be restoring and augmenting some effects of predation otherwise lost to species extirpation, providing an alternative view to its detrimental effects on resilience of Caribbean marine systems.

Keywords: Caribbean Sea, food webs, functional diversity, invasive species, lionfish, trophic behavior

Introduction

The introduction of non-native species due to globalization leads to the homogenization of biotas with impacts on economic welfare and conservation worldwide. Besides financial loss, non-native species have the potential to impact biodiversity, food webs, habitats, and ecosystem functions important to community structure and persistence (Ruiz et al. 1997; Mooney and Cleland 2001; Crooks 2002; Clavero and Garcia-Berthou 2005; Pimentel et al. 2005; Albins and Hixon 2008; Lockwood et al. 2013). Marine invasions are no exception and are now recognized as drivers of biotic and environmental change at multiple ecological scales (Ruiz et al. 1997). The Indo-Pacific red lionfish (*Pterois volitans* Linnaeus, 1758), introduced to the tropical

Western Atlantic as early as the mid-1980s, is now an invasive marine fish and is considered a major threat across an extensive range of habitats including reefs, mangroves, seagrasses, and artificial structures (Albins and Hixon 2008; Morris and Whitfield 2009; Sutherland 2010; Albins 2012). Its alleged introduction into Florida waters by aquarists resulted in a rapid expansion into marine habitats that now extend from North Carolina to Venezuela, and it is expected to advance even more southward in the future (Morris and Whitfield 2009; USGS Database 2017).

Given the extent of the invasion, ecologists are concerned about the potential impacts of lionfish on important fisheries, reef communities, and ecosystem functioning as coral reefs around the globe suffer additional anthropogenic-driven degradation and regime shifts (Jackson 1997; Hughes et al. 2003; Lesser and Slattery 2011). The voracious feeding behavior of the lionfish in its invasive range has been known to impact the structure of coral reef communities, with documented studies showing that the trophic habits of the lionfish alone alter the composition and abundances of herbivorous and piscivorous fish faunas within reefs (Albins and Hixon 2008; Green et al. 2011; Green et al. 2012; Lesser and Slattery 2011). For example, Albins and Hixon (2008) estimated that lionfish predation reduced native fish recruitment in the Bahamas by about 80%, while Green et al. (2012) observed that between 2008 and 2010 an increase in *P. volitans* abundance coincided with a 65% decrease in prey fish biomass in New Providence reefs.

Many vertebrates and higher trophic level consumers have been extirpated from Caribbean reef communities due to historical overfishing, vacating trophic roles and emptying niches that would otherwise be filled by native top predators (Jackson 1997; Paddock et al. 2009; Roopnarine and Hertog 2010). The absence of predators has initiated trophic cascades leading to

altered marine community structure and function (Friedlander and DeMartini 2002; Ritchie and Johnson 2009; O’Leary and McClanahan 2010; Estes et al. 2011; Frank et al. 2011) including subsequent secondary extinctions (Roopnarine and Hertog 2010). Ecologists speculate that lionfish have the potential to compete with the remaining native predators, thus affecting the biodiversity of already stressed environments and thwarting successful management efforts (Morris and Whitfield 2009; O’Farrell et al. 2014). However, it is also hypothesized that the establishment of lionfish in these predator-deprived communities could replace some of the trophic structure previously provided by the activities of endemic higher consumers (O’Farrell 2014; Bellwood and Goatly 2017; Roopnarine and Dineen 2018). The extent to which invasive lionfish compete with other species, however, or replace others functionally remains uncertain.

Currently, many studies of invasive lionfish document species-specific interactions observed during experimental and field research (Lowe et al. 2000; Green and Cote 2014). However, these approaches are often regionally limited and the species vulnerable to invasive species consumption vary over time and space (Green and Cote 2014). Past studies based on taxonomic data suggest that lionfish function as opportunistic generalists, yet the broad diet of the lionfish has been shown to have a degree of specialization (Layman and Allgeier 2012; Green et al. 2014; Chappell and Smith 2016; Peake et al. 2018). This observation conveys a necessity for further analyses of lionfish prey selectivity and trophic breadth at a time when other regions of the world, such as the Mediterranean, experience the impacts of lionfish invasion in its early stages (Turan et al. 2014; Kletou et al. 2016).

Functional diversity, a metric of the number of ways in which species interact with their environment, is an appropriate for predicting the trophic impacts of invasions in novel ecosystems and will be useful in understanding lionfish behavior in broader contexts. Functional

diversity is broadly recognized as essential for maintaining ecological resilience in systems affected by disturbance (Peterson et al. 1998; Elmqvist et al. 2003; Bellwood et al. 2003; Nystrom 2006). To date, little work has been done to explore lionfish diet preferences and the effects of its predation from a functional perspective (Green and Cote 2014).

In this study, we address whether *P. volitans* represents a functionally novel predator in the Greater Antilles and if it selects for specific functional characteristics in its prey. We also assess if the lionfish replaces any predatory function previously existing in reef systems that are now bereft of higher predators due to historical overfishing, using a network of trophic interactions to examine how its trophic behavior impacts reef dynamics at the community level. In future work, these analyses could aid in predicting which taxa might be detrimentally impacted by lionfish trophic behavior in invaded reef communities that are understudied, as well as provide important information for management and research efforts about how lionfish impact communities both functionally and structurally.

By using a functional or trait-based approach, we examine whether or not *P. volitans* forages indiscriminately and quantify the breadth of reef functions that are impacted by its diet. To do this, we developed a functional ecospace focused on three reef communities in the Greater Antillean region to assess the trophic impacts of lionfish on Caribbean reef functional diversity. In addition, we utilized a highly resolved Greater Antillean reef food web to assess the potential impacts of *P. volitans* on ecosystem structure. The food web model is used to estimate species trophic properties, including trophic level, food chain lengths and prey resource overlap, and the ecospace provides a metric for interspecific similarities based on functional traits.

Methodology

116 *The Functional Ecospace Model*

117 The foraging selectivity of lionfish was determined by projecting the functional traits and
 118 life habits of known lionfish prey into a Novack-Gotshall (2007) functional ecospace. This
 119 functional ecospace is comparable to the theoretical morphospaces used by morphologists, where
 120 a specimen's or taxon's position in multivariate morphometric or meristic state space
 121 summarizes their attributes relative to others included in the analysis. Characters (traits) used in
 122 the present model (see next section) were chosen based on their potential relevance to prey
 123 vulnerability and each prey's functional role in the reef. *N*-dimensional combinations of
 124 character states in the framework describe the ecological diversity of lionfish prey with respect to
 125 their community assemblages (fish only) in three regions within the Greater Antilles: Cuba,
 126 Jamaica, and the Cayman Islands.

127 Diversity data for these regions were derived from Roopnarine and Hertog (2012), an
 128 extensive food web study based on detailed occurrence data from REEF (<http://www.reef.org/>),
 129 GBIF (<http://www.gbif.org/>) and the published literature, encompassing decades of work
 130 describing the life habits and ecology of the species present. Though Roopnarine and Hertog
 131 (2012) contains a broad range of taxa, our model only focuses on the 177 species of fish which
 132 represent a pooled ichthyological composition across the three regions, with updates on changes
 133 to biodiversity over the past 10 years due to extirpation. Ecologies of the fishes included in this
 134 trait-based framework were obtained through extensive literature-based research and FishBase
 135 (2017).

