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Article

Taxonomic and functional diversity of mollusk assemblages in a tropical rocky intertidal zone

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ABSTRACT. We investigated the spatial variation of molluscan assemblages with different habitat-forming species and bare rock habitat in a rocky intertidal zone in northeastern Brazil. The high intertidal zone substrate was covered predominantly of barnacles [*Chthamalus bisinuatus* (Pilsbry, 1916)], the mid-intertidal of mussels [*Brachidontes exustus* (Linnaeus, 1758)] and the low intertidal of macroalgae chlorophytes [*Gayralia oxysperma* (Kützing) K. L. Vinogradova ex Scagel *et al.*, 1989 and *Ulva lactuca* Linnaeus, 1753], phaeophytes [*Sargassum vulgare* C. Agardh] and rhodophytes [*Palisada flagellifera* (J.Agardh) K. W. Nam, 2007]. A total of 3,861 mollusks were recorded, belonging to the classes Gastropoda (9 species; 3,800 individuals), Bivalvia (3 spp.; 54 ind.), and Polyplacophora (1 sp.; 7 ind.). Functional diversity was accessed through the trophic structure, in which we identified food guilds: suspension feeders, grazers, herbivores, and carnivores. The analysis revealed significant differences in mollusk abundance, species richness, diversity indices, and trophic diversity among barnacle belts, mussel beds, algae habitat, and bare rock habitats. The highest species richness and trophic diversity were detected in algae habitat and mussel beds, which showed low abundance. In contrast, barnacle belts registered low species richness and trophic diversity and a high number of individuals. Bare rock recorded low values in all surveyed indices. This result points to the effect of environmental modification caused by habitat-forming species in this system. These species increase environmental complexity and enable the establishment of organisms through facilitation processes. The various food guilds found in this study reaffirm the role of habitat-forming species in providing niches that support different occupation patterns.

KEYWORDS. Trophic groups, benthic ecology, ecosystem engineers, biological substrate, southwestern Atlantic.

RESUMO. Diversidade taxonômica e funcional das assembleias de moluscos em uma zona entre marés rochosa tropical. Nós investigamos a variação espacial das assembleias de moluscos em função de diferentes habitats formados por fauna séssil e substrato rochoso em uma zona entre marés rochosa no nordeste do Brasil. O substrato da zona entre marés superior era predominantemente recoberto por cracas [*Chthamalus bisinuatus* (Pilsbry, 1916)], da zona entre marés média por mexilhões [*Brachidontes exustus* (Linnaeus, 1758)] e da zona entre marés inferior por macroalgas clorofíceas [*Gayralia oxysperma* (Kützing) K. L. Vinogradova ex Scagel *et al.*, 1989 and *Ulva lactuca* Linnaeus, 1753], feofíceas [*Sargassum vulgare* C. Agardh, 1820] e rodofíceas [*Palisada flagellifera* (J. Agardh) K. W. Nam, 2007]. Foram registrados 3861 moluscos pertecentes às classes Gastropoda (9 espécies; 3800 indivíduos), Bivalvia (3 spp.; 54 ind.), e Polyplacophora (1 sp.; 7 ind.). A diversidade funcional foi analisada através da estrutura trófica, na qual identificamos as guildas alimentares: suspensívoros, raspadores, herbívoros e carnívoros. Abundância, riqueza de espécies, diversidade de Shannon, uniformidade de Pielou e diversidade trófica variaram em função dos habitats formados por cracas, mexilhões, algas e substrato rochoso. Habitats formados por algas e mexilhões apresentaram elevada riqueza de espécies e diversidade trófica, entretanto, apresentaram baixa abundância. Ao contrário, o habitat formado por cracas registrou baixa riqueza e diversidade trófica e elevado número de indivíduos. O substrato rochoso apresentou valores baixos em todos os índices investigados. Esse resultado mostra o efeito da modificação ambiental provocada pela fauna séssil nesse sistema. Esses organismos aumentam a complexidade ambiental e viabilizam o estabelecimento de organismos por meio de processos de facilitação. As diferentes guildas alimentares encontradas neste estudo reafirmam o papel dos substratos biológicos no fornecimento de nichos capazes de suportar diferentes padrões de ocupação.

PALAVRAS-CHAVE. Grupos tróficos, ecologia bentônica, engenheiros do ecossistema, substrato biológico, Atlântico sul ocidental.

Biodiversity can be quantified at many levels of biological organization, from the molecular to the ecosystem (Feld *et al.*, 2009; Moreno *et al.*, 2018). Classically, biodiversity has been described through diversity indices based on species richness or evenness, with relative abundance (Villéger *et al.*, 2010; Moreno *et al.*, 2018). Although they provide meaningful information about the structure of biotic systems, they do not consider the functional identity of organisms (Orwin *et al.*, 2014). Functional diversity is the component of biodiversity that describes the functions performed by organisms in an assemblage, community, or ecosystem (Tilman, 2001). It can be quantified by the functional characteristics of the species, described as biological attributes that influence ecosystem organization (Mlambo, 2014; Gusmão-Júnior *et al.*, 2016).

