

## Community structure of reef fishes on a remote oceanic island (St Peter and St Paul's Archipelago, equatorial Atlantic): the relative influence of abiotic and biotic variables

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**Abstract.** This study investigates the reef fish community structure of the world's smallest remote tropical island, the St Peter and St Paul's Archipelago, in the equatorial Atlantic. The interplay between isolation, high endemism and low species richness makes the St Peter and St Paul's Archipelago ecologically simpler than larger and highly connected shelf reef systems, making it an important natural laboratory for ecology and biogeography, particularly with respect to the effects of abiotic and biotic factors, and the functional organisation of such a depauperate community. Boosted regression trees were used to associate density, biomass and diversity of reef fishes with six abiotic and biotic variables, considering the community both as a whole and segregated into seven trophic groups. Depth was the most important explanatory variable across all models, although the direction of its effect varied with the type of response variable. Fish density peaked at intermediate depths, whereas biomass and biodiversity were respectively positively and negatively correlated with depth. Topographic complexity and wave exposure were less important in explaining variance within the fish community than depth. No effects of the predictor biotic variables were detected. Finally, we notice that most functional groups are represented by very few species, highlighting potential vulnerability to disturbances.

**Additional keywords:** depth, functional groups, isolation, low species richness.

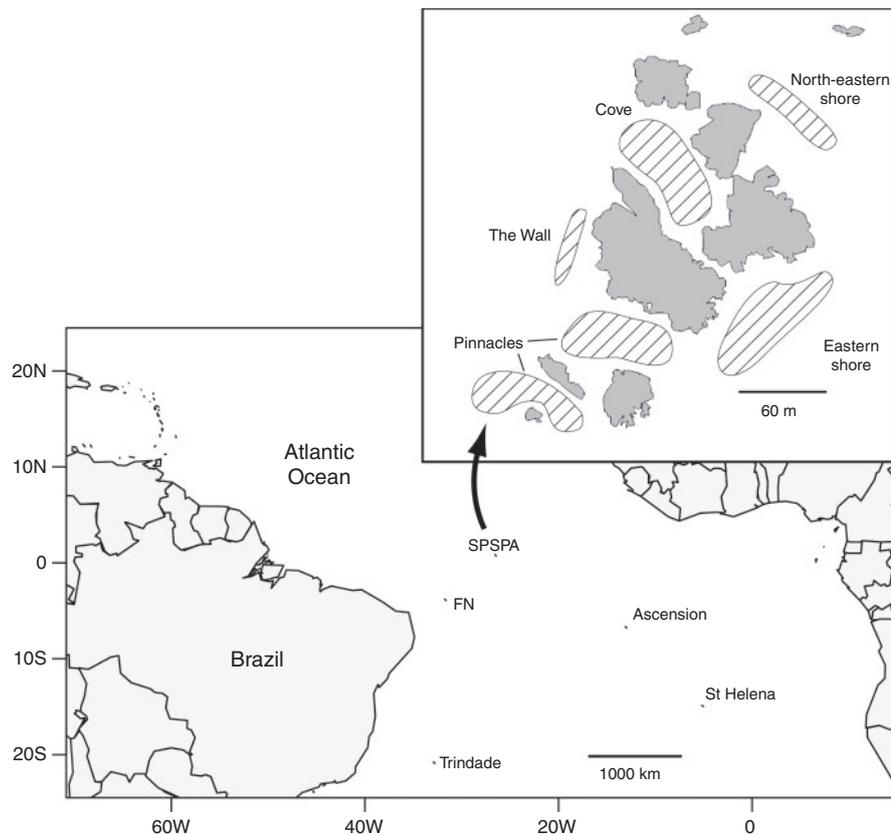
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### Introduction

Tropical reef fishes are extremely diverse and represent a substantial source of food for humans, sustaining commercially important fisheries worldwide (Teh *et al.* 2013); yet, they have been poorly managed (Paddack *et al.* 2009; Mora *et al.* 2011). Understanding the ecological processes structuring fish communities is therefore of prime importance in order to achieve proper management of reef fisheries and to safeguard critical ecosystem functions (Bellwood *et al.* 2003; Hoey and Bellwood 2009).

Most studies on reef fish community structure were conducted in large coral reef systems in the Caribbean and in the

West Pacific regions (Hixon 2011). Therefore, quantitative studies of reef fish communities on small, remote, and isolated islands are still very scarce. Such bias is not surprising given that logistical constraints imposed by remoteness often limit field-work time and raise research costs. As a consequence, we still have a poor understanding of the factors driving the community structure of reef fishes on remote islands and how they compare with larger coral reef networks (Hobbs *et al.* 2012). The high endemism per unit area in remote-island faunas makes these important targets for conservation (Roberts *et al.* 2002). Unfortunately, despite their isolation, remote oceanic islands are not



**Fig. 1.** Maps of the equatorial Atlantic, and Saint Peter and Saint Paul's Archipelago (SPSPA). Hachured areas indicate sampling locations.

exempt from human impacts (Graham *et al.* 2010; Luiz and Edwards 2011; Friedlander *et al.* 2013). It is therefore important to understand the mechanisms underlying the structure of reef fish communities on isolated islands.

Variability in habitat characteristics is one of the most studied factors influencing the structure of reef fish communities (Messmer *et al.* 2011; Komyakova *et al.* 2013). The structural complexity of the habitat, depth and wave energy affect fish abundance and diversity in different spatial and temporal scales (McGehee 1994; Ferreira *et al.* 2001; Srinivasan 2003; Fulton *et al.* 2005; Floeter *et al.* 2007; Komyakova *et al.* 2013). Likewise, biotic interactions among sympatric species such as damselfish territory partitioning (Ceccarelli *et al.* 2001) and top-down predation effects (Dulvy *et al.* 2004; Heinlein *et al.* 2010; Walsh *et al.* 2012) are also important factors affecting reef fish communities. Because combined effects between habitat and biotic interactions often complicate fish-habitat relationships (Almany 2004; Rilov *et al.* 2007), disentangling the relative importance of single habitat variables in the structure of reef fish communities has been a challenging task, particularly when they act synergistically with human impacts (Graham *et al.* 2006; Ruppert *et al.* 2013).

Reef fish communities in small remote islands possess a unique set of features that can influence their structure. First, island communities comprise a subset of the species pool found in the neighbouring mainland coastline, with species number

generally varying as a function of the island's size and isolation (Floeter *et al.* 2008; Hobbs *et al.* 2012). Second, island communities, when compared to the neighbouring mainland assemblage, typically contain a higher proportion of habitat-generalist species with good dispersal and colonisation abilities (Hobbs *et al.* 2010, 2012). Third, due to isolation and low connectivity with neighbouring reefs, self-recruitment is disproportionately more important for population maintenance on remote islands (Robertson 2001), which potentially makes reef communities on those islands more closed than larger continental-shelf reef systems. In essence, the interplay between lower species richness and limited connectivity makes remote oceanic islands ecologically simpler than mainland ecosystems (MacArthur and Wilson 1967), providing an invaluable model system for ecology and biogeography (Vitousek 2002).