136 Through scoring the presence or absence of categorical traits (and log-transforming the
 137 continuous trait data to account for additional variation), a principal components analysis (PCA)
 138 was used to ordinate the positions of species in ecospace (represented by points), by reducing the

multivariate dataset to fewer dimensions, representative of summary linear combinations of the original, higher dimensional data. These dimensions describe gradients of variation in the life habits of the included species. The ordination of species in the analysis reflect their positions in multidimensional functional space, with the relative distances between them maintained. As a result, species that are similar in function are closer to each other in the PCA-transformed space relative to those that are more different. PC analyses were performed with the software PAST 3.25 (Hammer et al. 2001) and STATA 14.2.

The PCA model was utilized to determine if lionfish are functionally distinct from other reef predators, comparing the dietary preferences of the lionfish to those of other extant species who occupy similar network trophic positions or which have been extirpated locally. Network trophic position (NTP), a measure of the relative position of species in a food web network, was calculated using the three food webs constructed for Jamaica, the Cayman Islands, and Cuba (Roopnarine and Hertog 2012). Roopnarine and Dineen (2018) defined NTP as the average shortest distance of a species' prey species to a primary producer in a metanetwork, where "distance" is the number of steps between species on a food chain. Predators with fewer than 15 known prey species were omitted from the analysis. Through this methodology, we can assess the degree to which lionfish diet overlaps with those of endemic species, as well as determine if the functional role of the lionfish potentially compensates for the loss of higher predators in the reef community due to local extinction.

Functional Traits

Characters (traits) were chosen based on their potential relevance to prey vulnerability and were divided into multiple states when applicable. The characters are logically distinct from

one another, with individual states representing different life habits in the framework. Only autecological characters were used and describe the following: 1) resources, such as general diet and habitat; 2) morphological features and characteristics relevant to resource acquisition and defense; and 3) other key characters, such as body size, depth distribution, and life history (Novack-Gotshall 2007).

A total of eight categorical and continuous life habits were used to describe the fish in this study. The presence of chemical and physical defenses together (e.g. barbs, spines, and toxins) were binary coded as presence or absence data. Common maximum depth was coded as continuous in meters and derived from FishBase (2017). Diel behavior was coded using four categories: diurnal, nocturnal, crepuscular, and diurnal and nocturnal, represented numerically. Body size was represented by total length in centimeters. Trophic habit was coded using the following categories describing the primary diet of each fish: planktivore, algal herbivore (consuming fleshy, filamentous, or macroalgae), seagrass herbivore (feeding on seagrass), mobile invertivore (feeding on invertebrates that are mobile such as crustaceans, gastropods, mobile bivalves etc.), sessile invertivore (feeding on invertebrates that are attached to a substrate such as ascidians, sponges, corals, etc.), piscivore (fish that consume other fishes), and omnivore (fish that consume both plant and animal material). Herbivore type was further divided into two categories as grazer or scraper. Foraging habitat was coded using three categories describing habitat type: reef, seagrass, and mangrove. NTP was coded as continuous, and the NTP of each species was derived from the food web work of Roopnarine and Hertog (2012) where the NTP of each species was averaged amongst the Jamaican, Cuban, and the Cayman Islands webs. All continuous trait data were log-transformed to account for variation at different scales.

Measuring the Functional Impacts of Lionfish

Functional diversity was measured as the distribution of species in the multidimensional trait space, with the relative distances between species representing the magnitude of functional differences, and the orientation of the distance representing the nature of the differences. The functional aspects of predator behavior, therefore, can be assessed when quantifying the functional diversity of their prey. To quantify the functional diversity of prey groups, we used the average dissimilarity among species (distance) as a measure of functional variability within ecospace, where the Euclidean distances between and amongst prey are measured for each predator under examination. This method is robust to variations in sample size, as the distances between and among species measure actual differences in function rather than scaling with the total amount of ecospace occupied. However, because this measure utilizes dissimilarity, we use the term functional disparity.

Two measures of functional disparity were used to compare the trophic breadth of the lionfish to those of endemic species that share a similar NTP and that may have been extirpated from our study region. The first measure of functional disparity is derived from Foote's morphological definition (1993), where disparity is represented as the mean squared Euclidean distance among species to the group centroid in unreduced morphospace, summarizing the absolute variance of each set. However, because our work consists of both continuous and categorical variables, we adapted this definition within the framework of our ecospace model by first reducing the space with a principal components analysis, and then summarizing the multidimensional functional space with the first 10 principal components, representing approximately 80% of the total variance. The formula we use for functional disparity is:

$$FD = \frac{\sum_{i=1}^n d_i^2}{(n-1)}$$

where n is the number of species within a group and d_i is the Euclidean distance of the i th species from the group centroid in principal component functional ecospace.

A second measure of dissimilarity utilizes the pairwise distances between all prey within a predator's set of prey. Although the data here are not summarized in a single metric, the distributions of pairwise distances for each prey set provide an alternative method for quantifying and visualizing functional disparity. Because the data are nonparametric, each prey set was compared to that of the lionfish using Kruskal-Wallis rank sum tests in STATA 14.2.

The Greater Antillean Food Web

Extensive work in the Greater Antilles, specifically, has provided a wealth of knowledge about Caribbean coral reef communities: their dynamics, biodiversity, and ecology (Hughes 1994). Moreover, studies documenting current and historic food webs in the Caribbean are conveniently accessible for use and provide crucial information for understanding the consequences of species extinctions and invasions (Roopnarine and Hertog 2012; Roopnarine and Dineen 2018). Published reports and syntheses of reef assemblages and species interactions in the Caribbean are publicly available online through Fishbase (2017) and REEF (2011). Peer-reviewed publications on lionfish diet, mainly derived from studies examining gut contents and direct field observations, are also abundant for this region (Albins and Hixon 2008; Green et al. 2011; Green et al. 2014).

Roopnarine and Hertog (2012) present detailed reconstructions of food webs from three different geopolitical regions of the Greater Antilles, including Cuba, Jamaica, and the Cayman Islands, with several coral reef and seagrass habitats highlighted in their dataset. This work is derived from a literature and database review (see references in Roopnarine and Hertog 2012). It

contains data on trophic interactions for the entire reef community, taxonomic composition, guild structure, and community dynamics of several Greater Antillean reefs.

Food webs derived from these reconstructions were used to examine how the presence of lionfish and the absence of extirpated predators may affect community structure and dynamics in the Greater Antilles. Species that share the same trophic habits and habitats were partitioned into groups, and members that share the same predators and prey (trophospecies) within those groups were further divided into trophic guilds. Trophic guilds are linked if members of one guild are likely to prey upon those in the other. This can occur unidirectionally between guilds (interguild predation), bidirectionally between guilds (bidirectional interguild predation), and within a single guild (intraguild predation).

Using this parameterization, three webs were constructed with the following treatments using community compositional data from REEF and reconstructions of food webs from Roopnarine and Hertog (2012) for the Greater Antilles region: 1) The Pristine Food Web contains 754 species partitioned into 265 trophic guilds, representing the entire reef community of the last 10+ years and without the invasion of the lionfish. 2) The Impacted Food Web contains 748 species and 259 trophic guilds, representing the reef community with the removal of locally extirpated predators and the introduction of lionfish into the region (representative of the actual community at present). For example, *Negaprion brevirostris* and *Epinephelus itajara* were removed from the food web since they have been recently extirpated from Jamaica (according to REEF observations) and being historically present in past records. 3) The Lionfish Free Food Web contains 747 species and 258 trophic guilds, representing the reef community with both the extirpated predators and the lionfish removed from the network (perhaps representing reef communities with successful lionfish eradication).