Among the methods for assessing functional diversity is the analysis of functional groups or trophic guilds (Gusmão-Júnior & Lana, 2015; Donnaruma *et al.*, 2018a). According to the original definition, guilds are groupings of species that exploit the same class of environmental resources in a similar way (Root, 1967). In turn, feeding guild refers to the assemblage of species with similarities in the size and composition of food particles, the mechanism of ingestion, and the mobility patterns associated with feeding (Fauchald & Jumars, 1979).

The feeding guild structure of intertidal benthic communities is affected by environmental heterogeneity (Gallucci *et al.*, 2020). In the rocky intertidal zone, sessile organisms, such as mussels and macroalgae, increase environmental heterogeneity, and host a diverse associated fauna (Borthagaray & Carranza, 2007; Bellgrove *et al.*, 2017). Sessile biota provides other organisms with protection from physical stress (Scrosati *et al.*, 2011), food source (Gosselin & Chia, 1995), and shelter from predation and desiccation (Gutiérrez *et al.*, 2003). Therefore, these organisms fulfill the role of habitat-forming species by creating and modifying the habitat in which they occur (Jones *et al.*, 1994). The habitat-forming species influence species richness, abundance, uniformity, and functional identity playing an important role in the organization and functioning of intertidal benthic communities (Lemieux & Cusson, 2014).

Mollusks are among the more diverse and abundant groups of marine intertidal benthic communities, occupying a wide range of habitats and ecological niches (Zuschin *et al.*, 2001; Ponder & Lindberg, 2008). Functional diversity through the use of feeding guilds, in molluscan assemblages, has been investigated in submerged environments (Rueda *et al.*, 2009; Donnaruma *et al.*, 2018a). In the intertidal zone, studies on mollusk feeding guilds have been carried out on sandy beaches (Arruda *et al.*, 2003) and on vermetid bioconstructions (Donnaruma *et al.*, 2018b). A study on the rocky intertidal community with a biological substrate was developed for medium- and macrofauna, with a secondary emphasis on mollusks (Gallucci *et al.*, 2020). To our knowledge there is only one previous study assessed the trophic structure of molluscan assemblages inhabiting different habitat types in a tropical rocky intertidal zone (Olabarria *et al.*, 2001).

Therefore, the goal of this study was to investigate the structure and function (through the use of feeding guilds) of molluscan assemblages inhabiting different habitat types in a rocky intertidal zone. We analyzed the taxonomic and functional diversity of molluscan assemblages in a tropical urban area in Bahia state, in Brazil's Northeast Region, investigating their spatial variation among three habitats-forming species, and bare rock habitat. We have tested the hypothesis that different biological substrates harbor different associated assemblages. We admit that the variation in taxonomic and functional diversity will be explained by environmental heterogeneity (Hutchinson, 1959; Villéger *et al.*, 2010). We, therefore, expect mollusk assemblages to exhibit differences in composition between the different habitats investigated. In this investigation, we first characterized habitats and feeding guilds and subsequently compared synecological indices and functional diversity. Finally, we discuss the taxonomic structure and trophic relationships identified and their association with described habitats.

MATERIAL AND METHODS

Study area. The study was performed in the south-west Atlantic, in the Northeast Region Brazil, on a hill called *Morro de Pernambuco* (14°48'S, 39°01'W), located at the limits of a peninsula at the mouth of the Cachoeira River. It is inserted in the urban area of Ilhéus, Bahia state. The climate is tropical, with a mean temperature of 24.6°C and an annual precipitation of 2,000 mm irregularly distributed throughout the year (Alvares *et al.*, 2013). Recreation and tourism activities are carried out in this place, which suffers from environmental impact due to garbage deposition, erosive tendencies, and inadequate traffic of motor vehicles (Silva, 2015). The site was selected because of land accessibility, and to provide a stable rocky substrate (no loose blocks). *Morro de Pernambuco* is formed by irregular rocky outcrops of volcanic origin (Oliveira *et al.*, 1989). The substrate of these outcrops stretch covered by sessile biota, including different species of invertebrates and macroalgae.

Data collection. Sampling was carried out in August 2012 on the rocky intertidal zone along the eastern side of *Morro de Pernambuco*, facing the Atlantic Ocean, at low spring tide. The molluscan assemblages were investigated in two rocky outcrops. In each of them, samples were obtained along three parallel transects measuring 1 by 30 m (30 m along-shore transects). The positioning of transects was chosen according to the intertidal zones. The upper boundary was determined using ecological indicators (barnacle zone). The intertidal range was then divided into three zones of equal vertical extent (high, mid, and low level) (Heaven & Scrosati, 2008). Samples with five aleatory replicates at each intertidal zone in each of the rocky outcrops were collected by visual estimate of percentage cover, totaling 10 samples per level. The percentage cover of sessile organisms was estimated using quadrats (60 x 60 cm) with 100 subdivisions (Dethier *et al.*, 1993). Samples with five aleatory replicates at each intertidal zone in each of the rocky outcrops were collected by scraping the hard bottom, totaling 10 samples per level. The biological substrate was removed by scraping a quadrat (25 × 25 cm) and the malacofauna present in each sample were manually removed using forceps and spatula and washed in a 0.5-mm meshsieve. The organisms retained were packed in plastic bags for transport to the laboratory, where they were refrigerated for 24 h and then fixed in 70% ethanol. Infaunal mollusks were not considered in this study.