Here we take the ecological simplicity of islands to the extreme by investigating the factors affecting the reef fish community of the smallest remote tropical island in the world, the St Peter and St Paul's Archipelago (hereafter SPSPA). The SPSPA – formerly known in the biological literature as Saint Paul's Rocks (Lubbock and Edwards 1981; Edwards 1985) – is a group of barren islets in the equatorial Atlantic Ocean, on the mid-Atlantic ridge (Fig. 1). The archipelago, which is considered a remote outpost of the Brazilian Province (Floeter *et al.* 2008), is only 400 m across at its greatest extent and, to the best of our knowledge, has the most limited area of shallow habitat

(<50 m deep) among oceanic islands, with less than 0.2 km<sup>2</sup> (Robertson 2001; Feitoza *et al.* 2003). The SPSPA possesses the most depauperate reef fish assemblage known for a single tropical island, with ~60 species recorded (Ferreira *et al.* 2009), and a high level of endemism (~9.5%) (Robertson 2001; Floeter *et al.* 2008).

In this study, we describe the reef fish community structure of the SPSPA, assessing all shallow habitats in the archipelago. We also examined the relationships between fish density, biomass, species diversity and trophic structure across a set of abiotic (depth, substrate complexity, wave exposure) and biotic (density of territorial damselfish, density of predators, benthic cover of the substrate) variables.

## Materials and methods

### Study site

Saint Peter and Saint Paul's Archipelago (SPSPA; 00°55'N, 29°21'W) is located at ~960 km off Cape of São Roque, north-eastern coast of Brazil and 1890 km south-west off Senegal, West Africa (Fig. 1). Data were collected during four expeditions between 2006 and 2010. Sampling around the SPSPA was divided among five sites (Fig. 1): (1) The 'Cove', a small inlet protected from the main westward surge, forming a very gentle slope from 3 to ~20 m deep. (2) 'North-eastern shore', highly exposed to the westward surge; it is a platform composed of boulders of several sizes 11–23 m deep. (3) 'Eastern shore', highly exposed to westward surge, characterised by a gravel-covered platform 10–21 m deep. (4) 'Pinnacles', the area situated between the main island and the islets on the south-west of the SPSPA, moderately sheltered from the predominant westward surge, characterised by a series of pinnacles rising from 40 to ~5 m deep. (5) 'The Wall', an almost vertical drop off on the eastern face of the SPSPA, starting at 20 m down to several hundred metres. Sampling at this zone was performed between 20 and 33 m.

### Data collection

We assessed the composition of the reef fish community in the SPSPA by underwater visual census (UVC). A total of 213 belt transect samples (20 × 2 m) were conducted across all sites at different depths. The range of depths surveyed was similar among all sites, except at The Wall, where only mid- and deep-depths (i.e. below 20 m) were surveyed. All transects were conducted at fixed depths ± 2 m. Each transect was sampled twice. During the first count, the diver swam along the transect and recorded all conspicuous swimming species. During the second count, cryptic and bottom-dwelling species were searched for by carefully scanning the substratum and looking beneath rocks and crevices. Along each transect the number of individuals of each species was tallied and grouped into size classes (10-cm intervals) of total length. The first size class was further divided into 0–5- and 5–10-cm classes in order to account for small recruits.

All species recorded in the surveys were grouped into the following trophic groups: macrocarnivores, mobile invertebrate feeders, omnivores, planktivores, roving herbivores, sessile invertebrate feeders and territorial herbivores, following previous studies on reef fish communities in Brazil (Ferreira *et al.*

2004; Floeter *et al.* 2007; Luiz *et al.* 2008). Fish biomass was estimated by length–weight transformations and allometric conversions:  $W = a * L^b$  where parameters  $a$  and  $b$  are constants for the allometric growth equation. Fish length was calculated as the mid-point for each size class. When coefficient values were not found for the species, we used coefficients for congeners.

Depth, topographic complexity and wave exposure were assigned for each transect. The topographic complexity of the substratum was visually classified according to four categories (adapted from Wilson *et al.* 2007), from low to high complexity: (1) sand bottom and flat gravel beds with no relief; (2) rock surface with shallow ledges and crevices (3) small boulders <1 m in size and holes <1 m in depth; and (4) large boulders >1 m in size and holes >1 m in depth.

Wave exposure was categorised into three levels based on our own observations. The Cove and The Wall are sites located on the western side of the SPSPA and protected from the predominant wind and currents. Transects on these sites were categorised as Levels 1 or 2 depending on whether they were located inside or outside the cove. Transects in the Pinnacles site, which faces south-east, and the North-eastern shore and Eastern shore sites, which face east, were assigned exposure Levels 2 or 3, depending on whether the transect locations were protected from the main surge by surrounding islets.

Benthic cover was assessed through photo quadrats sampled along replicated transects ( $n = 3$ ; 10 m long) at different depths. For each transect, a frame of 50 × 50 cm was positioned every 2 m over the substratum where a digital photograph was taken. A total of 253 digital photographs were analysed using the software Coral Point Count with Excel Extension (CPCe ver. 3.5) (Kohler and Gil 2006). Thirty random points were overlaid on each photograph in order to estimate the relative cover of each substratum type.

### Data analysis

For each of the 213 transects, we calculated the following community parameters: total fish density, total fish biomass and Shannon diversity. Shannon's diversity index ( $H$ ) is calculated as

$$H = \sum_{i=1}^S p_i \ln p_i$$

where  $S$  is the number of species in the sample, and  $p_i$  is the proportion of  $S$  in the  $i$ th species (Mason *et al.* 2005). For each transect, we also extract density for the seven trophic groups and for territorial damselfishes. Macrocarnivores were modelled both as a response and predictor to test their predatory and fear effects on the community parameters, and thus labelled as 'predator density' in models where it was used as a predictor.

We used boosted regression trees (BRT) in order to access the relative importance of habitat variables (depth, wave exposure, substratum complexity) on community structure parameters. We then evaluated the effects of biotic variables on fish density and Shannon diversity models by including density of both territorial damselfishes and predators among the predictor variables in two additional sets of models, one containing only the density of territorial damselfishes and the other containing density of predators. Density of both territorial damselfishes

and predators cannot be included in the full community models and their respective sets of models because their occurrences must be subtracted from the full community in order to avoid autocorrelation (i.e. the density of damselfishes predicts itself if it is included both in the response and predictor variables). BRT is a machine-learning technique that has several advantages over traditional regression-based approaches, including improved explanatory power, being insensitive to irrelevant predictors and outlying data points, and the automatic modelling of interactions (De'ath 2007; Elith *et al.* 2008; Harborne *et al.* 2012). All models were fitted in R (R Development Core Team 2014) using the 'gbm' package (Ridgeway 2014) plus customised code written and described by Elith *et al.* (2008).

We used cross validation in order to identify the best combination of parameters required by BRTs (learning rate, tree complexity and bag fraction) (Elith *et al.* 2008; Harborne *et al.* 2012). Cross-validation was automatically repeated for learning rates from 0.001 to 0.05 (steps of 0.002), tree complexities of 1–3 and bag fractions of 0.5 and 0.75, which span the range of likely optimal values (Elith *et al.* 2008). The combinations that generated the lowest mean cross-validation deviances, calculated from at least 1000 trees, were used for the final models (Harborne *et al.* 2012). Following the derivation of full models with all variables, models were investigated to establish whether irrelevant predictors could be removed (procedure as detailed in Elith *et al.* 2008). Response variables were either square-root-transformed or log-transformed in order to achieve a normal distribution.

