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Reef microhabitats mediate fish feeding intensity and agonistic interactions at Príncipe Island Biosphere Reserve, Tropical Eastern Atlantic

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Abstract

The benthic assemblage of reefs provides an important resource of food and habitat for reef fishes. However, how benthic composition mediates reef fishes' biotic interactions at isolated environments such as oceanic islands remains largely unknown. Here, we aimed to investigate the role of four different reef microhabitats over biological interactions of fishes in an understudied oceanic island, Príncipe Island. For that, we recorded a total of 46 Underwater Remote Videos (RUVs) to document benthic composition and fishes' trophic and agonistic interactions. We used benthic cover estimates to group the samples into four microhabitats (dominated by epilithic algal matrix [EAM], sand/rock, corals and sponges), then quantified fishes' trophic and agonistic interactions in each microhabitat. All microhabitats presented a different structure of trophic and agonistic interactions of the fish assemblage. Feeding pressure (FP) and agonistic interactions were higher on the EAM microhabitat and lower in coral microhabitat. Herbivores were the main responsible group for the FP in all microhabitats. Territorial damselfishes used microhabitats differently for both trophic and agonistic interactions. We demonstrated that reef fish diversity and intensity of biotic interactions varied according the spatial distribution of benthic resources, which suggests that benthic composition plays an important role on structuring biological interactions at isolated reef systems.

KEYWORDS
agonistic interactions, biodiversity hotspot, Gulf of Guinea, oceanic islands, trophic interactions

1 | INTRODUCTION

A habitat can be defined as the environment in which a species lives, being distinguished through their physical and biological characteristics such as substrate and resource availability (Clements & Shelford, 1939; Ricklefs & Relyea, 2018). In marine ecosystems, habitat characteristics, such as benthic composition, have been proposed to determine the structure and functioning of marine communities (Ferreira, Gonçalves, & Coutinho, 2001; Gratwicke & Speight, 2005). On tropical reefs, the benthic assemblages can provide food (e.g. invertebrates and algae) and shelter from predators (e.g. topographic complexity) for a wide variety of reef fishes (Hixon, 2015; Smith, Johnston, & Clark, 2014). Thus, it mediates the intensity and distribution of reef fish biological interactions, such as feeding rates on benthic substrate and agonistic disputes for refuge (Giglio et al., 2018; Longo, Ferreira,

& Floeter, 2014; Longo et al., 2015; Pereira & Munday, 2016). Moreover, the distribution of reef fish interactions is crucial for sustaining ecosystem functions and resilience (Nash, Graham, & Bellwood, 2013).

Quantifying the dependence of organisms on habitat characteristics is necessary for a better understanding of the dynamics on the structure of reef communities (Bellwood & Hughes, 2001; Ricklefs, 1987). Although widely studied in inshore reefs, the influence of benthic composition on structuring reef assemblages in isolated or difficult-to-access reefs, such as oceanic islands, remains largely unknown. Oceanic islands are characterized by being geographically isolated environments from continental areas, formed by volcanic activity or tectonic plate convergence (Gillespie, 2007; Hachich et al., 2015), and generally have low species richness and high endemism rates when compared to coastal areas (Floeter et al., 2008). These features make them unique ecosystems for studying evolutionary and ecological processes that sustain these isolated and vulnerable reef communities (Rominger et al., 2016).

Studies addressing oceanic islands fish and benthic assemblages concentrate mostly in Southwestern Atlantic (e.g. Krajewski & Floeter, 2011; Longo et al., 2015; Luiz et al., 2015), Tropical Eastern Pacific (e.g. Quimbayo, Mendes, Kulbicki, Floeter, & Zapata, 2017) and in the Indo-Pacific (e.g. Friedlander & Parrish, 1998; Williams et al., 2015). However, in the Tropical Eastern Atlantic (TEA), ecological aspects of fish and benthic assemblages remains understudied (but see Friedlander, Ballesteros, Fay, & Sala, 2014; Maia et al., 2018; Tuya, Bosch, Abreu, & Haroun, 2017). Thus, there is a gap in the knowledge concerning the relationship between habitat features and organisms' interactions. Located in TEA, Príncipe Island is part of the Gulf of Guinea biodiversity hotspot (Roberts et al., 2002) and a variety of microhabitats are found on its rocky and biogenic reefs (Maia et al., 2018). These habitats are constituted of some key benthic organisms, including Epilithic Algal Matrix (EAM), calcareous coralline algae, macroalgae, hard corals, sponges, zoanthids and gorgonians (Laborel, 1974; Maia et al., 2018), potential resources that could possibly mediate fishes' biological interactions and, consequently, shape community structure.