The mollusks were examined under a stereoscopic microscope and identified to the lowest possible taxonomic level. To each mollusk species, a feeding guild was assigned, according to Rios (2009) and Felder & Camp (2009). The following categories were considered: suspension feeders, grazers, herbivores, and carnivores (*e.g.*, Barroso *et al.*, 2018).All collected material was incorporated into the Malacological Collection "Prof. Henry Ramos Matthews" - series B of the Universidade Federal do Ceará (CMPHRM-B/UFC).

Data analysis. The habitat-forming species were described through the average percentage cover per level sampled in the intertidal zone. Subsequently, they were classified into different habitats.

Mollusk assemblages were analyzed using synecological indices, such as the total abundance of individuals (N), species richness, the Shannon-Weaver species diversity (H'), and the Pielou's Evenness (J). The quantitative and qualitative dominances (%DI and %DQ) and frequency (%F) were also calculated. The functional (trophic) diversity of the molluscan assemblages at each habitat was analyzed through the index of trophic diversity (ITD) (Heip *et al.*, 1985). The ITD ranges from 0 to 1 (high and low trophic diversity, respectively), and is calculated according to the following equation:

$$\mathrm{ITD} = \sum q_i^2$$

where q_i is the relative contribution of the number of individuals of each trophic group (i) to the total number of individuals. According to the modified version applied to mollusks (Antit *et al.*, 2016), ITD was calculated as 1-ITD to have the highest trophic diversity with the greatest weight (Donnarumma *et al.*, 2018a).

Analyses of variance (ANOVAs) were performed to test abundance, species richness, Shannon-Weaver diversity, Pielou's Evenness, and index of trophic diversity variation between habitat types. Each was based on a one-way model. When significance was identified, a Tukey test was used to evaluate differences between pairs of means. The assumptions of normality and homogeneity of variance were tested before all analyses using Shapiro–Wilk and Levene tests, respectively. When necessary, data were log (x + 1) transformed to remove heterogeneous variances (Zar, 1996).

To assess the relationship between food guilds and habitat types we use redundancy analysis (RDA). The response matrix of presence-absence data was Hellinger transformed and the explanatory matrix was standardized to zero mean and unit variance (Legendre & Gallagher, 2001). Normality and multicollinearity assumptions were tested before using the Shapiro-Wilk test and variance inflation factors, respectively (Fox & Monette, 1992). All analyses were performed in R ver. 3.6.1 (R CoreTeam, 2019).

RESULTS

Environmental characteristics. The high intertidal zone substrate was covered predominantly (68%) of barnacles [*Chthamalus bisinuatus* (Pilsbry, 1916)], and the mid-intertidal (52%) of mussels [*Brachidontes exustus* (Linnaeus, 1758)]. In the low intertidal there was a predominance (78%) of macroalgae chlorophytes [*Gayralia oxysperma* (Kützing) K. L. Vinogradova ex Scagel *et al.*,1989 and *Ulva lactuca* Linnaeus, 1753], phaeophytes [*Sargassum vulgare* C. Agardh] and rhodophytes [*Palisada flagellifera* (J. Agardh) K. W. Nam, 2007]. Substrate with no cover (bare rock) were identified at the high (31%), mid (4%), and low (5%) intertidal zones. Therefore, barnacles, mussels, and macroalgae were considered habitat-forming species, and the rocky substrate with no associated sessile biota were described as bare rock. For data analysis, each substrate (barnacle belt, mussel beds, algae habitat and bare rock) was treated as a habitat type (Fig. 1).

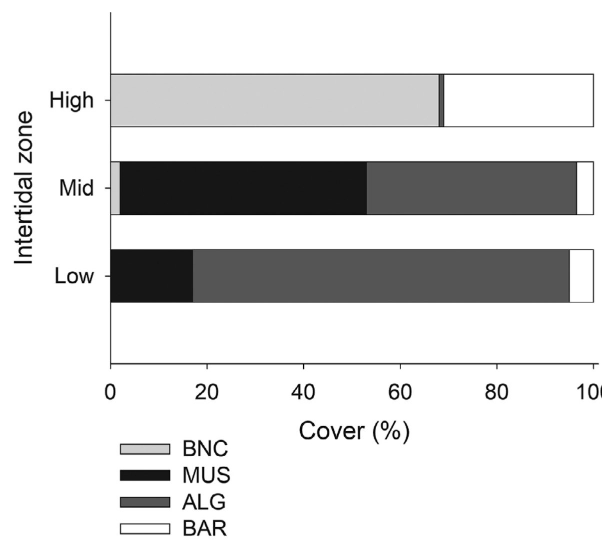

Fig. 1. Substrate characterization of the rocky intertidal zone of *Morro de Pernambuco*, Ilhéus, Bahia, Brazil. Intertidal zones (High, Mid and Low) and percent cover (mean) of algae habitat (ALG), bare rock (BAR), barnacle belt (BNC) and mussel beds (MUS).