Five hundred species-level networks were generated from each of these guild-level food webs, each representing a possible pattern of community interactions at a single instance of time. A species-level network specifies interspecific interactions, in context to the guild-level webs. These networks are drawn from a finite number of food web topologies that are consistent with and constrained by the actual observed ecologies and interactions of the community at the guild level, and encompass uncertainty of interspecific interactions (see Figure 1).

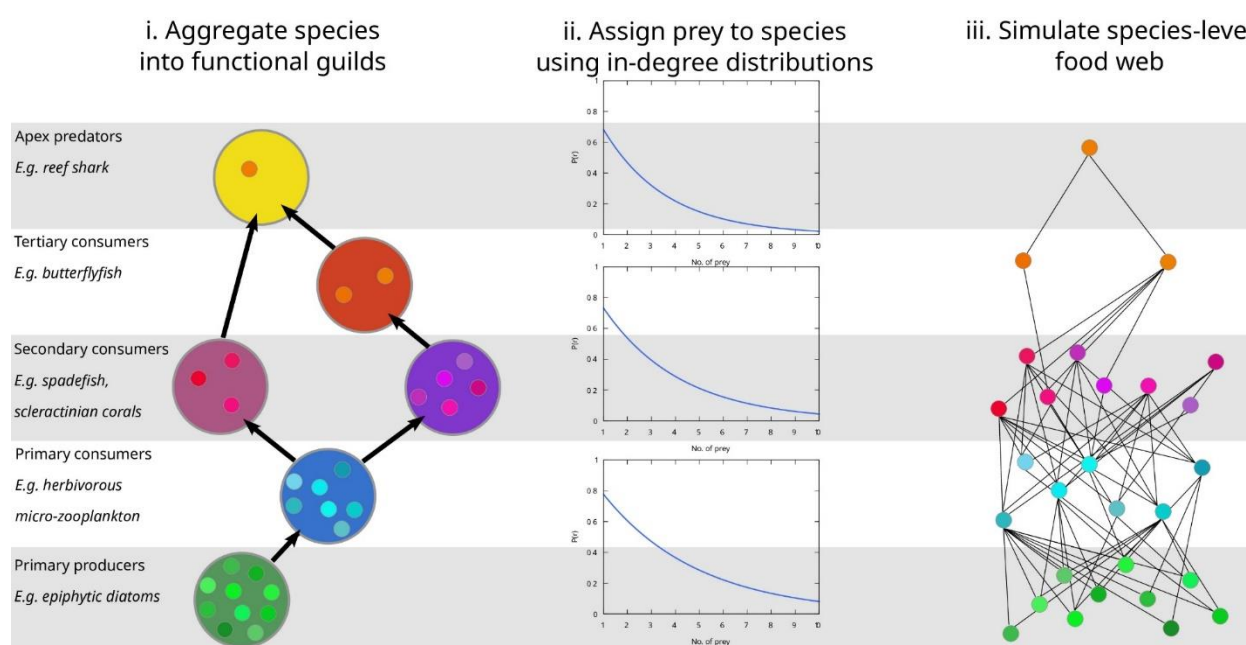


Figure 1. Schematic of estimation of a species-level food web from a guild-level, functional metanetwork. Consumer in-degree distribution models are shown in the middle column. Distributions vary according to the maximum number of prey available to any species in a particular guild. Random draws from the distributions determine the number of prey per consumer in the species-level food web.

To accomplish this, a trophic link distribution was used to describe the distribution of prey per species within a guild, stochastically determining the number of prey assigned to each species. The number of prey assigned to a species ranges from 1 to the total number of species in guilds specified as prey to the guild in focus in the food web (Figure 1). Past surveys of trophic

link distributions suggest that a majority in nature are hyperbolic “decay” distributions, where most species in food webs are biased toward low dietary breadths and are more specialized than generalized in their diet (Dunne et al. 2002; Roopnarine et al. 2007; Williams 2009; Roopnarine and Dineen 2018). The distribution used for the Greater Antillean web was determined empirically by a power law function (Roopnarine and Dineen 2018): $\ln(p) = 3.48 - 0.78[\ln(r)]$, where p is the number of consumer trophospecies and r is the number of prey trophospecies per consumer trophospecies. This repeatable methodology accounts for natural variation and observational uncertainty as community topology can vary temporally and spatially (Eveleigh et al. 2007; Roopnarine 2017).

Species-level networks were described using several network metrics, including modularity, connectance (the density of interspecific interactions), NTP distribution, the total number of interactions, and maximum food chain length. Modularity measures the partitioning of interactions within a network where subsets of nodes (species) interact more frequently with each other but less frequently with other subsets than expected if interactions occurred randomly (Newman 2004). To obtain modularity, we used a method developed by Blondel et. al. (2008) in the network visualization software Gephi, where Newman’s modularity algorithm was applied to generate replicate modularity measures for the three networks.

Results

Our ecospace analysis, comparing species scores on the first two principal components of the functional matrix of observed lionfish prey and non-prey, suggests that *Pterois volitans* selectively forages for prey with specific traits - namely herbivory, invertivory, omnivory, diurnal activity, smaller body size, species living higher in the water column, and not possessing

a physical defense (Hotelling's T^2 , $F(2, 174) = 10.352$, $p < 0.001$; Figure 2A). "Predicted" lionfish prey, that is, species sharing the same prey and predators as lionfish prey in the food web, but which have not been observed to be eaten by *P. volitans*, are encompassed in the functional space defined by the observed prey. The predicted prey are functionally indistinguishable from the observed prey that belong to the same trophospecies guilds (Hotelling's T^2 , $F(2,22) = 2.2195$, $p = 0.132$). Those species tend to be algal and seagrass herbivores, grazers and scrapers, and invertivores of mobile species (Figure 2B).

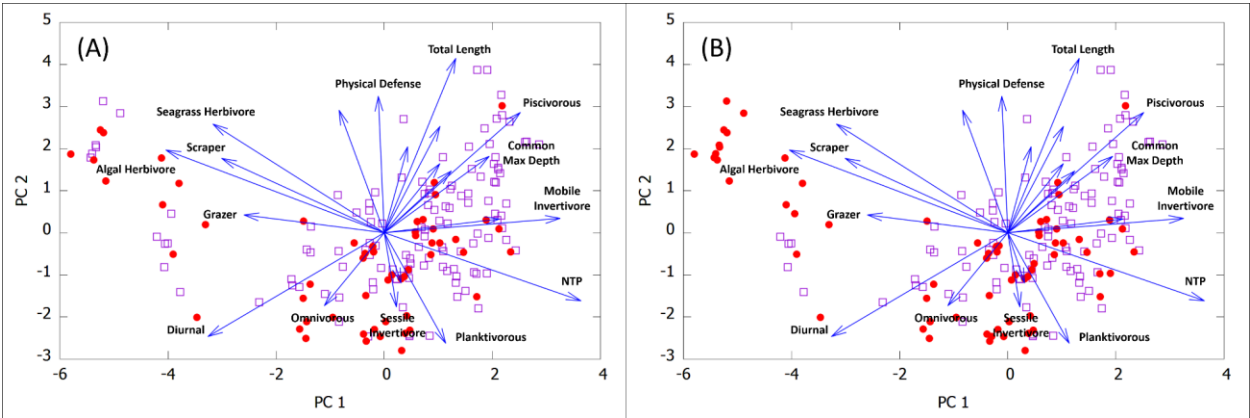


Figure 2. Lionfish diet in functional ecospace. Distribution of (A) observed lionfish prey in ecospace (red circles), and (B) complete set of lionfish prey (observed and predicted; red circles) in ecospace relative to other fishes concurrently living in the Greater Antillean coral reef ecosystem (purple squares). Blue vectors in ecospace represent the direction and strength of specific traits driving the position of species relative to Principal Components 1 & 2.