The influence of substratum benthic cover on the structure of reef fish community was analysed with two sets of redundancy analyses (RDA) (Legendre and Legendre 2012). Owing to logistical constraints, benthic and fish transects were performed at different expeditions. Therefore, for the RDA, data were averaged in three depth categories within each site: shallow (2–12 m), mid (>12–22 m), and deep (>22–33 m). Covariance on benthic categories was tested *a priori* whereas some categories were excluded from subsequent analyses. In the first RDA we tested the correlation of benthic cover against mean density of the seven most abundant fish species, whereas in the second RDA we used trophic groups of fish species. In each set of analyses, the overall correlation between both benthos and fish matrices was tested with permutation analysis using the package 'vegan' in R (Oksanen *et al.* 2013).

## Results

In total, 50 410 fish individuals belonging to 33 species were recorded. The three most abundant species (*Chromis multilineata*, *Stegastes sanctipauli* and *Melichthys niger*) accounted for 85% of all fishes recorded in this study, and 99% of all fishes corresponded to only 14 species (Table 1). Planktivores accounted for 49.1% of all fish individuals recorded, followed by territorial herbivores (23.4%), omnivores (19.4%), mobile invertebrate feeders (5.2%), macrocarnivores (2%), sessile invertebrate feeders (0.6%) and roving herbivores (0.2%) (Fig. 2). In terms of biomass, omnivores accounted for 74%, followed by planktivores (13.6%), mobile invertebrate feeders (3.5%), sessile invertebrate feeders (3%), macrocarnivores (2.8%), roving herbivores (2.4%) and territorial herbivores

(0.7%) (Fig. 2). Abundance and Shannon diversity of individuals were similar among sites (Fig. S1a, c) (ANOVA,  $F=0.003$ ,  $P=0.95$ ), and biomass was slightly lower at the Cove than at the North-eastern shore (Fig. S1b) (ANOVA,  $F=2.94$ ,  $P=0.02$ ). The proportional distribution of trophic groups was also very similar among sites (Fig. S1d). Overall, we did not find any evidence for site effects on the response variables. Some trophic groups comprised one or two species, indicating that patterns of abundance and biomass within groups were driven by very few species (Fig. 2).

Depth and complexity were respectively the first and second most influential predictors of density and biomass, and depth was the single most influential predictor for Shannon diversity (Fig. 3). However, the magnitude and direction of these effects varied. Depth correlated positively with density and biomass, and correlated negatively with Shannon diversity. Density peaked at ~12–15 m depth, and then decreased to slightly lower levels in transects deeper than 17 m (Fig. 3a). Biomass increased drastically at 10 m depth and then slowly grew as depth increased (Fig. 3b). Shannon diversity peaked at 10 m depth, and then decreased sharply towards deeper habitats (Fig. 3c). Complexity correlated positively with density, negatively with biomass, and did not affect Shannon diversity (Fig. 3).

The inclusion of biotic variables in the models (density of territorial damselfishes and predators) did not change the effects of the abiotic variables on community parameters (Fig. S2). Density of territorial damselfish correlated positively with the density and biomass of other species, suggesting that density of territorial damselfish broadly responds to the same abiotic factors affecting the whole community (Fig. S2a, b), and showed a negative relationship with Shannon diversity of small magnitude compared to depth effects (Fig. S2c). Predator density correlated positively with density and Shannon diversity (Fig. S2d, f), and a weak negative correlation with biomass (Fig. S2e).

Abiotic effects varied among trophic groups. Density of planktivores increased with depth, complexity and exposure, reaching a peak at the maximum depth surveyed and in the most exposed areas (Fig. S3a). This pattern is largely driven by *C. multilineata*, the most abundant planktivore in the SPSPA (Fig. 2). Density of territorial herbivores correlated negatively with depth and positively with complexity (Fig. S3b). It was higher at shallow depths (10–15 m) but decreased sharply towards deeper habitats (Fig. S3b). Density of omnivores increased with depth until 20 m depth and remained constant until 30 m (Fig. S3c). Depth and exposure were important predictors for density of macrocarnivores (Fig. S3d). A visual analysis of the BRT plots for density of macrocarnivores (Fig. S3d) shows two similar peaks at shallow and deep transects, and an increase of density with exposure. Density of mobile invertebrate feeders was negatively correlated with depth; it remained high and roughly constant until ~17 m and declined sharply in the deeper transects (Fig. S3e). Very low densities of roving herbivores and sessile invertebrate feeders prevented statistical analyses for these groups.

The benthic community was largely dominated by the epilithic algal matrix (EAM) at most sites, the exception being The Wall where brown algae from the genus *Dictyota* was the dominant item followed by EAM and *Caulerpa* being of

**Table 1. Density, relative abundance and frequency of occurrence estimates of fish species recorded during underwater visual census (213 transects)**  
Species are ranked in order of decreasing numeric abundance. Taxa with asterisks represent the 14 taxa that comprised 99% of the individuals. Trophic group: MAC, Macrocarivore; MIF, Mobile Invertebrate Feeder; OMN, Omnivore; PLK, Planktivore; SIF, Sessile Invertebrate Feeder; THE, Territorial Herbivore

Species	Mean density (individuals per 40 m <sup>2</sup> ) ± s.e.	Relative abundance (percentage of all individuals)	Frequency (percentage of transects)	Trophic group
<i>Chromis multilineata</i> *	114.8 ± 8.9	48.50	85.44	PLK
<i>Stegastes sanctipauli</i> *	47.8 ± 3.0	20.18	88.26	THE
<i>Melichthys niger</i> *	38.3 ± 2.2	16.20	94.83	OMN
<i>Ophioblennius trinitatis</i> *	7.7 ± 0.8	3.24	70.42	THE
<i>Abudefduf saxatilis</i> *	7.4 ± 1.1	3.12	47.88	OMN
<i>Myripristis jacobus</i> *	5.9 ± 1.0	2.49	50.70	MIF
<i>Halichoeres radiatus</i> *	3.2 ± 0.8	1.35	76.99	MIF
<i>Malacoctenus</i> sp.*	2.8 ± 0.37	1.17	47.41	MIF
<i>Muraena pavonina</i> *	2.5 ± 0.7	1.04	62.91	MAC
<i>Canthidermis sufflamen</i> *	1.3 ± 0.4	0.57	10.32	PLK
<i>Holacanthus ciliaris</i> *	0.1 ± 0.08	0.40	50.70	SIF
<i>Caranx lugubris</i> *	0.9 ± 0.3	0.37	30.04	MAC
<i>Aulostomus strigosus</i> *	0.8 ± 0.2	0.34	42.25	MAC
<i>Kyphosus</i> spp.*	0.6 ± 0.2	0.24	14.55	RHE
<i>Bodianus insularis</i>	0.3 ± 0.04	0.14	23.94	MIF
<i>Rypticus saponaceus</i>	0.3 ± 0.03	0.11	21.12	MAC
<i>Cantherhines macrocerus</i>	0.2 ± 0.03	0.09	17.84	SIF
<i>Chaetodon striatus</i>	0.2 ± 0.04	0.08	4.69	SIF
<i>Emblemariopsis</i> sp.	0.1 ± 0.04	0.04	4.22	MIF
<i>Pomacanthus paru</i>	0.1 ± 0.03	0.04	6.10	OMN
<i>Choranthias salmopunctatus</i>	0.08 ± 0.06	0.03	1.40	PLK
<i>Holocentrus adscensionis</i>	0.08 ± 0.03	0.03	3.75	MIF
<i>Enchelycore nigricans</i>	0.05 ± 0.01	0.02	5.16	MAC
<i>Aluterus scriptus</i>	0.04 ± 0.01	0.01	4.22	SIF
<i>Gymnothorax miliaris</i>	0.03 ± 0.01	0.01	3.28	MAC
<i>Muraena melanotis</i>	0.02 ± 0.01	0.01	1.87	MAC
<i>Sphyaena barracuda</i>	0.02 ± 0.01	0.009	15.02	MAC
<i>Caranx latus</i>	0.01 ± 0.01	0.007	0.46	MAC
<i>Lutjanus jocu</i>	0.01 ± 0.009	0.007	1.87	MAC
<i>Clepticus brasiliensis</i>	0.01 ± 0.01	0.005	0.93	PLK
<i>Enchelycore anatina</i>	0.01 ± 0.008	0.005	1.40	MAC
<i>Prognathodes obliquus</i>	0.01 ± 0.01	0.005	0.93	SIF
<i>Dactylopterus volitans</i>	0.01 ± 0.006	0.003	0.93	MIF