Taxonomic composition. A total of 3,861 mollusks were recorded at the 30 sampled points. Overall, 13 species, belonging to the classes of Gastropoda (9 species; 3,800 individuals), Bivalvia (3 spp.; 54 ind.), and Polyplacophora (1 sp.; 7 ind.) were identified in the four habitat types (Tab. I). The bivalve *Brachidontes exustus* occurred in a high-density aggregate distribution, forming a continuous patch covering the substrate. This bivalve was described as habitat-forming species (MUS - mussel beds) and was not included in the composition of mollusk assemblages.

Consistent effects of variation on sinecological indices of molluscan assemblages were identified in the habitat types studied. The ANOVA indicated that there were significant differences in abundance ($F_{3, 26}$=53.22; p<0.001), species richness ($F_{3,26}$=3.82; p=0.022), Shannon diversity ($F_{3,26}$=8.59; p<0.001) and Pielou's evenness ($F_{3,26}$=10.43; p<0.001) when comparing different habitats.

Barnacle belt (BNC) recorded lower species richness and diversity indices than mussel beds (MUS) and algae habitat (ALG). However, BNC showed the highest total abundance among these habitats. Algae habitat showed higher diversity indices than BNC and bare rock habitat (BAR) (Fig. 2).

Tab. I. Taxonomic list of mollusk species with their feeding guilds (suspension feeders, grazers, herbivores, and carnivores), abundance (N) and frequency (F%) for each habitat type (ALG, algae habitat; BAR, bare rock; BNC, barnacle belt; MUS, mussel beds) recorded in the rocky intertidal zone of *Morro de Pernambuco*, Ilhéus, Bahia, Brazil. References: [a]Rios, 2009 and [b]Felder & Camp, 2009.

CLASS Species	Feeding habitat	Barnacle belt		Mussel beds		Algae habitat		Bare-rock	
		N	F (%)	N	F (%)	N	F (%)	N	F (%)
GASTROPODA									
Anachis isabellei (d'Orbigny, 1839)	carnivore[a]	0	0	0	0	2	6.67	0	0
Anachis lyrata (G. B. Sowerby I, 1832)	carnivore[a]	0	0	0	0	2	6.67	0	0
Echinolittorina lineolata (d'Orbigny, 1840)	grazer[a]	2515	100.00	495	100.00	14	33.33	636	80.00
Eulithidium affine (C. B. Adams, 1850)	grazer[b]	0	0	0	0	19	6.67	0	0
Fissurella rosea (Gmelin, 1791)	herbivore[b]	0	0	0	0	6	13.33	0	0
Lottia subrugosa (d'Orbigny, 1846)	herbivore[a]	5	16.67	32	100.00	29	46.67	15	20.00
Mitrella dichroa (G. B. Sowerby I, 1844)	carnivore[b]	0	0	0	0	6	13.33	0	0
Stramonita brasiliensis Claremont & D. Reid, 2011	carnivore[b]	0	0	9	60	14	46.67	0	0
Stramonita sp.	carnivore[b]	0	0	0	0	1	6.67	0	0
BIVALVIA									
Isognomon bicolor (C. B. Adams, 1845)	suspension feeder[a]	0	0	13	20.00	17	20.00	0	0
Modiolus americanus (Leach, 1815)	suspension feeder[a]	0	0	0	0	14	26.67	0	0
Sphenia fragilis (H. Adams & A. Adams, 1854)	suspension feeder[a]	0	0	0	0	10	13.33	0	0
POLYPLACOPHORA									
Rhyssoplax janeirensis (Gray, 1828)	herbivore[a]	0	0	4	20.00	3	20.00	0	0

Gastropoda was dominant in all habitat types. Only gastropods occurred at BNC and BAR. Two species, *Echinolittorina lineolata* (d'Orbigny, 1840) and *Lottia subrugosa* (d'Orbigny, 1846), have been recorded in these habitats (Fig. 3).

In the MUS, gastropods were dominant both in abundance (DI 96.93%, 536 individuals) and species richness (DQ 60%, 3 species), followed by bivalves (DI 2.35%, 13 ind.; DQ 20%, 1 sp.) and polyplacophorans (DI 0.72%, 4 ind.; DQ 20%, 1 sp.) (Fig. 3). The most abundant and frequent species were *E. lineolata* and *L. subrugosa* (495 individuals; frequency: F 100% and 32 ind.; F 100%, respectively), followed by the bivalve *Isognomon bicolor* (C. B. Adams, 1845) (13 ind.; F 20%) (Tab. I).

In ALG, gastropods were also dominant both in abundance (DI 67.88%, 93 ind.) and species richness (DQ 69.23%, 9 spp.), followed by bivalves (DI 29.93%, 41 ind.; DQ 23.08%, 3 spp.) and polyplacophorans (DI 2.19%, 3 ind.; DQ 7.69%, 1 sp.) (Fig. 3). The most abundant and frequent species were the gastropods *L. subrugosa* and *Eulithidium affine* (C. B. Adams, 1850) (29 ind.; F 46.67% and 19 ind.; F 6.67%, respectively), followed by *I. bicolor* (17ind.; F 20%) (Tab. I).