Identical analyses were conducted for piscivores with the same NTP as *P. volitans* (Table 1; Figure 3), and for piscivorous species that have been recently extirpated from Cuba, Jamaica, and the Cayman Islands (Table 1; Figure 4). Though many of these species are considered generalist predators (Randall 1967), our results suggest that, like the lionfish, they also actively select for certain traits in their prey, and that non-prey species may possess life habits that constrain their predatory behaviors (Table 1; Figures 3 & 4). The positions of prey in our

functional ecospace model and the trait vectors drawn in Figures 3 and 4 illustrate how these species selectively forage for prey within our localities.

Table 1. Ecospace prey comparisons of the high trophic level predators and the lionfish.

Hotelling's T-squared results comparing the ecospace coordinates of the prey to the species not preyed upon (nonprey) by the species listed, the non-overlapping observed lionfish prey to the prey of the species listed, and the non-overlapping complete set of lionfish prey (observed and predicted) to the prey of the species listed.

Species	Category	vs. nonprey			vs. observed lionfish prey			vs. complete set of lionfish prey		
		T-sq.	df	p	T-sq.	df	p	T-sq.	df	p
<i>Negaprion brevirostris</i>	Same NTP	29.655	2, 174	<0.001*	0.078	2, 62	0.926	2.769	2, 52	0.072
<i>Rhizoprionodon porosus</i>	Same NTP	32.129	2, 174	<0.001*	0.058	2, 63	0.944	2.965	2, 53	0.060
<i>Scomberomorus cavalla</i>	Same NTP	9.190	2, 174	0.011*	17.442	2, 61	<0.001*	12.732	2, 65	<0.001*
<i>Scomberomorus regalis</i>	Same NTP	19.542	2, 174	<0.001*	5.943	2, 58	0.062	6.171	2, 62	0.055
<i>Carcharhinus acronotus</i>	Extirpated	39.148	2, 174	<0.001*	0.544	2, 63	0.583	0.329	2, 53	0.721
<i>Carcharhinus longimanus</i>	Extirpated	6.188	2, 174	0.048*	10.259	2, 64	<0.001*	6.567	2, 58	0.003*
<i>Galeocerdo cuvier</i>	Extirpated	10.124	2, 174	0.008*	0.367	2, 101	0.294	0.325	2, 89	0.723
<i>Sphyrna tiburo</i>	Extirpated	37.081	2, 174	<0.001*	0.005	2, 63	0.995	2.094	2, 53	0.133

*Indicates significant p-values

For instance, *Scomberomorus regalis* (Bloch, 1793) primarily feeds on prey that are invertivorous (feeding on both sessile and mobile invertebrates), planktivorous, omnivorous, smaller in total length, found in relatively shallow depths, lacking physical and chemical defenses, and have low NTP (Table 1; Figure 3A). *Scomberomorus cavalla* (Cuvier, 1829) selects for similar prey, feeding on those that are invertivorous, planktivorous [but found at both shallow and deeper depths], lacking physical and chemical defenses (Table 1; Figure 3B). The elasmobranchs *Negaprion brevirostris* (Poey, 1868), *Rhizoprionodon porosus* (Poey, 1861), *Sphyrna tiburo* (Linnaeus, 1758), and *Carcharhinus acronotus* (Poey, 1860) feed across a larger array of functions including species that are algae and seagrass herbivores, omnivores, invertivores of sessile and mobile invertebrates, planktivores, found at relatively shallow depths, and lacking chemical and physical defenses (Table 1; Figure 3C-D; Figure 4A-B). *Galeocerdo cuvier* (Péron and Lesueur, 1822) is the least selective, foraging across all of the functions listed

in addition to foraging on species that are nocturnal, piscivorous, and larger in total length (Table 1; Figure 4C). On the other hand, *Carcharhinus longimanus* (Poey, 1861) forages on fewer species ($n = 15$) and across fewer functions compared to the other sharks, primarily feeding on invertivores, planktivores, and piscivores that can be found across a variety of depths (Table 1; Figure 4D).