Given the importance of benthic habitat components in structuring reef fish communities, we aimed to investigate the role of reef microhabitats over biological interactions of fishes in this poorly known oceanic island. We expected the spatial distribution of benthic resources (e.g. sand, EAM and coral) to shape distinct microhabitats and influence the structure of biological interactions of reef fishes. Also, we hypothesized that (a) microhabitats with a large cover of EAM (i.e. mostly composed by turf algae and detritus) which includes important food resources for reef fishes (Wilson, Bellwood, Choat, & Furnas, 2003), will present the highest feeding interactions and (b) microhabitats with a potentially higher structural complexity, such as coral-dominated microhabitats, will present more agonistic interactions among reef fishes. Understanding ecological interactions among species is essential to perceive community structure and the resilience of this unique system.

2 | MATERIAL AND METHODS

2.1 | Field and lab procedures

Sampling was conducted in five reefs at Príncipe Island (1°37′N, 7°24′E), between 18 and 24th of January 2016. This island belongs to the São Tomé and Príncipe Archipelago, located along the Cameroon Volcanic Line in the Gulf of Guinea, Africa (Figure 1) (Lee, Halliday, Fitton, & Poli, 1994). In these reefs, we recorded a total of 46 underwater remote videos (RUVs) during daytime (from 09:00 to 14:00 hr), in shallow waters between 3 and 12 m of depth. A RUVs sample consisted of a 15-min video shot by a high-definition camera (GoPro Hero 4 model) settled on the reef substrate and focused on a 2 m^2 (2 × 1 m) reef area, previously delimited by a diver with a measuring tape (Longo et al., 2014). The diver kept a distance of at least 10 m from the camera to avoid disturbing the behaviour of the fishes (Longo & Floeter, 2012).

In the laboratory, we took a single frame from each video to visually estimate the percentage cover of major benthic components inside the 2 m^2 delimited area. On each video frame, we quantified the percentage of benthic cover (%) for each of the following benthic categories: EAM, sand/rock, coral, sponge, calcareous algae, macroalgae and zoanthids. For quantifying fish feeding pressure (FP) on the benthic substrate and agonistic interactions among fishes, we analysed the central 10 min of each video, since the initial and final minutes were discarded in order to minimize the diver effects over fishes' behaviour (Longo et al., 2014). Each fish recorded biting the substrate or performing agonistic interactions inside the 2 m^2 area was identified, had its total length (cm) visually estimated and assigned to a trophic guild, according to Mouillot et al. (2014) and Maia et al. (2018). We focused on individuals larger than 5 cm in total length, because identification of smaller individuals in RUVs can be unprecise (Fontoura et al., 2020; Longo & Floeter, 2012).

We counted the number of bites on the reef substrate for each fish recorded biting on the benthos. We considered a bite every time a fish stroked the benthos with its jaws opened, closing its mouth subsequently, regardless ingestion (Longo et al., 2014). We calculated the FP of each individual fish in the benthic community through the equation FP = (number of bites × biomass)/(2 m^2 × 10 min) (Longo et al., 2014). The body mass (kg) is considered to account for potential body size variation in the bite impact (Hoey & Bellwood, 2009), and the estimated biomass of fish was obtained from length–weight relationships from the literature (Froese & Pauly, 2019).

We considered as agonistic interactions all events in which a fish chased another without any obvious feature that could be associated to predation. We defined as a chase an event in which a given individual fish swam rapidly towards another fish with subsequent escape of the latter, with or without contact between them. For each video, we recorded all agonistic interactions observed between all