Functional composition. Four feeding guilds were identified: suspension feeders, grazers, herbivores, and carnivores. The feeding guild grazers showed high dominance in BNC (DI 99.80%, 2515 ind.; DQ 50%, 1 sp.), BAR (DI 97.60%, 636 ind.; DQ 50%, 1 sp.) and MUS (DI 89.51%, 495 ind.; DQ 20%, 1 sp.). Suspension feeders occurred in greater quantitative abundance in ALG (DI 29.93%, 41 ind.; DQ 23.08%, 3 spp.), followed by herbivores (DI 27.74%, 38 ind.; DQ 23.08%, 3 spp.). The highest qualitative contribution in ALG was observed in carnivores. (DQ 38.46%, 5 spp.) (Fig. 4).

The most abundant species in each feeding guilds were: the grazer *E. lineolata* (3,660 ind.), the herbivore *L. subrugosa* (81 ind.), the suspension feeder *I. bicolor* (30 ind.) and the carnivore gastropod *Stramonita brasiliensis* Claremont & D. Reid, 2011 (23 ind.) (Tab. I).

The index of trophic diversity (ITD) differed between habitats ($F_{3,26}$=8.68; p<0.001). In ALG, trophic diversity was higher than in BNC and BAR. The least ITD was recorded in BNC (Fig. 5).

Redundancy analysis (RDA) showed that the habitat variable explained 49.27% (ANOVA: $F_{4,25}$=5.80; p=0,001) of variability in the occurrence of feeding guilds. The first axis explained 37.89% variability and was positively related

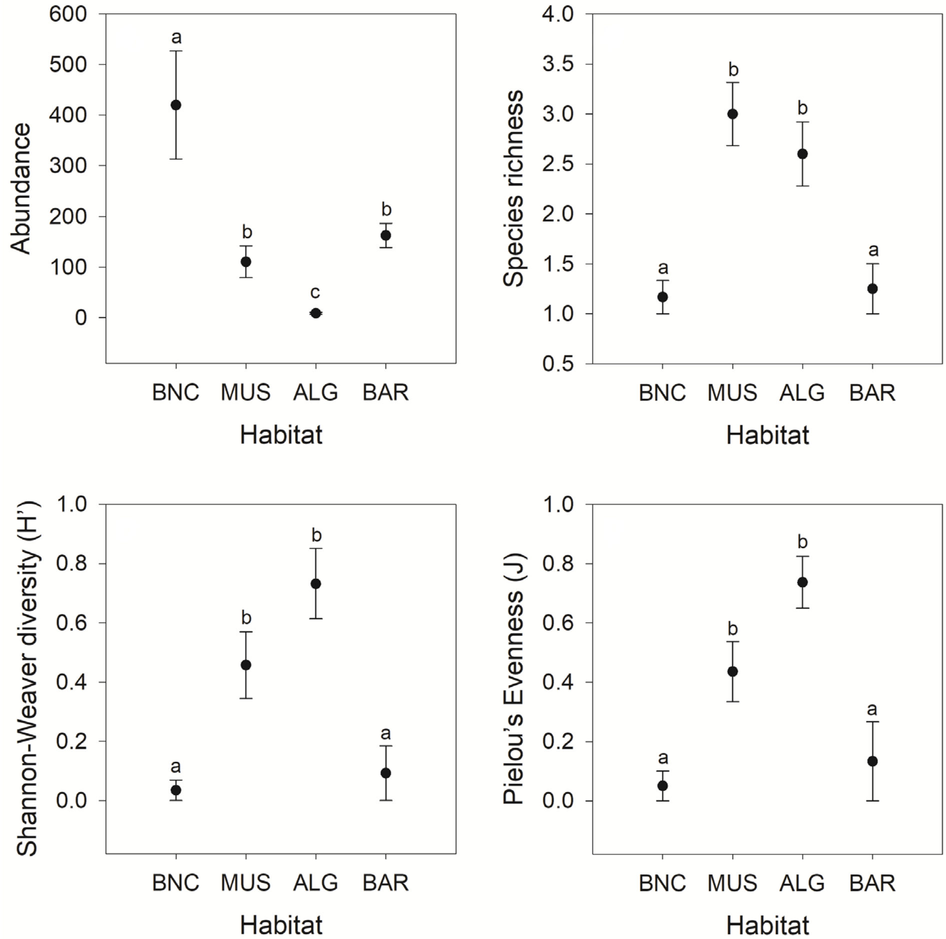

Fig. 2. Mollusk assemblages: number of individuals (Abundance), number of species (Species richness) and diversity indices (Shannon-Weaver H' and Pielou's evenness J) calculated (mean ± SE) measured for each habitat (ALG, algae habitat; BAR, bare rock; BNC, barnacle belt; MUS, mussel beds) in the rocky intertidal zone of *Morro de Pernambuco*, Ilhéus, Bahia, Brazil. Significant differences are indicated with different letters (Tukey's test: $p<0.05$).

to variables ALG (0.86) and MUS (0.67) and negatively to variables BNC (-0.93) and BAR (-0.65). The tri-plot showed an association between carnivores and ALG and between grazers, BNC, and BAR. Herbivores were related to MUS. Guild suspension feeders had a low association with investigated habitats (Fig. 6).