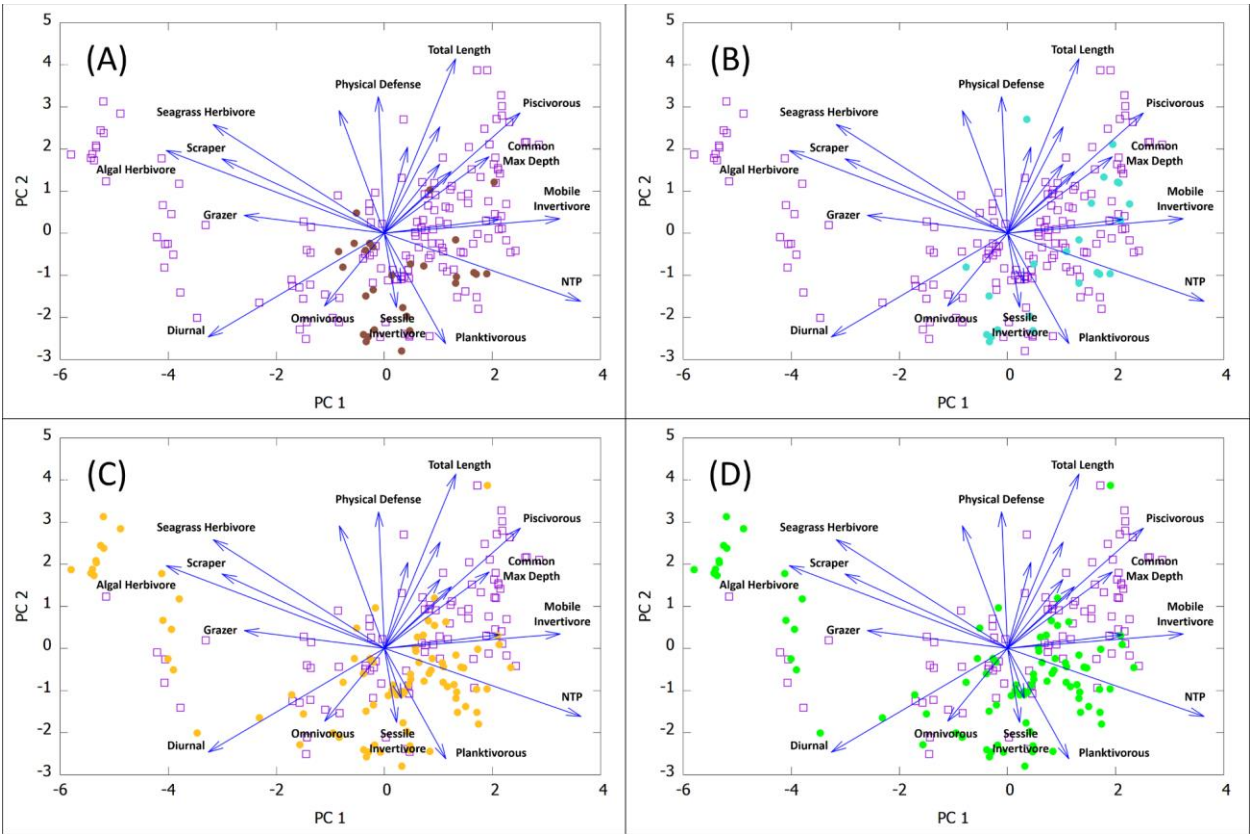


Figure 3. Functional ecospace for the diets of predators that share a similar NTP. The prey of predators with the same NTP as the lionfish (colored circles): (A) Cero (*Scomberomorus regalis*) (B) King Mackerel (*Scomberomorus cavalla*) (C) Lemon Shark (*Negaprion brevirostris*) (D) Caribbean sharpnose shark (*Rhizoprionodon porosus*) in ecospace relative to other fishes concurrently living in the Greater Antillean coral reef ecosystem (purple squares). Blue vectors in ecospace represent the direction and strength of specific traits driving the position of species relative to Principal Components 1 & 2.

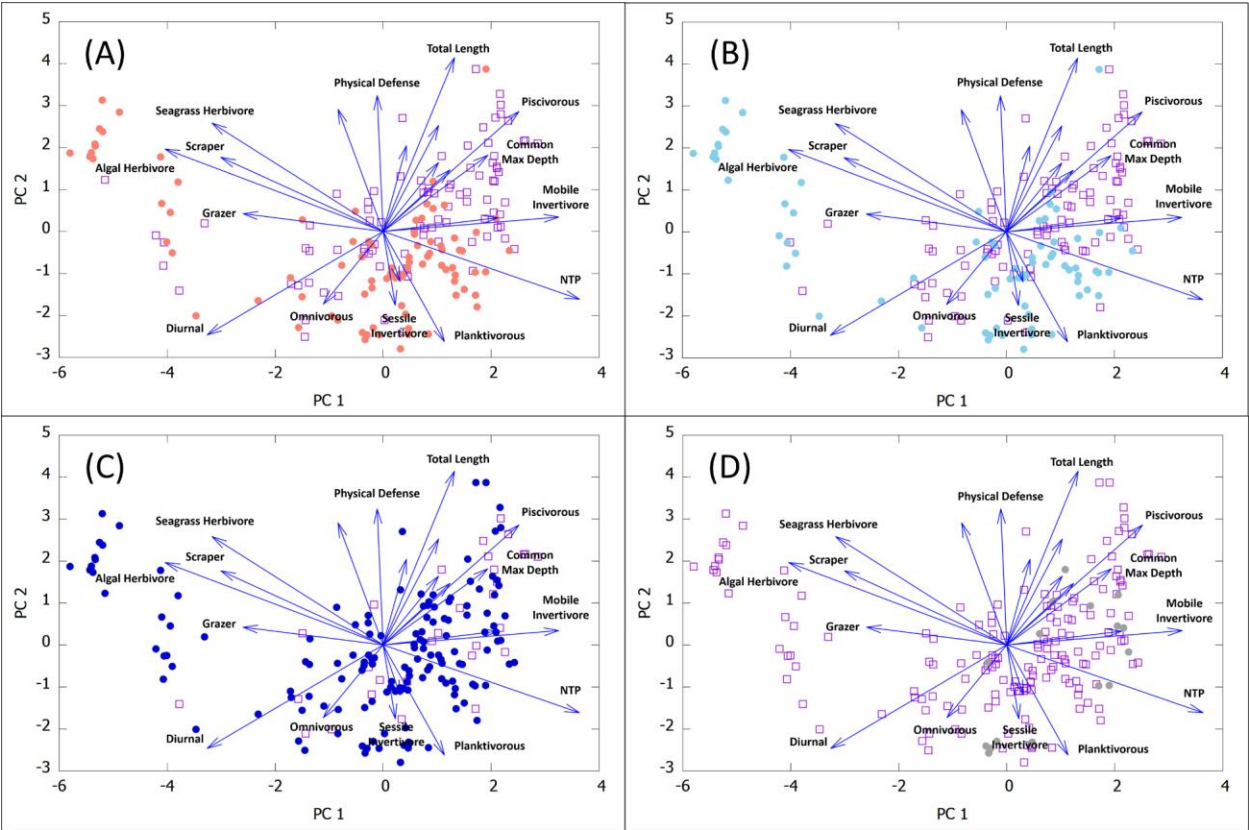


Figure 4. Functional ecospace for the diets of extirpated predators. The prey of predators extirpated from Cuba, Jamaica, and the Cayman Islands (colored circles): (A) Bonnethead shark (*Sphryna tiburo*) (B) Blacknose shark (*Carcharhinus acronotus*) (C) Tiger Shark (*Galeocerdo cuvier*) (D) Whitetip shark (*Carcharhinus longimanus*) in ecospace relative to other fishes concurrently living in the Greater Antillean coral reef ecosystem (purple squares). Blue vectors in ecospace represent the direction and strength of specific traits driving the position of species relative to Principal Components 1 & 2.

To determine if *Pterois volitans* has significant functional predatory overlap with other predatory species, we isolated the prey unique to each species and the lionfish, omitting prey species that the lionfish shares with each other species. We compared the prey distributions of each predator in ecospace with the observed and complete (observed plus predicted) prey distributions of the lionfish using the prey principal component scores. Pairwise Hotelling's T-squared tests show that the cero (*Scomberomorus regalis*), lemon shark (*Negaprion brevirostris*), and Caribbean sharpnose shark (*Rhizoprionodon porosus*), predatory species with the same NTP

as the lionfish, select for prey that are statistically indistinguishable in ecospace from the observed and complete lionfish prey sets (Hotelling's T^2 , Table 1). Similarly, the bonnethead shark (*Sphryna tiburo*), blacknose shark (*Carcharhinus acronotus*), and tiger shark (*Galeocerdo cuvier*), extirpated predatory species that previously occupied the Greater Antillean region, select for prey that are indistinguishable from both the observed and complete lionfish prey sets, suggesting that lionfish occupy a trophic niche that is similar to those of larger-bodied native piscivores (Hotelling's T^2 , Table 1).

Functional disparity (FD) was greatest among observed prey of the blacknose shark (FD = 42.435, $n = 77$), and lowest for the cero (FD = 14.139, $n = 28$). Except for the whitetip shark (FD = 17.244, $n = 16$), the other sharks had high prey disparity, ranging from 37.971 to 42.435. Disparity values for both the observed and complete lionfish prey sets were 36.852 and 42.529 respectively, coinciding with the range of the sharks. While these results suggest that lionfish have a substantial impact on functions in reefs that parallel many generalist shark species, examination of disparity across the entirety of the food web was used to determine if large disparities are simply more common amongst higher trophic level predators. The distribution of pairwise Euclidean distances between the observed lionfish prey and the prey of the tiger shark, lemon shark, sharpnose shark, and bonnethead were indistinguishable from each other, signifying similarities in the ecospace distributions of prey species (Kruskal-Wallis, $p > 0.05$; Figure 5). Conversely, the distribution of pairwise distances between the complete lionfish prey set and all other species differed significantly (Kruskal-Wallis, $p < 0.01$; Figure 5), owing to the addition of predicted prey items primarily representing a number of herbivorous and invertivorous reef fishes.