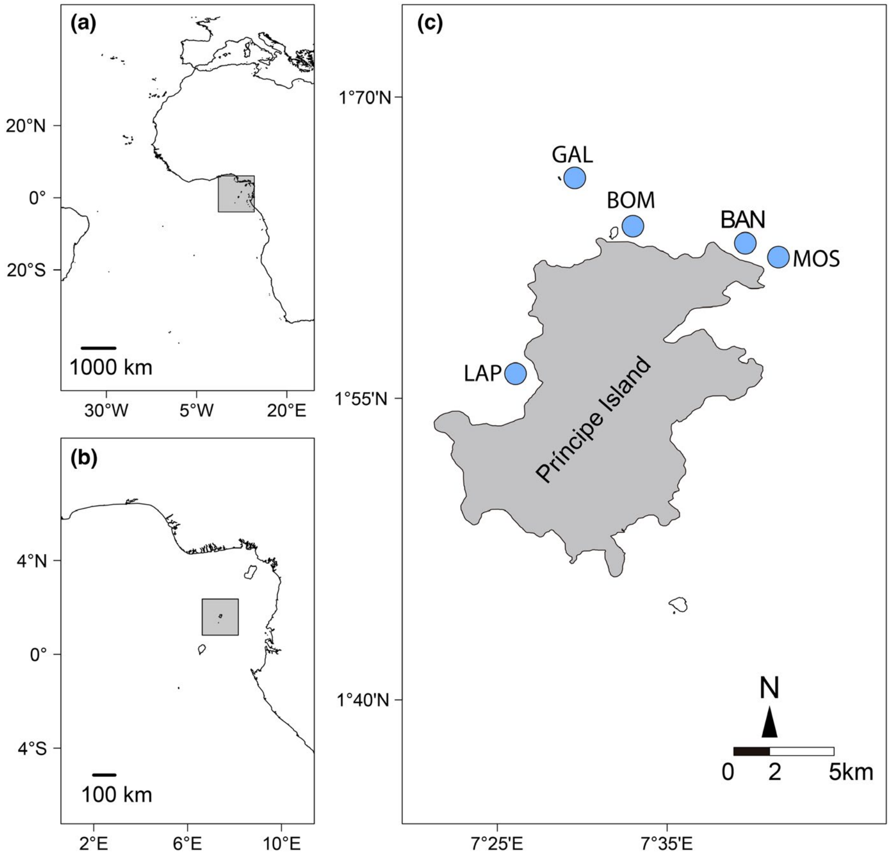

FIGURE 1 The location of Príncipe Island in the African Coast (a), in the Gulf of Guinea (represented by a grey square) (b); The Príncipe Island (c). Blue circles in "c" represent the sampled reefs in the island. BAN, Praia Banana (*N* = 8); BOM, Ilhéu Bombom (*N* = 10); GAL, Pedra Galé (*N* = 10); LAP, Praia Lapa (*N* = 10); MOS, Mosteiro (*N* = 8)

species pairs and quantified the total number of agonistic interactions performed by each species.

2.2 | Statistical analyses

First, we aimed to identify the dominant microhabitat types in relation to their main benthic composition in island of Príncipe. We identified four microhabitats (see Figure 2) based on the benthic composition (percentage of cover) of videos samples using a cluster analysis, with Euclidian distance and a similarity profile analysis (Simprof) to test for significance.

To visualize the distribution of agonistic interactions among reef fishes, we applied a network approach. We compiled one interaction matrix for each microhabitat to create a total of four one-mode directed networks and calculated the centrality degree of the species using the sum of connections of each species on them. In each network, species are represented by nodes and connected by arrows whenever an agonistic interaction between (interspecific) or within (intraspecific) them was recorded in the video samples. Thickness of the arrows represents the total number of agonistic interactions observed in all samples between species pairs or within a species. Direction of the arrows indicates the aggressor (outward) and receptor (inward) of the agonistic interaction. The colour of the nodes represents species trophic group.

To investigate the influence of benthic composition on fishes' feeding and agonistic interactions, we performed a redundancy analysis (RDA), with a subsequent analysis of variance (ANOVA) of the canonical axes, using the intensity of interactions as a response variable and benthic composition as explanatory variable. All analyses were performed using the "clustsig" (Whitaker & Christman, 2014), "vegan" (Oksanen et al., 2013), "ggdendro" (Vries & Ripley, 2016), "ggplot2" (Wickham, 2009) and "igraph" (Csardi & Nepusz, 2006) packages of R software (R Core Team, 2019).