DISCUSSION

This study documented the spatial variation in taxonomic and functional diversity of mollusk assemblages in different types of habitat in a tropical rocky intertidal zone. Species of Gastropoda, Bivalvia, and Polyplacophora were identified and classified according to the feeding guilds suspension feeders, grazers, herbivores, and carnivores. Variations in the mollusk assemblage structure were identified between barnacle belt, mussel beds, algae habitat, and bare rock habitats.

Of the three taxonomic classes recorded, gastropods showed high abundance, species richness, and trophic diversity, having occurred in the four habitats investigated. This result is in line with that described for the rocky intertidal zone in other tropical regions (Flores-Rodríguez*et al.*, 2012; Martinez *et al.*, 2012), confirming gastropods affinity for these environments. The grazer *Echinolittorina lineolata* was the dominant species in this study. Species of *Echinolittorina* are described as dominant gastropods in the highest levels of intertidal rocky zones at tropical coasts (Reid, 2009). The highest species richness among gastropods was detected in the carnivores feeding guild. *Stramonita brasiliensis* was the most abundant in this guild. All bivalve species recorded in this study, such as *I. bicolor* and *Modiolus americanus* (Leach, 1815), belong to feeding guild suspension feeders. The guild occurs only in mussel beds and algae habitats and is a significant trophic category of marine hard-bottom communities (Donnarumma *et al.*, 2018b). Polyplacophorans, in turn, were poorly represented both in the number of individuals and in species richness, with the herbivore *Rhyssoplax janeirensis* (Gray, 1828) being the only species recorded. Although polyplacophorans are common in rocky intertidal zones on the Brazilian coast (Rios, 2009), their occurrence is commonly associated with the presence of pebbles (Jörger *et al.*, 2008) and the formation of rocky pools (Souza & Matthews-Cascon, 2019). The system

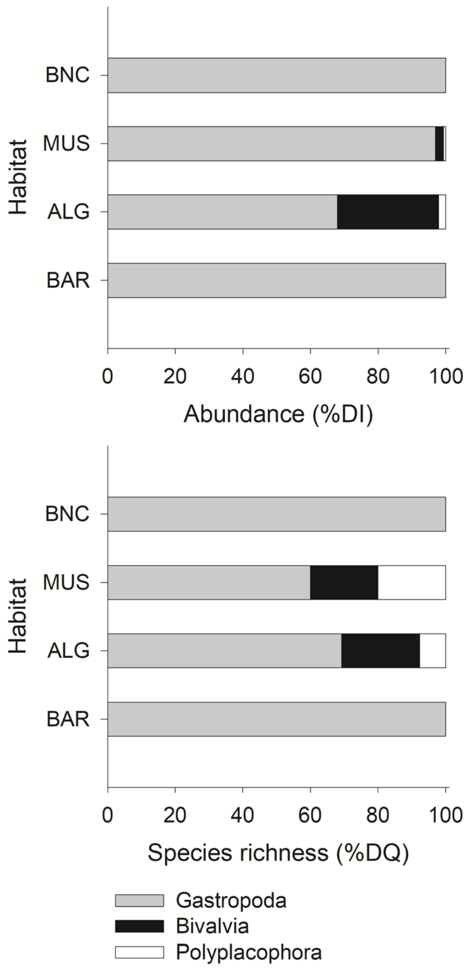

Fig. 3. Contribution of taxonomic groups (Gastropoda, Bivalvia, Polyplacophora) to quantitative (Abundance %DI) and qualitative (Species richness %DQ) dominances for each habitat (ALG, algae habitat;BAR, bare rock; BNC, barnacle belt; MUS, mussel beds) in the rocky intertidal zone of *Morro de Pernambuco*, Ilhéus, Bahia, Brazil.

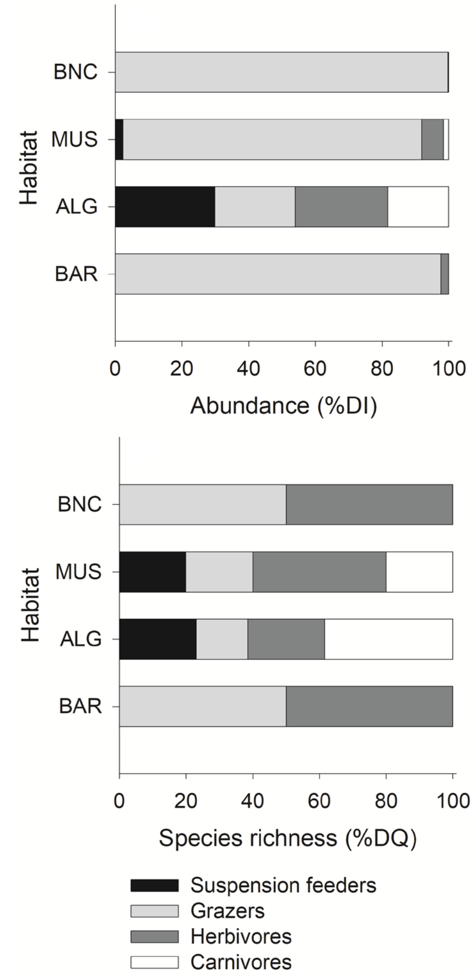

Fig. 4. Contribution of feeding guilds (suspension feeders, grazers, herbivores, and carnivores) to quantitative (Abundance %DI) and qualitative (Species richness %DQ) dominances for each habitat (ALG, algae habitat; BAR, bare rock; BNC, barnacle belt; MUS, mussel beds) in the rocky intertidal zone of *Morro de Pernambuco*, Ilhéus, Bahia, Brazil.

investigated in this study is characterized by the absence of loose blocks and continuous rocky substrate covered by sessile biota. This environment may not be conducive to the expressive establishment of polyplacophorans.