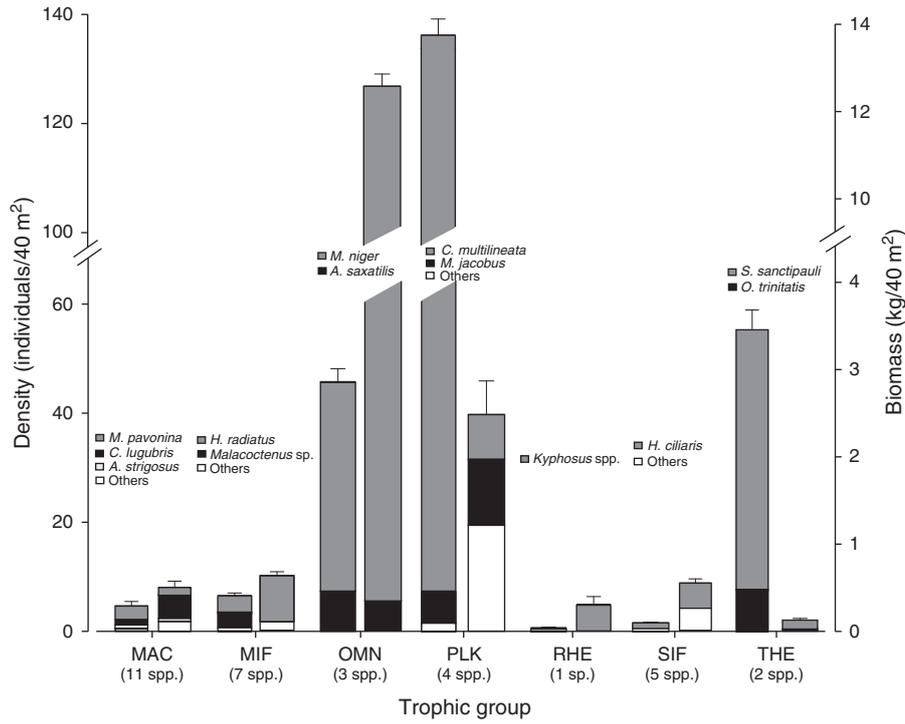
secondary importance. At Pinnacles and the Cove, the zoanthid *Palythoa* and rubble were respectively the second most important items, whereas at Eastern shore and North-eastern shore, *Caulerpa* followed EAM in total cover (Fig. S4). A weak correlation was detected between benthic cover and the mean density of the seven most abundant fish species ( $P = 0.01$ , adjusted  $R^2 = 0.48$ ) (Fig. 4). The most evident were the associations between *Halichoeres radiatus* and rubble, *M. niger* and crustose coralline algae (CCA), *Abudefduf saxatilis* and *Caulerpa*, and *Ophioblennius trinitatis* and EAM. For fish trophic groups, the correlation was slightly higher ( $P = 0.01$ , adjusted  $R^2 = 0.62$ ) (Fig. 4b). Both territorial herbivores and omnivores were correlated with sites with high rubble and CCA cover, mobile invertebrate feeders were more correlated with EAM and macrocarivores exhibited no correlation with any benthic category.

## Discussion

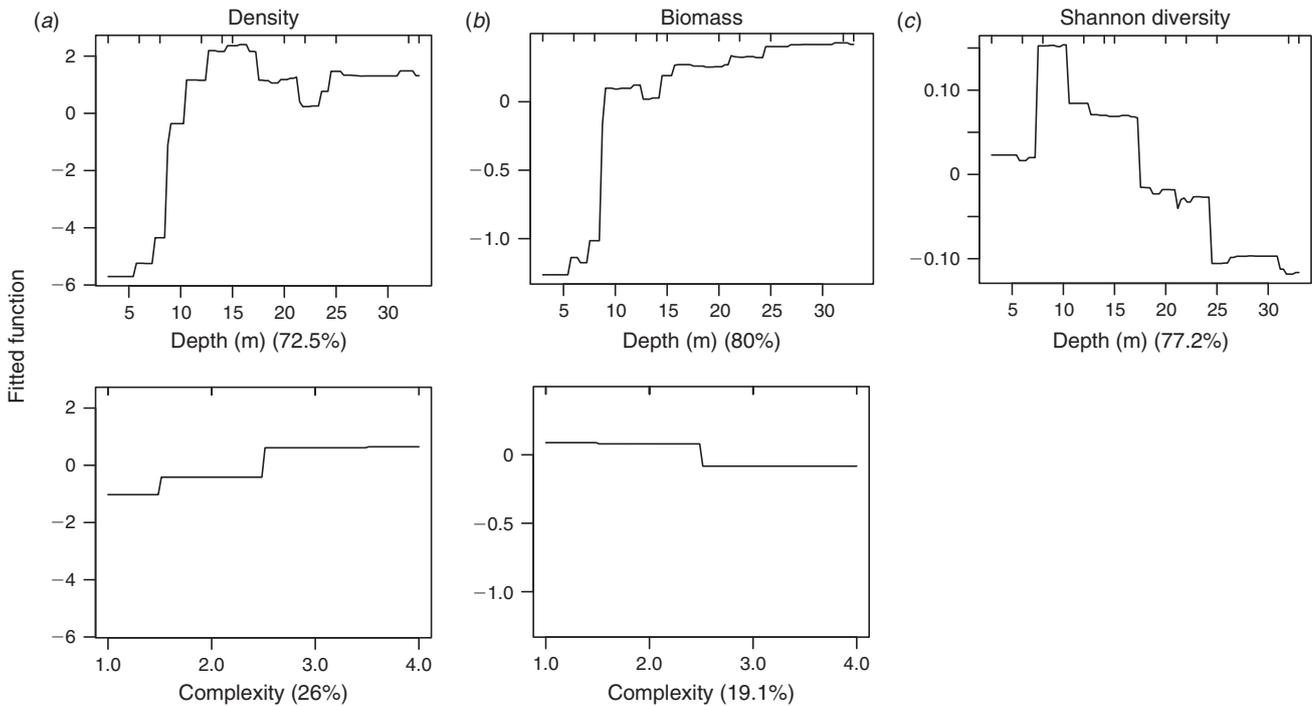
The SPSPA has the most depauperate fish community reported among the world's tropical oceanic islands. The peculiar characteristics of isolation, high endemism, low species richness,

and small reef area make the SPSPA of major interest for testing hypotheses in ecology and biogeography (Robertson 2001; Hobbs *et al.* 2012). The abundance of the few dominant fishes was similar all over the archipelago, and site location had negligible effects on total fish density, biomass, diversity, and the relative abundance of major trophic groups (Fig. S1). The fish community seems broadly homogeneous across the SPSPA, probably as a consequence of low species richness and dominance of generalist species. However, some patterns have emerged after examining the reef fish community structure at a finer scale, comparing transects rather than averaging them among sites.

