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Resource partitioning and adequacy among ontogenetic groups in a hermit crab and gastropod shell network

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Abstract In ecology, interaction networks allow the investigation of how interactions among species affect community structure and functioning. The structure of interaction networks can be nested and/or modular. Ecologically, the nested structure minimizes competition and increases the number of coexisting species, creating high diversity, while the modular structure occurs when there are non-overlapping groups of highly interacting consumer-resource species. Despite the importance of gastropod shells to hermit crabs, currently, few studies explored the structure of hermit crabs communities through a resource-usage perspective. Therefore, network analyses appear as an important tool to unveil how the use of empty shell as a resource rules hermit crabs communities through competition among species and rules hermit crabs populations through competition among distinct ontogenetic groups. This study investigated the resource usage pattern of empty gastropod shells by distinct ontogenetic stages of the hermit crab *Calcinus tibicen* from two different locations, using a network approach and the "Shell Adequacy Index" (SAI) analysis. The present results show that the interaction network between ontogenetic groups and gastropod shells was non-nested and modular and the SAI reflected the differences between males and ovigerous females in both locations, regarding shell size adequacy. We suggest that the modular structure may be a result of resource partitioning, which, in turn, is favored in habitats with a high degree of heterogeneity. The modular network structure may indicate habitat heterogeneity and resource partitioning. Future studies including other hermit crab species from the same areas should help determine how shells are partitioned interspecifically.

Keywords Modularity · Nestedness · Paguroidea · Rocky shore · SAI · Shells of gastropods

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Introduction

Understanding how intraspecific coexistence is maintained by resource partitioning is a major research goal in ecology and conservation biology (Chesson 2000; Shipley et al. 2019). Intraspecific competition for resources can lead to niche partitioning between sexes throughout ontogeny, which allows sympatric conspecifics to coexist (De Souza et al. 2015; Shiffman et al. 2019). In this sense, ecological networks can help us to understand intraspecific resource partitioning mechanisms that allow functionally similar conspecifics to coexist. Among the interaction network patterns, nested and modular structures stand out.

The nested structure occurs when generalist species interact with each other, while extremely specialized species also interact with generalist species (Thompson 2006). The modular structure occurs when a group of species (referred to as module) interacts more closely with each other than with other species in the same network (Lewinsohn et al. 2006; Mello et al. 2011). A nested pattern may emerge when certain species interact more frequently and with more partners than others and by the lack of coadaptation in the interaction (Guimarães et al. 2007). Meanwhile, modularity may be generated by resource heterogeneity, leading to low overlap in resource use, in which competition would be expected to decline (Pinheiro et al. 2019).

In general, studies about ecological networks traditionally focus on species interactions whereby each node represents individuals of different species (Thompson 2002; Vázquez and Aizen 2003). Although this species-based analysis is important to comprehend fundamental aspects of community structures, information about interactions on an individual level may be lost (Ings et al. 2009) since there are biological differences between individuals of the same species (Tur et al. 2014). Recent studies have discussed the importance of individuals in ecological networks by exploring the mechanism acting on the individual level and have evidenced that intrapopulation variations are essential for shaping the network interaction (Olesen et al. 2010; Dupont et al. 2011; Koch et al. 2018; Ballarin et al. 2019).

Hermit crabs and their interactions with gastropod shells may be an optimal model for understanding intraspecific resource partitioning, since the resource in question acts as a limiting factor to these crustaceans and is easily quantified (Hazlett 1989). Hermit crabs use empty gastropod shells as shelter due to their generally soft and non-calcified abdomen (Reese 1963; McLean 1974). Gastropod shells not only provide protection against predators but also protect eggs and increase resistance against desiccation, providing a microhabitat to deal with environmental stressors (Vance 1972; Fotheringham 1976; Bertness 1981).

Shell occupation of hermit crabs does not occur randomly, as choice or rejection of shells involves specific exploratory behaviors (Hazlett 1981; Ayres-Peres et al. 2012). Hermit crabs analyze and select their shells by considering various characteristics such as size, weight, aperture, internal volume, form, color, state of repair and maneuverability (Mitchell 1976; Conover 1978).

Moreover, their diversity patterns of shell occupation can also be affected by shell abundance and mainly by competition among individuals (Reese 1963; Bertness 1982; Mantelatto and Garcia 2000; Sant'Anna et al. 2006). In this sense, the ontogenetic stage and the sex each individual belongs to plays an important role in reducing intraspecific competition (Abrams 1988). The difference in body size between sexes (in which males are typically larger than females) prevents agonistic conflicts. As stronger competitors, male hermit crabs tend to pick larger shells (Neil and Elwood 1985; Asakura 1995), while ovigerous females tend to be more meticulous with their shell occupation as they need space to carry embryos, and thus prioritize shell aperture and inner volume (Fotheringham 1976; Mantelatto and Garcia 2000; Frameschi et al. 2013).