The barnacle belt habitat showed high abundance, however, with low species richness and diversity. Predators are less common in these regions, increasing competition for space and food. This condition can lead to competitive exclusion and consequent dominance of the system by a few species (Menge *et al.*, 1987; Clarke 2004). There was a predominance of gastropods in the barnacle belt, with the occurrence of two species, the grazer *E. lineolata*, and the herbivore *L. subrugosa*; these species were the most abundant in their respective feeding guilds. The high density of litorinids in the barnacle belt is characteristic in tropical rocky substrates (Apolinário *et al.*, 1999). Littorinid *E. lineolata* also occurred in high abundance in bare rock habitat. This result is in accordance with the habitat described for the distribution of this species (Reid, 2009). In addition, rocky surfaces in the intertidal zone are primarily covered by periphyton (Aguilera *et al.*, 2013), which is the main food source for benthic grazers (Liess *et al.*,2009). Grazers' dominance in barnacle belt and bare rock explains the low trophic diversity in these habitats. This condition also clarifies the association between grazers and these habitats identified in redundancy analysis.

The highest species richness and trophic diversity were detected in algae habitat and mussel beds, which showed low abundance. In contrast, barnacle belts registered low species richness and trophic diversity, and a high number of individuals. The inverse relationship between species richness and abundance is common in ecological systems and has already been described for mollusk assemblages (Donnarumma *et al.*, 2018a). According to a hypothesis describing this pattern, the greater the number of species, the smaller the size of their populations due to the partitioning of resources (Griffin *et al.*, 2008;Donnarumma *et al.*, 2018a). This result also indicates competition in habitats with the

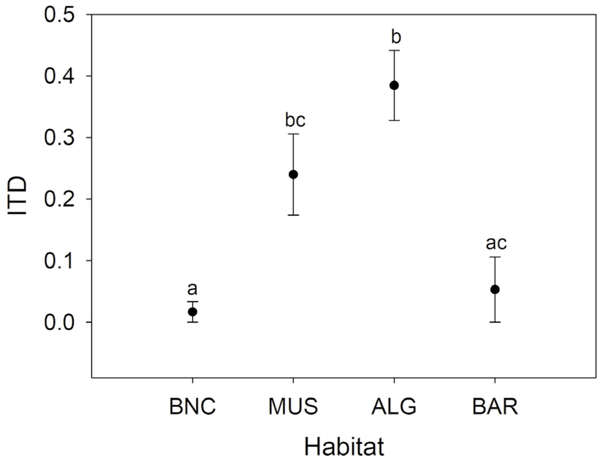

Fig. 5. Index of trophic diversity (ITD) calculated (mean ± SE, standard error) for each habitat (ALG, algae habitat; BAR, bare rock; BNC, barnacle belt; MUS, mussel beds) in the rocky intertidal zone of *Morro de Pernambuco*, Ilhéus, Bahia, Brazil. Significant differences are indicated with different letters (Tukey's test: p<0.05).

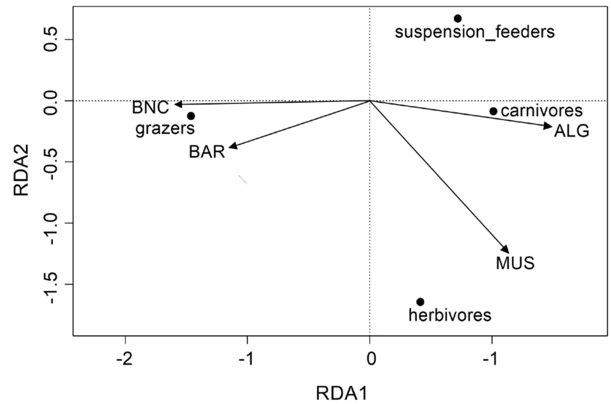

Fig. 6. Redundancy analysis (RDA) tri-plot on habitats types (ALG, algae habitat; BAR, bare rock; BNC, barnacle belt; MUS, mussel beds) and feeding guilds (suspension feeders, grazers, herbivores, and carnivores) in the rocky intertidal zone of *Morro de Pernambuco*, Ilhéus, Bahia, Brazil.

highest diversity. Resource competition can lead to increased niche variation and drive diversity via changes in foraging behaviour (Svanbäck & Bolnick, 2007).

Algae habitat and mussel beds hosted all feeding guilds identified in this study. In these habitats, grazers were mostly represented by *E. affine*, herbivores by *L. subrugosa*, carnivores by *S. brasiliensis*, and suspension feeders by *I. bicolor*. The co-occurrence of these guilds explains the high taxonomic diversity in such habitats due to environmental heterogeneity (Tews *et al.*, 2004; Ortega *et al.*, 2018). The habitat-forming species increase structural complexity to support a diverse associated fauna (Lemieux & Cusson, 2014; Gallucci *et al.*, 2020). Different types of macroalgae along with their complex architecture, promote diversity in mollusk assemblages (Chemello & Milazzo, 2002; Pitacco *et al.*, 2014). Mussel beds, in turn, increase complexity by aggregating living individuals, empty shells and byssal threads, providing shelter and reducing physiological and mechanical stress (Borthagaray & Carranza, 2007; Arribas *et al.*, 2014).