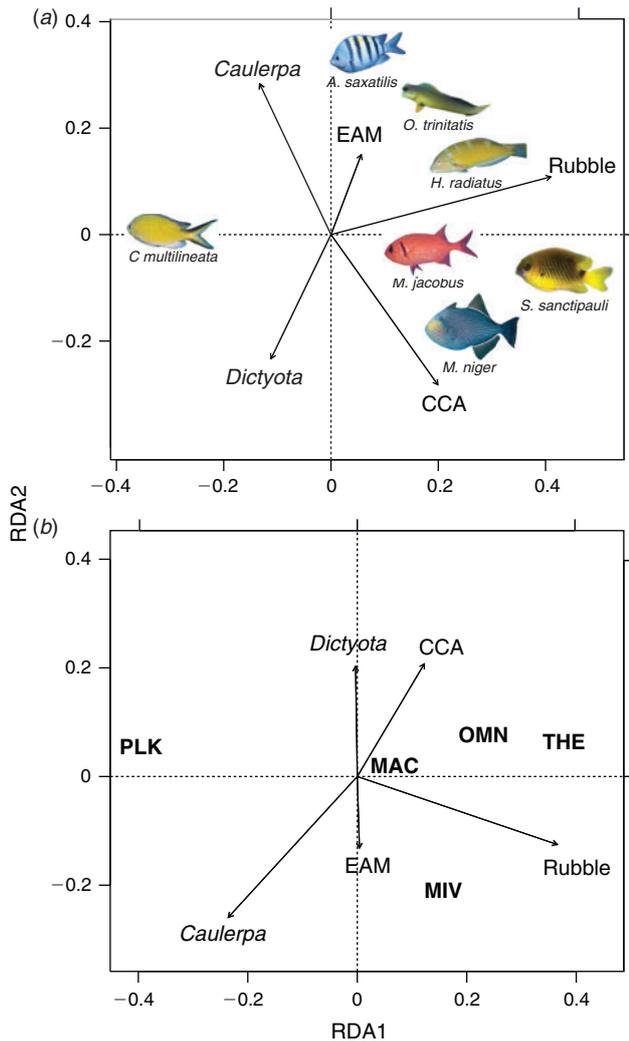
Depth is an influential variable determining fish distribution and its effects usually interact with other abiotic variables such as wave exposure (Denny 2005) and topographic complexity (Srinivasan 2003; Milazzo *et al.* 2011). In the SPSPA, fish density was very low in the shallow zone but peaked at ~15 m deep, probably because of the strong and prevalent wave surge all around the archipelago. Biomass increased with depth and reached higher values at the deep habitats (25–30 m), indicating



**Fig. 2.** Density (mean  $\pm$  s.e.) and biomass (mean  $\pm$  s.e.) of trophic groups on the SPSPA, number of species and composition. MAC, Macrocarivore; MIF, Mobile Invertebrate Feeder; OMN, Omnivore; PLK, Planktivore; SIF, Sessile Invertebrate Feeder; THE, Territorial Herbivore. For each trophic group, the right and left bars represent density and biomass respectively.



**Fig. 3.** Partial dependence functions for the most important abiotic factors influencing reef-fish community parameters across all sampled sites.



**Fig. 4.** Redundancy analysis (RDA) diagram for the relationship between benthic categories and the density of the seven most abundant species (a) and the trophic groups (b).

that smaller fish (both small species and juveniles of larger species) are more common in the intermediate depths and large individuals dominate the deep reefs. In fact, species commonly found in shallow areas were mostly the small territorial damselfish *Stegastes sanctipauli*, the cryptobenthic species *Ophioblennius trinitatis* and *Malacoctenus* sp., and juveniles of *Abudefduf saxatilis*, *Chromis multilineata* and *Halichoeres radiatus*. In contrast, species reaching high densities in deep habitats are the larger black jack (*Caranx lugubris*), and adults of *A. saxatilis*, *C. multilineata* and *H. radiatus*. The peak in biodiversity at 10–12 m, with decrease both to shallow and to deep habitats, indicates that most fish species are restricted to intermediate depths.

Much research has been conducted on the effects of reef benthic cover and topography on the structure of reef fish communities and their response to disturbance (Luckhurst and Luckhurst 1978; Roberts and Ormond 1987; Caley and St John 1996; Jones and Syms 1998; Ferreira *et al.* 2001; Komyakova

*et al.* 2013). Despite yielding mixed results, syntheses of previous research suggest that reef topographic complexity is more important for fish density, and that live benthic cover is more important for reef fish diversity (Messmer *et al.* 2011; Komyakova *et al.* 2013). In the SPSPA, topographic complexity was important for fish density, even though the territorial damselfish *S. sanctipauli* largely drove this pattern. Damselfishes are mostly bottom-attached species elsewhere (Ceccarelli *et al.* 2001). In the SPSPA, *S. sanctipauli* is the third most abundant species, establishing territories over a wide depth range (7–30 m deep). Juveniles share space with adults, generating high densities per transect. The density of territorial damselfishes in the SPSPA is higher than in any other assemblage recorded elsewhere along the Brazilian Province (Ferreira *et al.* 2004), and adult damselfishes tend to establish their territories in areas with medium to high complexity, which provides optimal refuge. Topographic complexity was not significant for biomass, likely because species composing the bulk of biomass are relative large schooling species, such as *Melichthys niger* and *Caranx lugubris*, which are highly mobile species, not closely associated with the bottom. Exposure was a poor predictor for distinguishing habitat selectivity within the fish community, likely because of the high intensity of wave surge associated with little degree of embayment in the SPSPA. Nevertheless, a marginal positive effect of exposure influenced the density of planktivores, a general pattern noted elsewhere (Thresher 1983; Hamner *et al.* 1988; Ferreira *et al.* 2004).

None of the predictor biotic variables had significant effects on the reef fish community, although a few species showed an apparent preference for specific types of benthic cover. Reef fish communities on isolated islands are characterised by a large proportion of generalist species, which may compensate for local (or global, if endemics) extinction risk (Hobbs *et al.* 2010). The large proportion of generalist species, associated with low species richness, could result in less competition for space, which may explain the lack of correlation between fish community and biotic variables.