3 | RESULTS

The structure of the feeding and agonistic interactions varied among the four microhabitats. A total of 28 species were recorded biting on the substrate and the FP (mean ± *SE*) was higher in the EAM microhabitat (4.9 ± 1.3), followed by the sponge microhabitat (1.74 ± 0.6), sand/rock (1.73 ± 0.8) and coral (0.24 ± 0.02, Figure 3a). In the EAM microhabitat, 25 species (representing all the functional groups found in this study) were recorded biting on the substrate. The scraper herbivores, such as *Acanthurus monroviae*, were the main responsible for the FP in this microhabitat (Figure 3a). In the sand/rock microhabitat, 13 species were recorded biting the substrate, with emphasis on the scraper herbivore *Sparisoma choati* and the territorial herbivore *Stegastes imbricatus*. In the coral microhabitat, only five species were recorded biting on the substrate, with the highest FP performed by the territorial herbivore *St. imbricatus*. In the sponge microhabitat eight species were recorded feeding. Among them, the scrapers *A. monroviae*

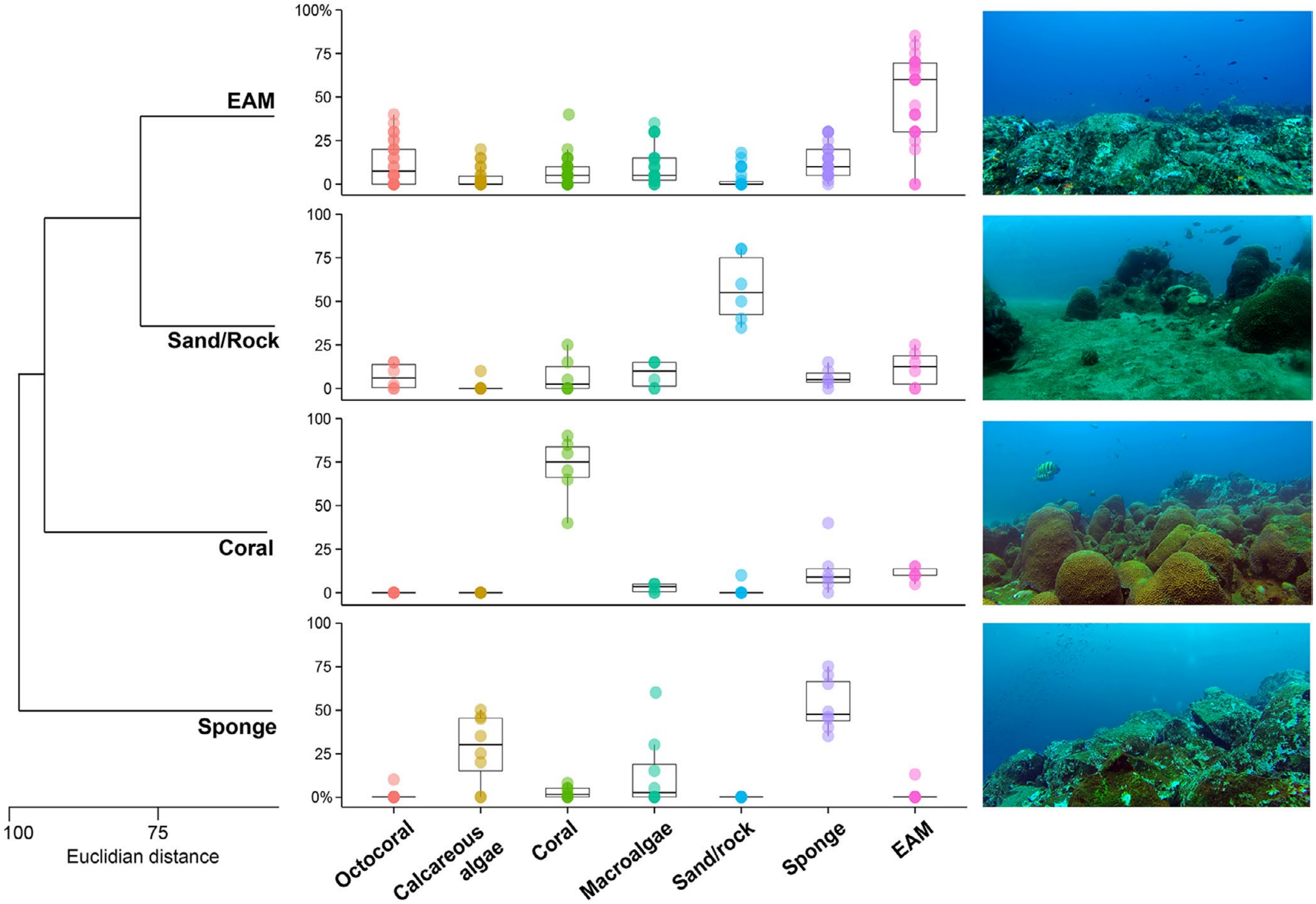

FIGURE 2 The four microhabitats (Epilithic Algal Matrix – EAM, Sand/rock, Coral and Sponge) according to the percentage of benthic composition based on a cluster analysis. On the middle, boxplot and scatter plot indicating the percentage cover of benthic groups (*y*-axis) in each microhabitat. The *x*-axis represents the benthic groups. On the right, a visual representation of each microhabitat

and *S. choati*, and the territorial herbivore *Microspathodon frontatus* were the most representative.