The algae habitat also registered a high qualitative contribution to carnivores. This accounts for the association found between this guild and algae habitat, as well as the high species richness in this habitat. Predator gastropods, such as *S. brasiliensis*, keep their prey below their carrying capacity, enabling the coexistence of a higher number of species (Paine, 1966). Predators modify their prey's population growth rates by direct consumption or by inducing behavioral and physiological changes (Preisser & Bolnick, 2008). In general, predation prevents a monopoly on food resources and reduces the intensity of competitive interactions between species at lower trophic levels (Paine, 1966; Griffin *et al.*, 2008). In addition to this top-down effect, the habitat algae discussed here comprises different macroalgae species, and may, therefore, hold diverse micro-habitats in them. Furthermore, macroalgae are primary producers in intertidal regions (Mann, 1973; Tait & Schiel, 2011), including resource availability and increasing species coexistence (Cardinale *et al.*, 2009). Increased bottom-up resource base in the food chain leads to an increase in all trophic levels (Menge, 2000).

A relative abundance of gastropod *E. lineolata* was detected in the mussel beds habitat. This periwinkle is normally distributed on bare rocks, between barnacles and mussels in upper and mid intertidal zones (Reid, 2009). This occupation pattern is explained by group physiological characteristics (Garrity, 1984), and predation pressure (Perez *et al.*, 2009) faced in the low intertidal zone. However, *E. lineolata* occurred at all sampled points in mussel beds habitat, including the low intertidal, characterized by frequent submersion. This result differs from traditional models (Stephenson & Stephenson, 1949) and from the one described for the Brazilian coast (Coutinho *et al.*, 2016). Although the environmental conditions in the low intertidal zone are not suitable to host litorinids, mussels can act as facilitators for these snails (Borthagaray & Carranza, 2007; Cartwright & Williams, 2012), facilitating an increase in the spatial range of fundamental niche species by mitigating the effects of niche reduction factors (Bruno *et al.*, 2003). Thus, the fundamental niche of *E. lineolata* may be increased by the facilitation provided by mussel beds. This habitat-forming species decreases the effect of factors that, in its absence, would limit the distribution of *E. lineolata* on barnacle belt and bare rock habitats.

The bivalve *I. bicolor* was detected at mussel beds and algae habitat. It was the suspension feeder species most abundant in these feeding guilds. The presence of this invasive species is well documented in Brazil (Dias *et al.*, 2013; Barroso *et al.*, 2018). *Isognomon bicolor* is native to Jamaica and was originally distributed in the Caribbean region (Domaneschi & Martins,2002). This bivalve is an example of a successful invasion in Brazilian coastal areas

(Dias *et al.*, 2013), and has sufficient dispersion capacity to interfere with the survival of native species (Breves-Ramos *et al.*, 2010; Martinez, 2012). During fieldwork, we observed predation of *I. bicolor* by *S. brasiliensis*, in which this gastropod consumes the invasive bivalve instead of the native mussel *Brachidontes exustus*. Taking into account the dispersive capacity and the potential to modify systems where it occurs, *I. bicolor* and its interactions with native species need to be further studied.

Rocky surfaces with no associated biological substrate presented low values in all taxonomic and functional components investigated. This is attributed to the high desiccation stress experienced on bare areas in rock intertidal systems. Diversity in these environments can be maintained by positive interactions that ameliorate physical stress (Silliman *et al.*, 2011). This result confirms the effect of environmental modification caused by the presence of habitat-forming species. *Chthamalus bisinuatus*, *Brachidontes exustus*, and the macroalgae group act as habitat-forming species in the system studied. By providing habitat and protection, habitat-forming species facilitate distributions of organisms by reducing desiccation stress (Silliman *et al.*, 2011). Furthermore, such organisms modify the landscape, increasing heterogeneity and, consequently, affecting associated communities (Lemieux & Cusson, 2014; Gallucci *et al.*, 2020). Thus, the habitat-forming species identified provide niches capable of supporting different occupation patterns and therefore affect taxonomic and functional diversity in mollusk assemblages.

In summary, our results showed that the taxonomic and functional structure of mollusk assemblages in the tropical rocky intertidal zone varies between different types of habitat investigated. The structure of mollusk assemblages is a result of the interplay of many different biotic and abiotic drivers, many of them not considered here. Intertidal elevation, wave exposure gradients, seasonality, bottom-up and top-down effects, for example, are some of these features. These are interconnected processes that have a strong influence on the structure of rocky intertidal communities. These processes and their relation to the taxonomic and functional diversity of mollusk assemblages will be analyzed and discussed elsewhere.

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Data availability. The datasets generated and analysed during the current study was deposited in the Open Science Framework repository, https://osf.io/6fhjr/. The data are available from the corresponding author on reasonable request and will be publicly available as soon as the manuscript is accepted for publication.

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