Low species richness also reflects on low functional redundancy with potential direct effects on ecosystem functioning (Duffy 2003; Hooper *et al.* 2005; Halpern and Floeter 2008). For instance, *Halichoeres radiatus* and *Bodianus insularis* are the only invertebrate feeders with high mobility on that system. Because *B. insularis* is not common and is more restricted to deeper areas, *H. radiatus* is the only broadly distributed species around the SPSPA performing that role. Likewise, as sand and other soft sediment habitats are virtually non-existent on the SPSPA, sand-foragers that are common elsewhere, such as soles and goatfishes, are absent in the SPSPA. The only sand-forager specialist recorded at the SPSPA is *Dactylopterus volitans*; yet, it is extremely rare, with very few records across many years of fieldwork. Roving herbivores represent another extremely rare functional group in the SPSPA. There are no reports of any resident surgeonfish species in the SPSPA; and only scarce records of parrotfishes (*Sparisoma axillare* and *S. frondosum*) exist to date (Feitoza *et al.* 2003; Ferreira *et al.* 2009). Although other herbivores such as chubs (*Kyphosus sectatrix* and *K. cineracens*) are frequently observed in shallow areas of the SPSPA, they are strictly macroalgal browsers and thus are not functionally redundant with any Atlantic surgeonfish or

parrotfish, the diets of which are based on detritus and filamentous algae (Ferreira and Gonçalves 2006). In the SPSPA, the omnivorous *M. niger* apparently replaces roving herbivores as the main species feeding on detritus and filamentous algae. Other trophic groups are also represented by few rare species (Fig. 2). All these examples illustrate the low functional redundancy of the SPSPA fish community.

Different processes shape reef fish communities, including historical (e.g. biogeography) and contemporary (e.g. pre- and postrecruitment effects). Fishes must overcome additional ecological filters beyond the island isolation in order to become established in the SPSPA. Some shallow-water habitats do not exist due to the small area. Moreover, human exploitation has been progressively eliminating species from the food web of the SPSPA's reef (Luiz and Edwards 2011). It is not well understood how species-poor systems with low functional redundancy can sustain critical ecosystem functions (Halpern and Floeter 2008). The lack of key trophic groups observed elsewhere may induce niche displacement; for instance, *M. niger* acting as the main roving herbivore foraging over the EAM. Moreover, niche expansion is also observed, as in the case of juveniles of *Stegastes sanctipauli* presenting an invertivore diet (Gasparini *et al.* 2008). This extreme low functional redundancy may have undesirable consequences when overfishing occurs.

Some oceanic islands are still pristine because of their isolation (Friedlander and DeMartini 2002; Stevenson *et al.* 2007; Sandin *et al.* 2008). However, the increasing intensity of oceanic fishing, with the aid of high-tech devices aimed at finding and catching fish, has resulted in there being very few pristine islands left (Myers and Worm 2003; Ward and Myers 2005; Baum and Worm 2009). The SPSPA sustains high values of fish biomass when compared to other sites along the Brazilian coast (Ferreira *et al.* 2004, 2009; Krajewski and Floeter 2011; Pinheiro *et al.* 2011). However, such high levels of biomass are not derived from top predators (e.g. macrocarnivores), as one might expect, but rather from medium-sized omnivores (Fig. 2). This suggests that the community food chain in the SPSPA is subsidised by means of trophic links with oceanic pelagic species (Barneche *et al.* 2014). This potential link between SPSPA's demersal and pelagic compartments has been largely overlooked in local fisheries management and is a topic for urgent future research.

It has long been assumed that ecological processes in species-rich systems are buffered against species loss due to their high functional redundancy among species (Fonseca and Ganade 2001). However, for some species-rich assemblages, including reef fishes, recent evidence has demonstrated that distinct combinations of functional traits are supported by a large number of rare species (Mouillot *et al.* 2013), with little redundancy among a large proportion of these functional groups (Mouillot *et al.* 2014). If high-diversity tropical reefs are vulnerable to functional diversity loss due to local extinctions (Mouillot *et al.* 2014), we may also expect low-diversity reefs to be at a high-level risk. Especially in the ASPSP, the reef-fish assemblage with lowest richness among all tropical islands, the loss of a few species can potentially impair important ecological processes and generate trophic cascades.

The SPSPA is part of a multiple-use Marine Protected Area (APA de Fernando de Noronha – Rocas – São Pedro e São Paulo)

with a major research program supported by the Brazilian Government. Fisheries are meant to be sustainably managed; however, the interplay of frail enforcement and commercial fishing around the SPSPA for more than 40 years (Vaske *et al.* 2010) targeting pelagic species, are largely responsible for the few large top-predator fishes remaining. For instance, the local population of Galapagos sharks (*Carcharhinus galapagensis*), once extremely abundant, is now locally extinct in the SPSPA (Luiz and Edwards 2011). Anecdotal observation from the *HMS Beagle's* captain Robert Fitzroy in 1832, described groupers being caught with hand lines but being voraciously eaten by sharks before the crew could take them out of the water (Luiz and Edwards 2011). Groupers are apparently absent in the SPSPA nowadays, despite a single record of a coney (*Cephalopholis fulva*) (Feitoza *et al.* 2003). Abundant and still persistent predators include carangids (*Caranx lugubris*, *Caranx crysos* and *Elagatis bipinnulata*) and moray eels (mainly *Muraena pavonina*). However, these remaining predatory species are more likely to perform the ecological role of mesopredators, thus not fulfilling the vacant niche of extinct top-predators. The extent to which the current fishing effort aimed at pelagic species affects the demersal food web is still to be determined. The interplay of low species richness, high biomass, and unique endemism, make the tropical reefs of SPSPA an important natural laboratory of marine ecology. However, current fishing practices have drastically reduced the abundance of top-predators (Luiz and Edwards 2011), hindering opportunities to understand trophic processes comprehensively. As a precautionary action we argue that more strict fishing regulations, with a larger buffer zone around the SPSPA, should be implemented and enforced.

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**Supplementary material**

**Community structure of reef fishes on a remote oceanic island (St Peter and St Paul's Archipelago, equatorial Atlantic): the relative influence of abiotic and biotic variables**