A total of 26 species were observed engaging in agonistic interactions. The EAM microhabitat had the greatest number of species (17) performing agonistic interactions (Figure 3b). The sand/rock, coral and sponge microhabitat networks had respectively 11, 12 and 7 species interacting. In all microhabitats, the territorial herbivores occupied the central position in agonistic networks and showed a higher number of agonistic interactions towards other species. In the microhabitats dominated by EAM, sand/rock and coral, the most aggressive and central species was *St. imbricatus*. On the other hand, in the sponge microhabitat, the most aggressive and central species was *M. frontatus*.

The RDA demonstrated that benthic composition explained feeding and agonistic interactions of fishes on Príncipe Island (Figure 4). Overall, we found that reef fish FP and agonistic interactions varied among microhabitats. FP of the two territorial herbivores differed between microhabitats. While *M. frontatus* fed mainly on the sponge-dominated microhabitat, *St. imbricatus* FP was higher in the coral microhabitat (Figure 4a). In contrast, the roving herbivores *S. choati* and *A. monroviae* were more associated with the EAM microhabitat. In terms of agonistic interactions, four species showed disproportionally higher number of agonistic interactions on specific microhabitats. *Microspathodon frontatus* engaged in agonistic interactions with other fishes mostly in the sponge-dominated microhabitat, *St. imbricatus* interacted more in the EAM, sand/rock and coral microhabitats (Figure 4b) and *Myripristis jacobus* was observed interacting more in the coral microhabitat.

4 | DISCUSSION

We demonstrated for the first time the influence of benthic composition on shaping a mosaic of microhabitats that mediated the distribution and intensity of both trophic and agonistic interactions of reef fishes in an oceanic island. The microhabitat dominated by EAM sustained a higher number of interacting species and functional groups, principally herbivores. Nonetheless, the variation of interspecific interactions among microhabitats highlights the importance of habitat heterogeneity for the maintenance of species' local coexistence in isolated systems.

The higher diversity and intensity of fishes feeding on the EAM microhabitat (Figure 3a) is potentially explained by its composition. The EAM, commonly known as "turf", comprises a complex matrix