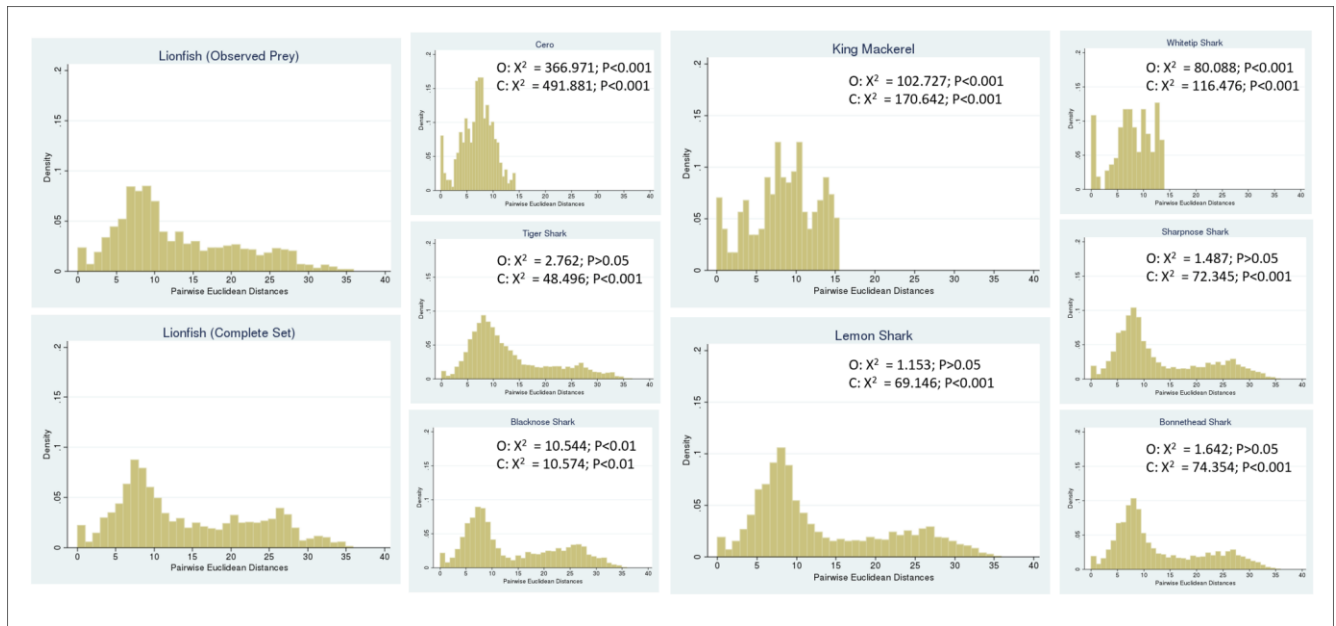


Figure 5. Functional disparity of the lionfish vs. other predators. Distributions of pairwise Euclidean distances between principal components scores of the lionfish's observed and predicted prey, species that share the same NTP, and species that have been extirpated locally. Species were compared to the lionfish's observed (O) and complete (C; observed and predicted) prey using several Kruskal-Wallis rank sum tests.

Greater Antillean food web results show that connectance and maximum food chain length did not vary across web treatments (pristine, lacking extirpated species, lacking extirpated species but with invasive lionfish; Kruskal-Wallis, $\chi^2 = 1.947$, $p > 0.05$ and $\chi^2 = 2.339$, $p > 0.05$ respectively; Table 2). However, simulations of plausible interactions based on the food web model show that the total number of trophic interactions in the network increases significantly with addition of *Pterois volitans*, while connectance does not, signifying the unusual breadth of the invader's interactions (Kruskal-Wallis, $\chi^2 = 47.556$, $p < 0.001$, Table 2). Despite the loss of higher predators and the addition and subsequent removal of the lionfish among web treatments, modularity remained intact (ANOVA, $F(2, 87) = 0.740$, $p = 0.482$). The distribution of NTP was

overall greater on average for the historical web when compared to the impacted web (Kruskal-Wallis, $\chi^2 = 26.404$, $p < 0.001$; Figure 6) and lionfish-free web (Kruskal-Wallis, $\chi^2 = 29.274$, $p < 0.001$; Figure 6). Similarly, predators foraging across guilds of the impacted and lionfish-free communities primarily exhibited lower values of NTP than the historical reef (Hotelling's T^2 , $F(2, 235) = 6.863$, $p = 0.001$ and $F(2, 217) = 27.697$, $p < 0.001$), with approximately 20.63% and 22.49% of predators from the impacted and lionfish-free webs having significantly lower NTP from their counterparts in the historical web (ANOVA, $p < 0.05$, Scheffe's multi-comparison test; please refer to Supplementary III for a full table of results). These pairwise analyses reveal that there are significant differences specifically between the distribution of NTP for predators foraging across the impacted and lionfish free reefs (Kruskal-Wallis, $\chi^2 = 7.431$, $p = 0.006$), suggesting that the presence of lionfish alters coral reef trophic structure at the community level.

Table 2. Structural parameter results across the pristine, impacted, and lionfish-free food webs. Kruskal-Wallis rank sum test results comparing the connectance, number of interactions, and maximum food chain lengths across web treatments.

	Connectance			Number of Interactions			Max. Food Chain Length		
	<i>n</i>	<i>Mean ± SD</i>		<i>n</i>	<i>Mean ± SD</i>		<i>n</i>	<i>Mean ± SD</i>	
Food Web	500			500			500		
<i>Pristine</i>		$0.012 \pm 5.081 \times 10^{-4}$			6640.654 ± 288.850			5.716 ± 0.748	
<i>Impacted</i>		$0.012 \pm 4.922 \times 10^{-4}$			6557.836 ± 275.412			5.642 ± 0.766	
<i>Lionfish Free</i>		$0.012 \pm 4.849 \times 10^{-4}$			6519.978 ± 270.584			5.656 ± 0.779	
Kruskal-Wallis Results	<i>df</i>	<i>Chi-sq.</i>	<i>p</i>	<i>df</i>	<i>Chi-sq.</i>	<i>p</i>	<i>df</i>	<i>Chi-sq.</i>	<i>p</i>
	2	1.947	0.378	2	47.556	<0.001	2	2.339	0.311

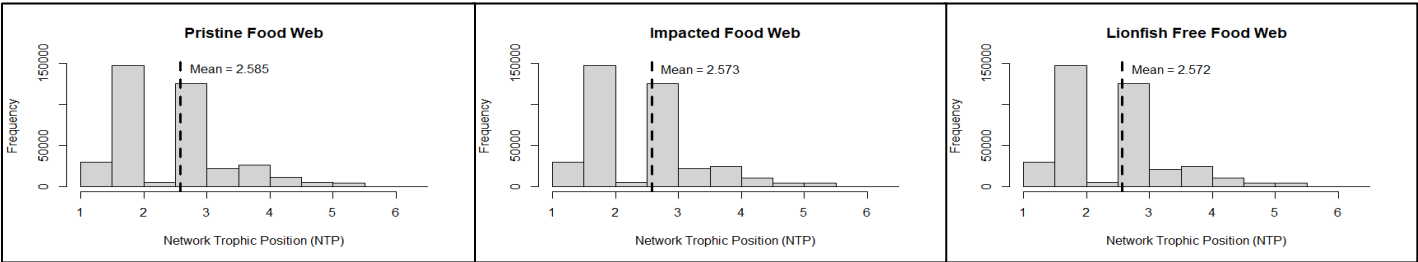


Figure 6. Network trophic position across food webs. Distributions of network trophic position (NTP) for each of the food webs (pristine, impacted, and lionfish free) used assess the impacts of lionfish on Caribbean reef communities. This figure was created using RStudio.