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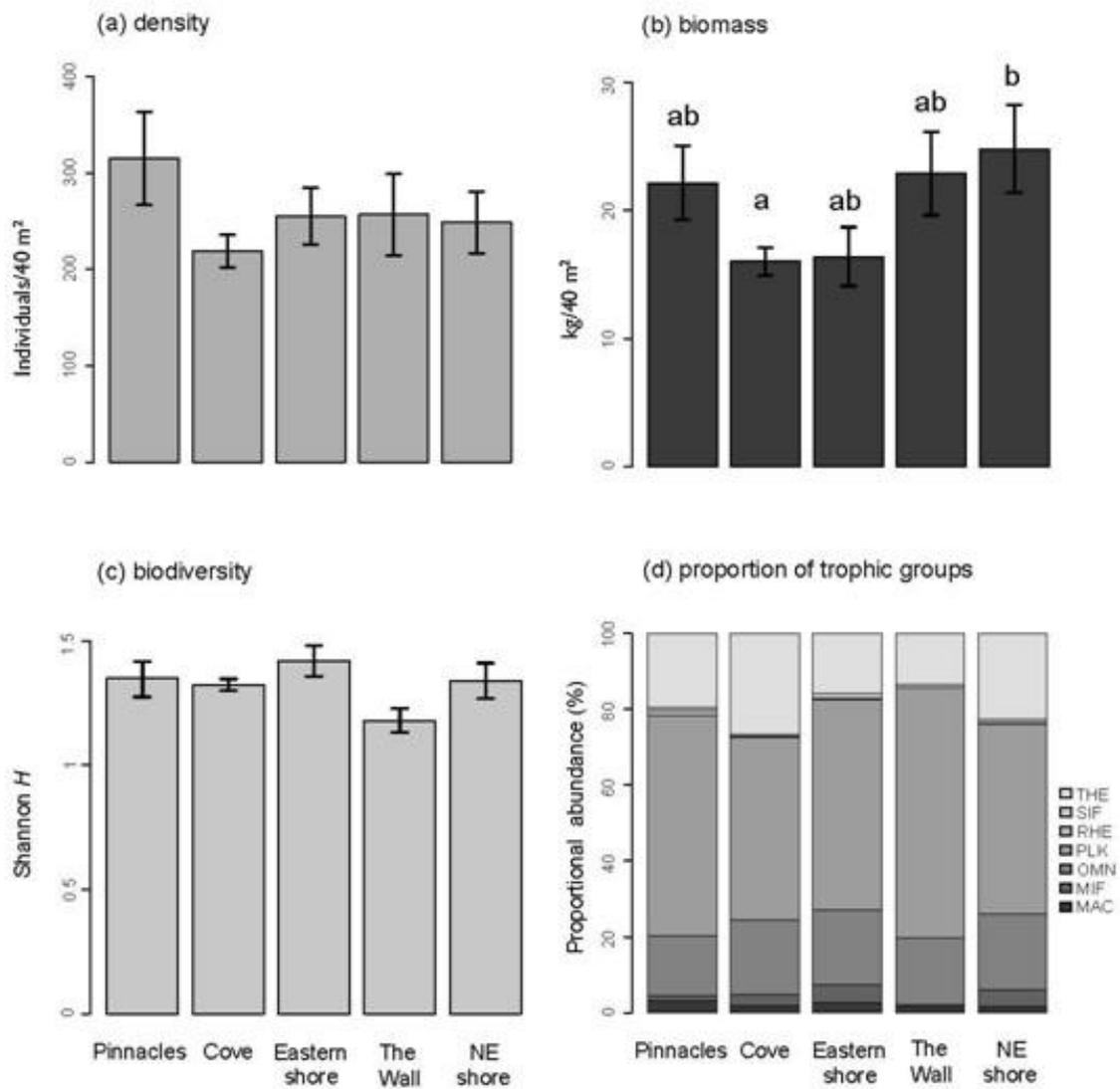
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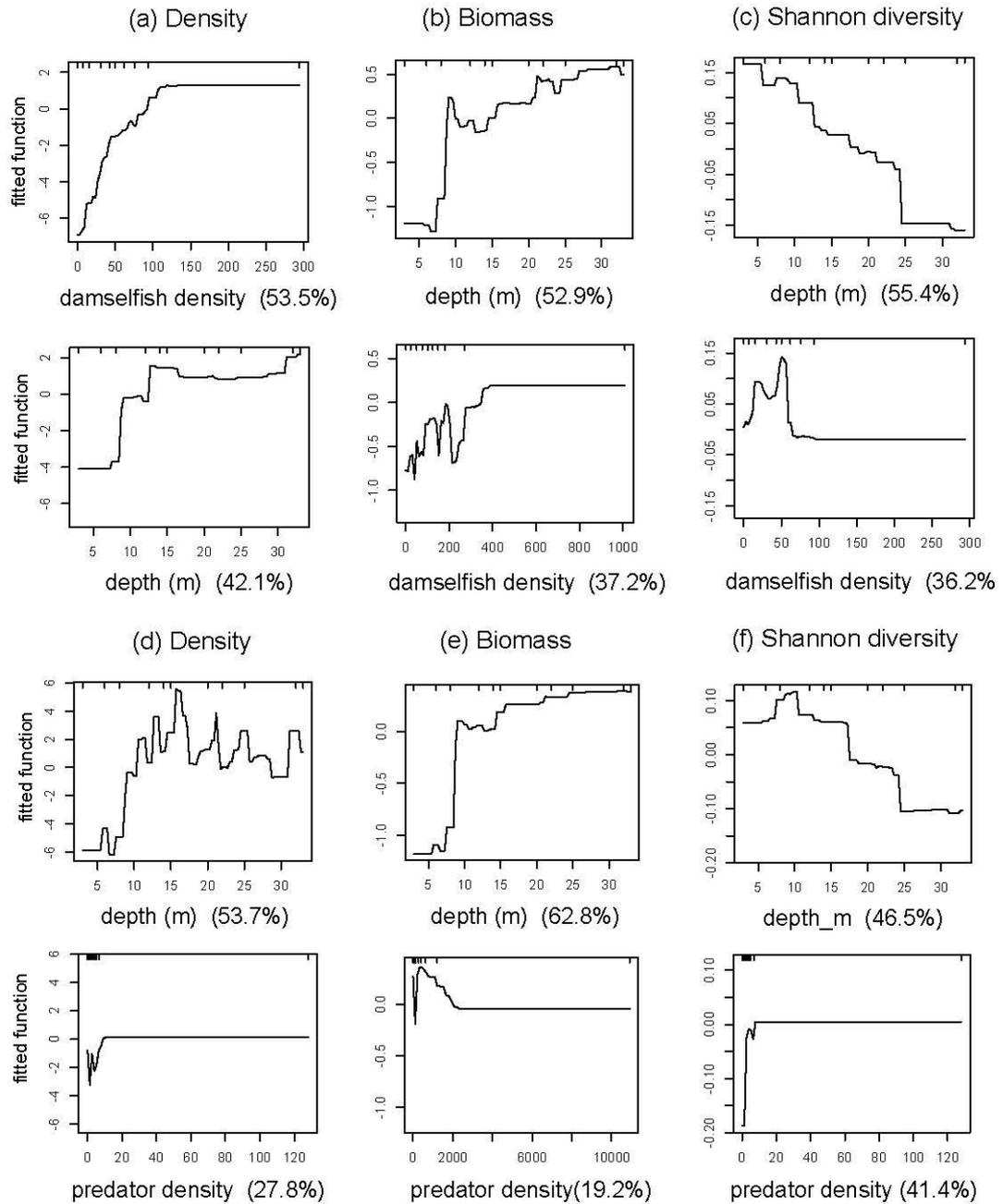
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Vitória, ES, Brazil.