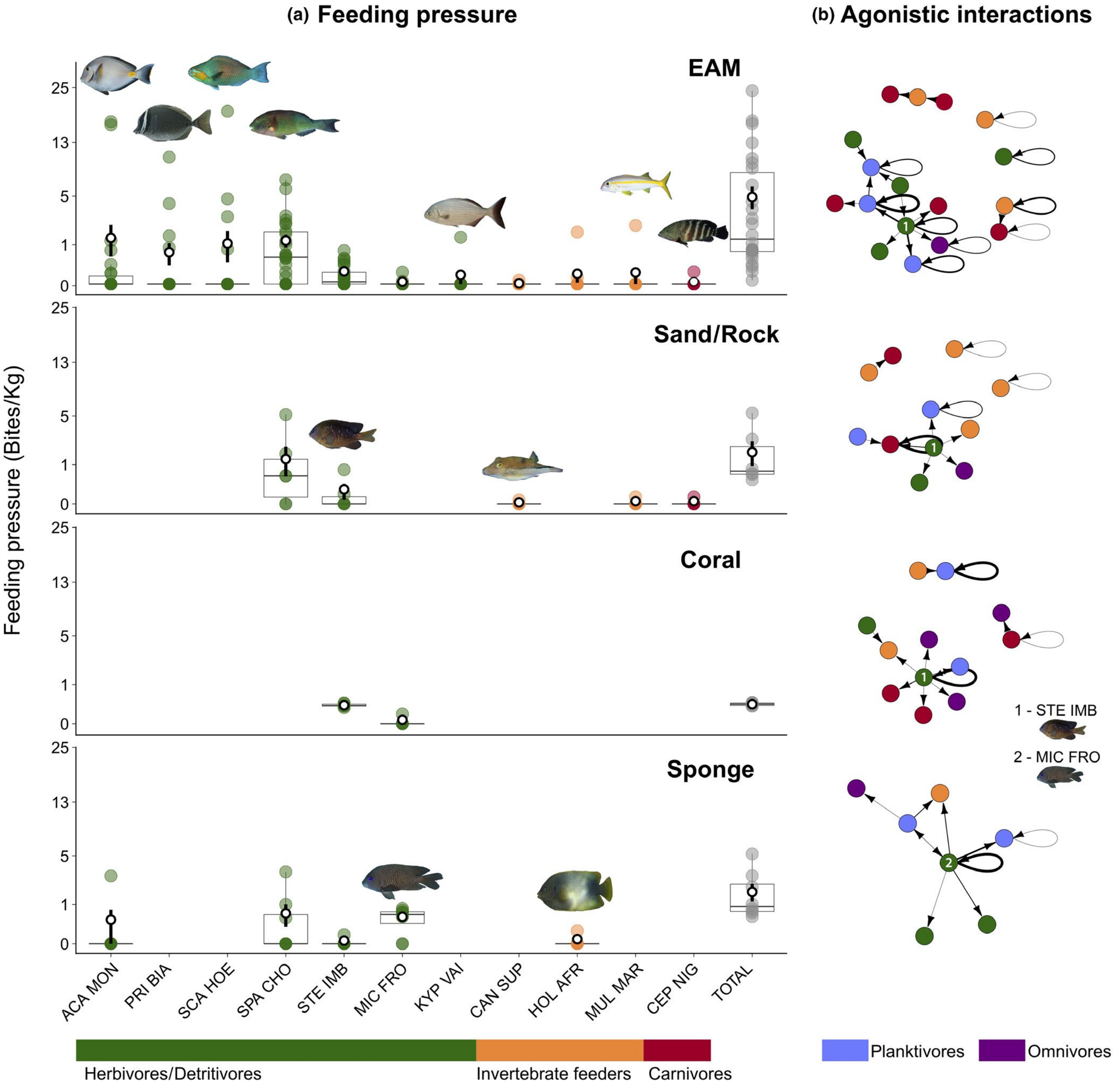

FIGURE 3 (a) Feeding pressure (FP) performed by different fishes and their respective functional groups on the benthic community in four microhabitats. ACA MON, *Acanthurus monroviae*; CAN SUP, *Canthigaster supramacula*; CEP NIG, *Cephalopholis nigri*; HOL AFR, *Holacanthus africanus*; KYP VAI, *Kyphosus vaigiensis*; MIC FRO, *Microspathodon frontatus*; MUL MAR, *Mulloidichthys martinicus*; PRI BIA, *Prionurus biafraensis*; SCA HOE, *Scarus hoefleri*; STE IMB, *Stegastes imbricatus*. Circles represent samples, white circles and black bars represent the species mean feeding pressure and standard error, respectively. Only species with mean feeding pressure values equal or greater than 0.05 are represented. (b) Agonistic interactions networks for the five microhabitats. Thickness of the arrows represents the total number of agonistic interactions observed in all samples between or within species. Direction of the arrows indicates the aggressor (outward) and receptor (inward) of the agonistic interaction. The colour of the nodes represents species trophic group. The numbers (1 and 2) indicate the central species for each microhabitat

composed of algae, invertebrates and detritus which are important in the food chain due to its high nutritional value (Wilson et al., 2003). Detritus is one of the most important component of the EAM, and it is considered the main food source for many herbivores and detritivores (Bonaldo & Bellwood, 2008; Ferreira & Gonçalves, 2006; Wilson et al., 2003). In addition, the invertebrate cryptofauna inhabiting the EAM possibly provides a significant food resource for upper trophic levels as omnivores and invertivore fishes (Enochs & Manzello, 2012; Klumpp, McKinnon, & Mundy, 1988; Kramer, Bellwood & Bellwood, 2013; Kramer, Bellwood & Bellwood, 2014).

In the sand/rock and coral-dominated microhabitats, the lower intensity of fish feeding is possibly due to their lower nutritional