Discussion

The trophic ecology of *Pterois volitans* has been a focus of ecological research owing to it being one of the most expansive and successful invasive marine fishes (Albins 2012). The dramatic increases in its abundance concurrent with declines in prey fish biomass in the Caribbean support a need for community-level studies as reef communities suffer degradation and regime shifts (Green et al. 2012). In addition, the presence of *Pterois miles* (an almost identical species of lionfish) in the southeastern Mediterranean Sea has been previously recorded in the literature, but a permanent invasion may have begun recently, likely due to continual migration through the Suez Canal from the Red Sea (Golani and Sonin 1992; Bariche et al. 2013; Turan et al. 2014). Few studies document the trophic impacts of *P. miles*, though significant numerical increases have been recorded throughout the Mediterranean, raising concerns for another impending invasion and invoking a need for *a priori* studies evaluating its potential impacts on Mediterranean reefs (Dailianis et al. 2016; Kletou et al. 2016; Azzurro et al. 2017; Azzurro and Bariche 2017).

Previous studies on lionfish diet focused on taxon specific interactions and largely characterize lionfish as generalist predators, albeit with a tendency to exhibit a certain degree of specialization both individually and at the species level (Layman and Allgeier 2012; Green et al. 2014; Chappell and Smith 2016; Peake et al. 2018). As such, assemblage specific studies of lionfish diet cannot always capture the nuances of its trophic behavior in newly invaded or understudied systems (such as the Caribbean or Mediterranean), information critical for effective

management. Studies focused on functional traits, however, can augment past work by providing further insight into how traits confer vulnerability to predation and are applicable across varying taxon assemblages (Green et al. 2014).

Here, we used a trait-based model to test if specific functional or morphological traits of Caribbean reef fishes confer vulnerability to predation by *P. volitans*. In total, our ecospace model consisted of 177 fish species described by eight different categorical and continuous traits. Through an extensive literature and database search, we found that lionfish forage on a total of 25 taxonomic families, 39 genera, and 55 species present in Cuba, Jamaica, and the Cayman Islands. Despite their apparently broad trophic breadth, our work suggests that invasive lionfish select for prey on the basis of distinct characteristics, with the likelihood of predation being greater for, or increasing for species that are diurnal, herbivorous, invertivorous, or omnivorous, smaller in total length, found higher in the water column, and that do not generally possess a physical defense. The diurnality and tendency of lionfish to forage in the sunlight zone in our results may be influenced by observational biases because most peer-reviewed studies on lionfish diet are often conducted during the daytime and within relatively shallow depths. Future work documenting lionfish trophic ecology at lower depths and nocturnally, as well as genomic gut content analyses (Valdez-Moreno et al. 2012; Harms-Tuohy et al. 2016), may aid in refining or corroborating the trends found here, as lionfish have also been reported to forage crepuscularly and at mesophotic depths in both their native and invaded ranges (Brokovich et al. 2008; Lesser and Slattery 2011; Andradi-Brown et al. 2016). Additional studies on lionfish diet in seagrass habitats may provide further insight into lionfish trophic selectivity, since many past diet studies focus on reef systems specifically.

Using our functional ecospace model encompassing prey trait data from the Greater Antilles, we also demonstrate that lionfish select for prey that are functionally indistinguishable from the prey of several endemic predators of similar trophic level, and that have become locally extinct in much of the study area. These predators include several chondrichthyans and larger-bodied teleosts, many of which function in coral reefs as mesopredators or apex predators, connecting multiple trophic levels via omnivory (Roff et al. 2016). For example, extant endemic predators such as the Caribbean sharpnose shark (*Rhizoprionodon porosus*), lemon shark (*Negaprion brevirostris*), and cero (*Scomberomorus regalis*) select for prey that are functionally indistinguishable from lionfish prey. In addition, the functional overlap between the prey of the red lionfish and the tiger shark (*Galeocerdo cuvier*), blacknose shark (*Carcharhinus acronotus*), and bonnethead shark (*Sphyrna tiburo*), all species that have been extirpated from many areas of the Greater Antilles, suggest that lionfish may be fulfilling functional roles that have been vacated or eroded due to fishing-driven local extinction.

Metrics of functional disparity complement these results by demonstrating that lionfish forage over a set of functionally diverse species in the Greater Antilles, paralleling the diet of many mesopredatory fish and sharks in our analysis. These prey groups contain taxa that are responsible for a number of functions on the reef, including species that are grazing and scraping herbivores, omnivores, planktivores, predators of both sessile and immobile invertebrates, and piscivores. It is important to note that an examination of disparity across the entirety of the food web is needed to statistically assess how the disparity of lionfish prey compares to those of other species. It would then be possible to measure the extent to which the red lionfish directly impacts the functions of the reef in the context of the entire community.

Finally, three types of species level food webs were utilized to test if the red lionfish impacts the trophic structure of reefs in the Greater Antilles at the community level. These food webs represented reefs where the community is historical (without extirpation of native species and invasion of the lionfish), impacted (with extirpation and the invasion of the lionfish), or lionfish free (with extirpation of native species, and eradication of the lionfish). Some structural components of the Greater Antillean community were preserved among all the treatments, such as connectance, food chain length, and modularity. The number of trophic interactions increased significantly with the addition of the lionfish, however, demonstrating the breadth of the invader's predatory activities and its function as a mesopredator on Greater Antillean reefs.

Trophic level structure also varied among these model webs, differing primarily between the trophospecies guilds of historical and impacted webs, and between the historical and lionfish-free webs. The same trend occurred when specifically comparing the average NTP of predators foraging across all three webs, showing structural changes at higher trophic levels. This indicates that, although the diet of *Pterois volitans* overlaps significantly with historical predators over a set of functionally and taxonomically diverse species, its trophic activities alone cannot fully replace those of native predators on Greater Antillean reefs. The differences observed here primarily reflect a number of changes occurring across webs, including the extirpation of predatory fishes that connect numerous food chains through omnivory, the invasion of a new predator that forages across a broad range of prey functions, and the alteration of food chains compositionally. It is important to note, however, that there were also structural differences between the impacted and lionfish free webs where the only compositional distinction between the two was the removal of lionfish. According to our analysis, the implication of this result is that the lionfish alone can alter the trophic structure of an entire reef community.