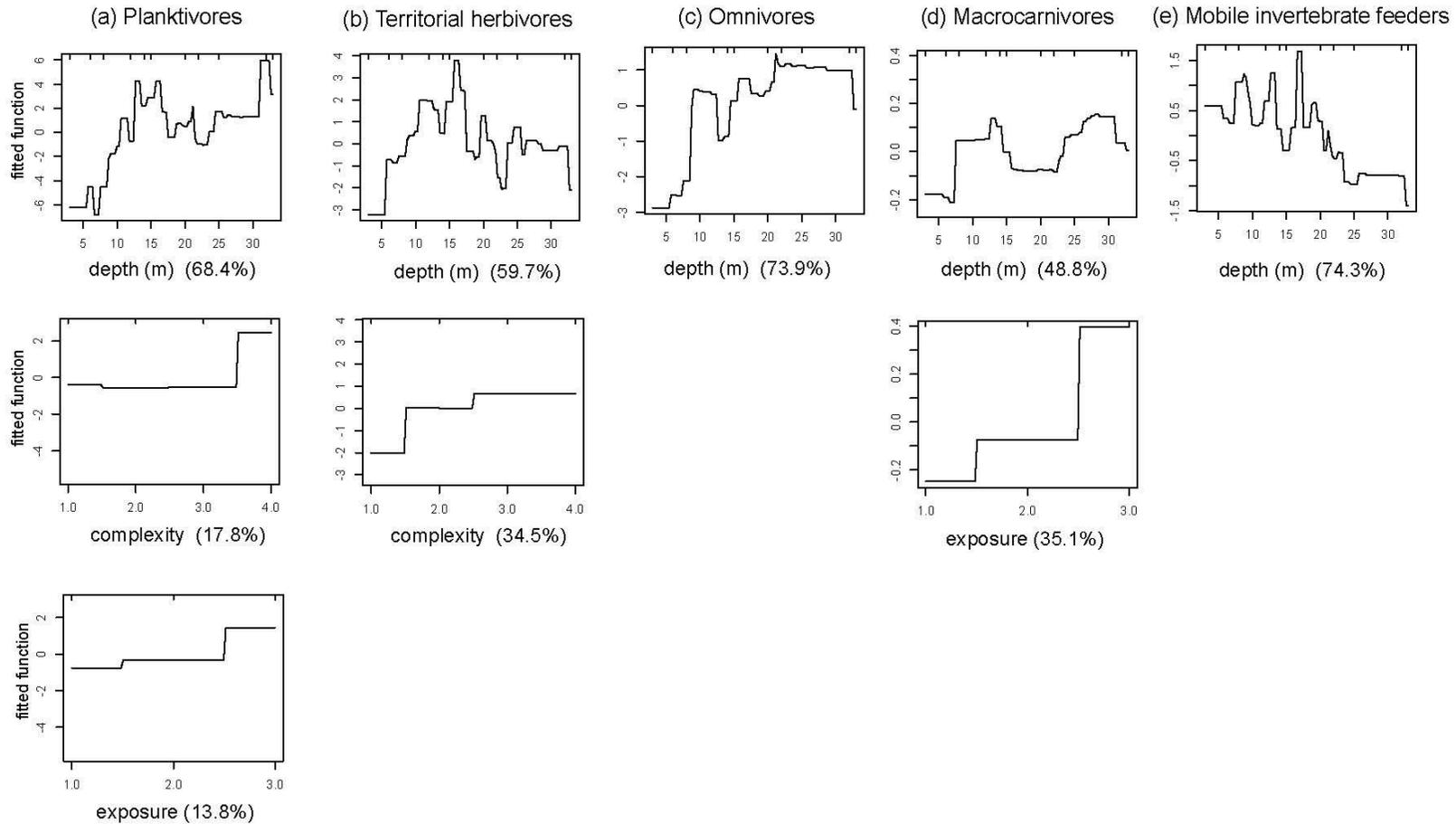
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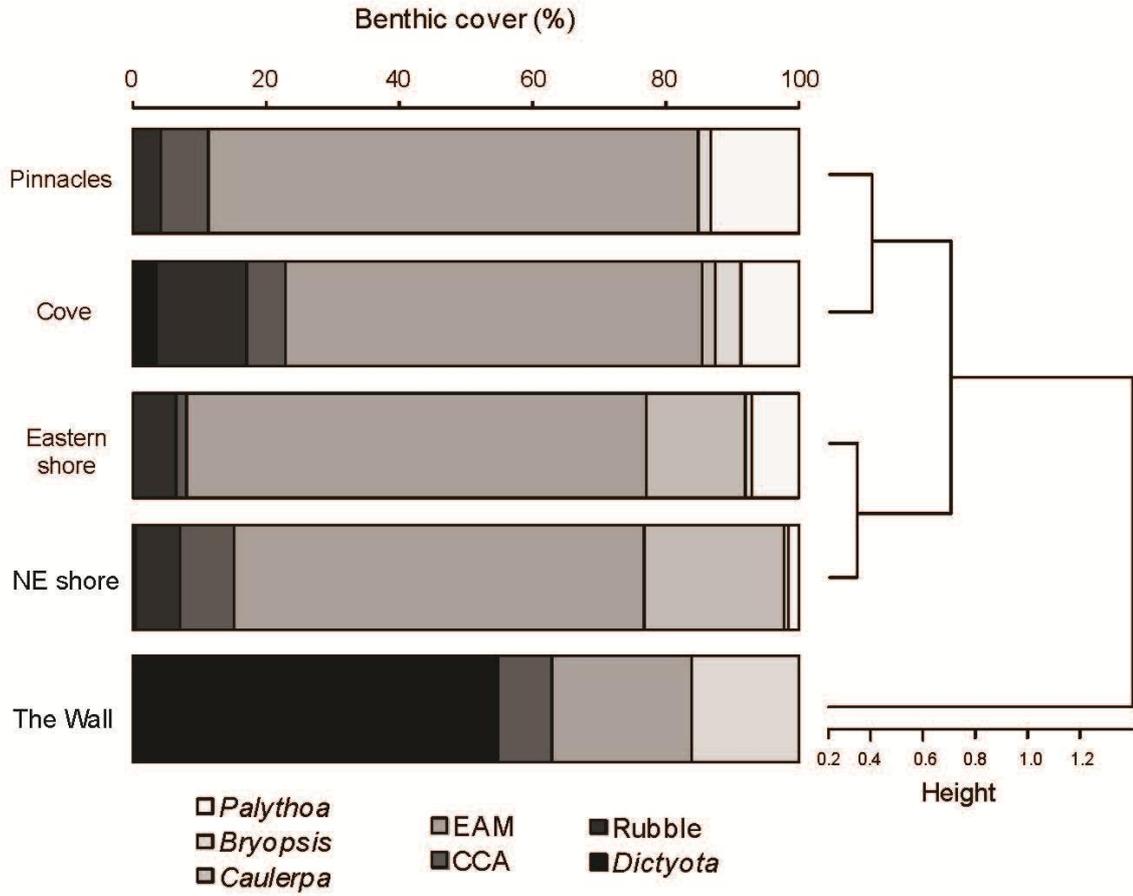
**Fig. S1.** Comparative (a) density (mean  $\pm$  s.e.; ANOVA,  $F = 0.003$ ,  $P = 0.95$ ), (b) biomass (mean  $\pm$  s.e.; ANOVA,  $F = 2.94$ ,  $P = 0.02$ ), (c) biodiversity (mean  $\pm$  s.e.; ANOVA,  $F = 1.707$ ,  $P = 0.15$ ) and (d) relative abundance of trophic groups on each site. Differences among sites were not significant for mean density (ANOVA,  $F = 2.94$ ,  $P = 0.02$ ). Contrasts groups in (b) generated with Tukey's HSD *post hoc* test. MAC, Macrocarnivore; MIF, Mobile Invertebrate Feeder; OMN, Omnivore; PLK, Planktivore; SIF, Sessile Invertebrate Feeder; THE, Territorial Herbivore.



**Fig. S2.** Partial dependence functions for the most important abiotic and biotic factors influencing reef-fish community parameters across all sampled sites. (a–c) All abiotic factors plus damselfish density, and (d–f) all abiotic factors plus predator density.



**Fig. S3.** Partial dependence functions for the most important abiotic factors influencing the density of individuals in each of the trophic groups across all sampled sites (RHE and SIF not included due to very low densities).



**Fig. S4.** Composition of the benthic community on each site, showing the similarity among them. EAM, epilithic algal matrix; CCA, crustose coralline algae.