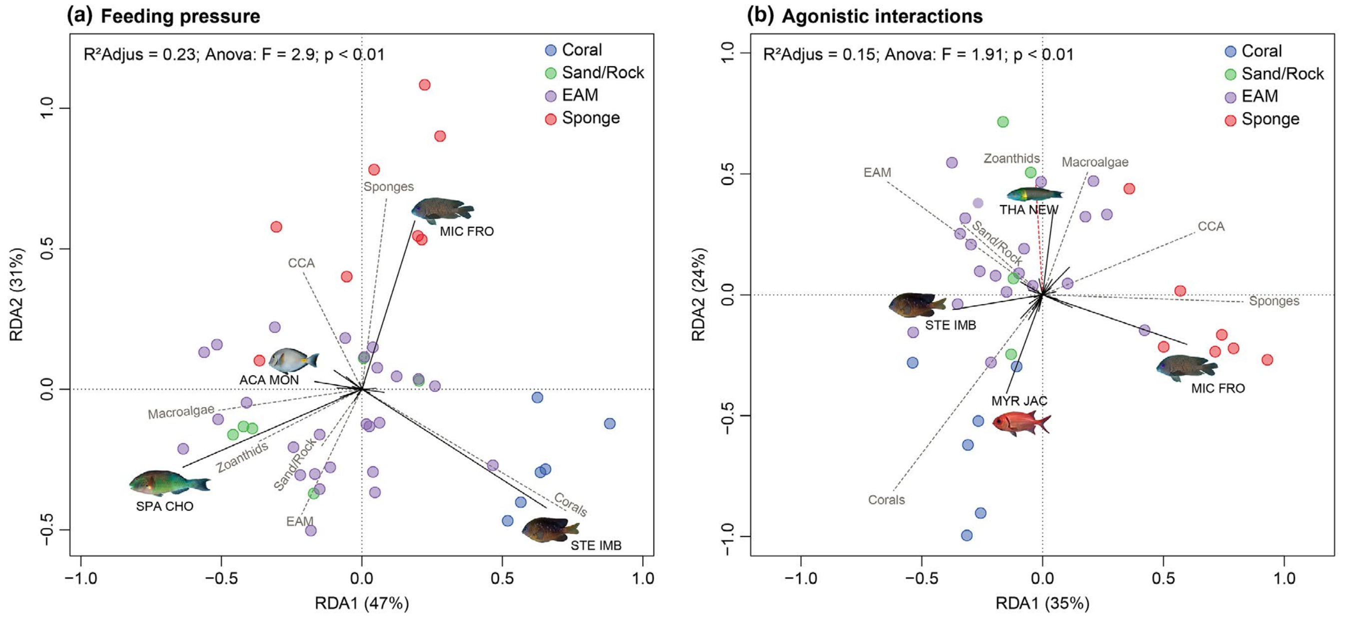

FIGURE 4 Redundancy analysis (RDA) between the benthic community and the biological interactions of fishes (a—feeding pressure and b—agonistic interactions). Circles indicate samples, colours indicate microhabitats. Grey dashed lines indicate benthic composition and black continuous lines represent fishes. ACA MON, *Acanthurus monroviae*; MIC FRO, *Microspathodon frontatus*; MYR JAC, *Myripristis jacobus*; SPA CHO, *Sparisoma choati*; STE IMB, *Stegastes imbricatus*; THA NEW, *Thalassoma newtoni*. Percentages represents the proportion of the constrained values explained for each axis

value and absence of structures that have the small-scale intricate complexity of the EAM (Wilson, 2002). Moreover, there are no corallivore reef fishes in Príncipe Island (Cole, Pratchett, & Jones, 2008). The species that most interacted in the coral microhabitat was the territorial *St. imbricatus*, possibly due to the behaviour of these damselfish of cultivating algae inside its territories (Lassuy, 1980), usually located between coral patches. In contrast, the other territorial herbivore, *M. frontatus*, was more frequently observed interacting in the sponge microhabitat and showed a distinct habitat-association compared to *St. imbricatus*, that interacted more frequently in the other three microhabitats. This differentiation in habitat use by territorial herbivores (Figure 4a) have already been documented for other damselfishes (Chaves, Ormond, McGinty, & Ferreira, 2012) and emphasizes the importance of habitat heterogeneity to sustain biodiversity.

Herbivores were the main responsible for the total FP in all microhabitats (Figure 3a). The dominance of FP by herbivores (specially from the genus *Acanthurus*, *Scarus* and *Sparisoma*) in different habitats was already documented for other coastal and oceanic systems (Lefcheck et al., 2019; Longo et al., 2014, 2015). In marine ecosystems, herbivory is known as a fundamental process that affects the structure and functioning of coral and rocky reefs, and kelp forests (e.g. Carter, Van Blaricom, & Allen, 2007; Mumby, 2006; Poore et al., 2012; Sala & Boudouresque, 1997). By keeping parts of the substrate free from algae, coral recruits can settle and grow (Ogden & Lobel, 1978). Among herbivore fishes, scrapers are important as they ingest detritus and organic matter present in the EAM where they feed (Choat, Clements, & Robbins, 2004). Detritus is a highly nutritional food material, since it includes several microorganisms such as cyanobacteria and other protein-rich organisms, targeted by scrapers such as parrotfishes (Clements, German, Piché, Tribollet, & Choat, 2017; Wilson, 2002). Thus, scraper fishes help organic matter cycling on reefs (Crossman, Choat, & Clements, 2005).