Though this may be alarming, our overall results beg the question of whether the activities of *Pterois volitans* partially compensate for the trophic structure lost because of the extirpation of native predators and if *P. volitans*, because of its functional overlap with several other predators, serves as a functionally redundant predator in the Caribbean. If further evidence were to corroborate this concept that lionfish could be replacing overfished endemic predators and, in turn, restoring historical community structure, it is possible that the consequences of their establishment in Caribbean reefs may not be all negative. The extent to which *P. volitans* acts as a redundant predator, however, remains a question that needs further study. This would necessitate experimental and field research focused on the synergistic interaction of population size and the per capita consumption rates of lionfish compared to those of its potential competitors.

Moreover, most Caribbean coral reefs have already undergone catastrophic changes due to bleaching, chronic overfishing, disease, and frequent storm events, resulting in the decline of important reef building corals, the rise of algal dominance, and the local extirpation of keystone predators and herbivores (Hughes 1993; Burke et al. 2004). Our work suggests that the presence of the invasive lionfish in degraded Caribbean coral reefs and in other affected communities could have unprecedented effects on account of its broad trophic breadth (affecting stocks of important forage fishes), its potential to compete with already overfished top predators, and its apparent impacts on food web structure. Continual action to restore the trophic level structure of historical webs by targeted efforts to understand the implications of lionfish invasion, to protect key species from overexploitation, and to facilitate the success of endemic predators will be necessary for systems to recover and maintain their hierarchical structure. Additional study focused on quantifying the impacts of lionfish at the community scale will augment this effort as

we refine our understanding of how invasive marine predators affect the communities in which they become established.

Conclusions

In this paper, we applied a novel approach to evaluating invasive species impacts by utilizing a multivariate ecospace previously used by paleontologists to describe the functional roles of species over time, and employed a species level food web to examine the consequences of species introduction at the community level. We first applied the ecospace model to the following question: “Do lionfish select for their prey randomly within reef communities or do they prefer prey with distinct traits?” By selecting a number of traits to describe a comprehensive list of reef fish endemic to Cuba, Jamaica, and the Cayman Islands, we were able to characterize the trophic selectivity and functional role of the red lionfish (*Pterois volitans*), a species previously described merely as an opportunistic predator in the Caribbean. We also examined if the lionfish represents a functionally novel predator by comparing its trophic breadth to that of several native predators of a similar trophic level, including predators that have been extirpated locally. Our results indicate that lionfish select for distinct traits in their prey and suggest that the functional role of lionfish significantly overlaps with a number of these higher trophic level and extirpated predators. Our food web analysis shows how the introduction of the lionfish alone can alter the trophic dynamics of an entire reef community by changing trophic level structure and significantly increasing the number of interactions.

Given that our findings suggest some functional overlap between lionfish and several high trophic level predators, it is worth considering the extent to which the invasion of lionfish proves to be detrimental to the resilience of Caribbean marine systems, given that it may be

restoring and augmenting some effects of predation otherwise lost to species extirpation. If further work were to corroborate this idea that lionfish could be restoring historical community structure at some capacity, it is likely that their establishment in the Caribbean may not be completely negative.

Supplementary Materials Supplementary I (SupplementaryI_Functional_Ecospace_traits.xlsx) contains the complete trait matrix utilized in the functional ecospace analysis. Please refer to the Methodology section for a full description of its contents. Supplementary II (SupplementaryII_Reference_list_FE.docx) contains a full list of references used to determine the assigned values for the trait matrix in Supplementary I. Finally, Supplementary III (SupplementaryIII_ANOVA_Scheffe.xlsx) is a table of statistical results for the ANOVA and Scheffe's multi-comparison test, analyzing predator NTP by guild across the three food webs. This is referred to at the end of the Results section.

Data Accessibility Additional information regarding the food web including guild assignments, its construction, and coding methods are made available through Roopnarine and Hertog (2012) and Roopnarine and Dineen (2018).

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Author Contributions C. T. Cameron and P. D. Roopnarine designed the study, executed the statistical work, and edited the manuscript. P. D. Roopnarine constructed the food web and wrote the code for its framework and analysis. C. T. Cameron drafted the text, edited the food web model to test hypotheses, determined traits for the ecospace model, and conducted the literature search. Both authors have discussed the results of this work, reviewed its contents, and have consented to its submittal.

Conflicts of Interest There are no conflicting interests between the authors.

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Figure Legends

Table 1. Ecospace prey comparisons of high trophic level predators and the lionfish.

Hotelling's T-squared results comparing the ecospace coordinates of the prey to the species not preyed upon (nonprey) by the species listed, the non-overlapping observed lionfish prey to the prey of the species listed, and the non-overlapping complete set of lionfish prey (observed and predicted) to the prey of the species listed.

Table 2. Structural parameter results across the pristine, impacted, and lionfish-free food webs. Kruskal-Wallis rank sum test results comparing the connectance, number of interactions, and maximum food chain lengths across web treatments.

Figure 1. Schematic of estimation of a species-level food web from a guild-level, functional metanetwork. Consumer in-degree distribution models are shown in the middle column. Distributions vary according to the maximum number of prey available to any species in a particular guild. Random draws from the distributions determine the number of prey per consumer in the species-level food web.

Figure 2. Lionfish diet in functional ecospace. Distribution of (A) observed lionfish prey in ecospace (red circles), and (B) complete set of lionfish prey (observed and predicted; red circles) in ecospace relative to other fishes concurrently living in the Greater Antillean coral reef ecosystem (purple squares). Blue vectors in ecospace represent the direction and strength of specific traits driving the position of species relative to Principal Components 1 & 2.

Figure 3. Functional ecospace for the diets of predators that share a similar NTP. The prey of predators with the same NTP as the lionfish (colored circles): (A) Cero (*Scomberomorus regalis*) (B) King Mackerel (*Scomberomorus cavalla*) (C) Lemon Shark (*Negaprion brevirostris*) (D) Caribbean sharpnose shark (*Rhizoprionodon porosus*) in ecospace relative to other fishes concurrently living in the Greater Antillean coral reef ecosystem (purple squares). Blue vectors in ecospace represent the direction and strength of specific traits driving the position of species relative to Principal Components 1 & 2.

821

822 **Figure 4. Functional ecospace for the diets of extirpated predators.** The prey of predators
823 extirpated from Cuba, Jamaica, and the Cayman Islands (colored circles): (A) Bonnethead shark
824 (*Sphryna tiburo*) (B) Blacknose shark (*Carcharhinus acronotus*) (C) Tiger Shark (*Galeocerdo*
825 *cuvier*) (D) Whitetip shark (*Carcharhinus longimanus*) in ecospace relative to other fishes
826 concurrently living in the Greater Antillean coral reef ecosystem (purple squares). Blue vectors
827 in ecospace represent the direction and strength of specific traits driving the position of species
828 relative to Principal Components 1 & 2.

829

830 **Figure 5. Functional disparity of the lionfish vs. other predators.** Distributions of pairwise
831 Euclidean distances between principal components scores of the lionfish's observed and
832 predicted prey, species that share the same NTP, and species that have been extirpated locally.
833 Species were compared to the lionfish's observed (O) and complete (C; observed and predicted)
834 prey using several Kruskal-Wallis rank sum tests.

835

836 **Figure 6. Network trophic position across food webs.** Distributions of network trophic
837 position (NTP) for each of the food webs (pristine, impacted, and lionfish free) used assess the
838 impacts of lionfish on Caribbean reef communities. This figure was created using RStudio.

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