The EAM microhabitat also presents the highest number of fishes engaged in agonistic interactions. Since this microhabitat has a wide variety of items (Wilson et al., 2003) and attracts more species for feeding, the chances of agonistic interactions are likely intensified (Peiman & Robinson, 2010). On the other hand, as FP was lower in sand/rock, coral and sponge microhabitats, a possible cause for the agonism observed in these microhabitats is the existence of competition for refuge places rather than food (Bonin, Boström-Einarsson, Munday, & Jones, 2015). Three-dimensional complex habitats, such as corals, are often used by small fishes as a refuge to avoid predation (Smith et al., 2014). The relatively large number of agonistic interactions observed between soldierfish *My. jacobus* individuals in the coral microhabitat (Figure 4b) might be an effect of the potential three-dimensionality shaped by the abundant coral colonies. As soldierfishes resides in caves and reef crevices during the day and forage during the night, their agonistic interactions are possibly related to refuge defence (Randall & Greenfield, 1996).

The territorial herbivore *St. imbricatus* is central in the agonistic networks in EAM, sand/rock and coral microhabitats (Figure 3b). Fishes from the genus *Stegastes* are key species for structuring agonistic interactions in coral reefs (Fontoura et al., 2020), and display intra and interspecific aggressiveness towards other fishes by defending their "algal gardens", especially from other herbivores (Lassuy, 1980). These territories are highly productive and have greater algal biomass and diversity than adjacent areas, features that makes worth spending energy on defending them (Hinds & Ballantine, 1987; Sammarco, 1983). In addition to primary productivity, there is a greater diversity of invertebrates in their territories, thus attracting invertebrate feeders (Ceccarelli, Jones, & McCook, 2001). Both the aggressive behaviour of these damselfishes and the possible greater demand of other fishes for the higher quality territories are factors that explain the great amount of agonistic interactions observed (Ceccarelli et al., 2001; Lassuy, 1980).

The only microhabitat with a different central species in the network was the sponge-dominated microhabitat, where *M. frontatus* engaged more frequently in agonistic disputes. This species is also classified as a territorial herbivore and presented an increased aggressive behaviour towards *St. imbricatus*. However, *M. frontatus* is a non-selective consumer that consumes algae in its territory in the proportion that they occur (Montgomery, 1980). Both central species from the Pomacentridae family were observed feeding and engaging into disputes at the same microhabitats (on EAM and sponge) but at different intensities. This observation reinforces the differentiation of habitat use between the two territorial damselfishes and the importance of habitat heterogeneity on creating ecological opportunities for species that hold similar niches to coexist locally in an isolated reef system (Robertson, 1996).

The influence of microhabitats on fishes' biological interactions was also recorded in different marine and freshwater ecosystems. At Rocas Atoll, for example, the feeding interactions, performed mostly by herbivore surgeonfishes, differ according to tide pool regimes and benthic composition (Longo et al., 2015). The importance of habitat characteristics in fish interactions was also observed in a freshwater system, where three different habitats (Plant, Lake, Rock) have shown different functions for mediating fishes' agonistic and trophic interactions. The rock habitat concentrated most of feeding interactions, while the lake habitat hosted most of the agonistic interactions (Nunes, Morais, Longo, Sabino, & Floeter, 2020).

We demonstrated that biological interactions are, in part, dependent on microhabitat characteristics, especially for herbivore fishes which are critical for maintaining ecosystems functions and the resilience on reef environments (Cheal et al., 2010; Hoey & Bellwood, 2009; Lefcheck et al., 2019; Longo et al., 2015). Príncipe island, as well as other oceanic islands, present low fish species richness comparing to coastal environments (Hachich et al., 2015) consequently resulting in low functional redundancy and higher vulnerability (Mouillot et al., 2014). Since spatial distribution of fishes' interactions might be dependent on different microhabitats, maintaining habitat heterogeneity is essential to preserve the fish diversity in oceanic islands. Therefore, different microhabitats sustaining a diverse array of interactions among species are essential for the resilience of this unique system.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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