Nevertheless, due to limited availability of shells in the environment, it is common to find hermit crabs occupying inadequate shells, evidenced either by the disproportionate size of a hermit crab compared to its shell or because the shell is colonized by epibionts and/or has some degree of damage (Mantelatto et al. 2007; Silva et al. 2019). Besides that, the limited availability of shells in the environment might lead to inadequate occupancy by hermit crabs, resulting in major intraspecific and interspecific competition for shells (Reese 1962; Bertness 1980; Angel 2000; Mantelatto and Garcia 2000). Studies have revealed that inadequate shell occupancy can have negative consequences for hermit crabs, such as reduced growth rate, increased mortality and variations in fecundity rates (Brooks 1988; Angel 2000). A tool that is commonly used to check if hermit crabs are occupying a suitable shell is the Shell Adequacy Index (SAI), which indicates suitability based on hermit crab size (Vance 1972).

Several studies on shell occupation have been conducted over the last decades (Hazlett and Baron 1989; Mantelatto and Garcia 2000; Garcia and Mantelatto 2001; Lima et al. 2018). However, only a few have applied ecological networks to describe hermit crab–gastropod shell interactions (Silva et al. 2020; Rodrigues et al. 2020), and none of them evaluated networks properties in a downscaled perspective. The goal of this study was to use the ecological network analysis to describe and compare the interactions between ontogenetic groups of *C. tibicen* and gastropod shells in two locations on the southern coast of Bahia, Brazil, and the shell adequacy index (SAI) to evaluate the suitability of shells used by each ontogenetic group of *C. tibicen*. For the intertidal hermit crab species *C. tibicen*, we considered the following hypotheses: (1) the ecological interaction networks will present a modular pattern since ontogenetic groups should interact differently with shell resources and (2) ontogenetic groups will differ in shell adequacy (estimated through SAI) due to the higher degree of affinity with a given resource.

Materials and methods

Study area

This study was conducted in the municipality of Itacaré and Ilhéus, on the southern coast of Bahia, Brazil. The sampling location in Itacaré was Concha beach (14° 16′ 28.1″ S 38° 59′ 13.0″ W) and in Ilhéus, the shores of Batuba (14° 56′ 25.6″ S 39° 00′ 38.6″ W) and Olivença (14° 56′ 52.5″ S and 39° 00′ 31.9″ W) were used. These locations were chosen because of their rocky shores and distinct morphologies. In Itacaré, the rocky shore is sheltered with no significant elevations, while in Ilhéus it is exposed and more susceptible to wave action.

Species distribution

Calcinus tibicen (Herbst 1791) is distributed in the Western Atlantic Ocean from the Bermudas, Florida and the Antilles to the northern region of South America and Brazil (from Ceará to Santa Catarina and in the Fernando de Noronha archipelago) (Coelho and de Ramos 1972; Melo 1999).

Sampling and analysis of hermit crabs

From October 2013 to September 2014 in Itacaré and from November 2016 to October 2017 in Ilhéus, bimonthly collections of hermit crab specimens were carried out randomly by two collectors for 30 min each, during daytime low tide. We packed the crustaceans in plastic bags, labeled them by location, and then refrigerated and transported them to the laboratory for analyses. Afterward, the hermit crabs were identified according to Melo (1999) and those belonging to the target species (*C. tibicen*) were placed in glass recipients filled with 70% methyl alcohol at the II Zoology Laboratory of the "State University of the Southeastern of Bahia" (UESB), Vitória da Conquista Campus, State of Bahia, Brazil.

The *C. tibicen* specimens were removed manually from their shells, which were broken carefully when necessary, to avoid damaging the paguroidean. We measured cephalothoracic shield length (SL) (in millimeters) and classified the specimens according to Fransozo et al. (2003), into four ontogenetic groups: males (M), non-ovigerous females (F), ovigerous females (OF), and juveniles (J). We designated the individuals with gonopores situated on the ventral side of the coxa of the fifth pair of pereiopods as males; individuals with gonopores situated on the ventral side of the coxa of the third pereiopods as non-ovigerous females; individuals with eggs adhered on their pleopods as ovigerous females; and individuals with SL smaller than the smallest SL from ovigerous females as juveniles.

The gastropod shells were identified according to Rios (1994), and their biometric parameters were shell aperture height (AH) and shell aperture width (AW), which were measured with Mitutoyo caliper (0.01 mm accuracy). For sex identification, we used a stereoscope microscope (Tecnival SQF-L II) with an optic micrometric scale.

Network-level metrics

We constructed quantitative interaction matrices using the abundance of *C. tibicen* in each occupied shell species to describe and compare the structure of network interactions between ontogenetic groups and gastropod shells in both locations, in which rows (i) represent shell species and columns (j) represent the ontogenetic stage of *C. tibicen*. Each shell i was found occupied by a hermit crab j, and the interaction frequency for each pair of species (a_{ij}) was represented in the matrix. All analyses were performed using R programming language version 3.5.3 (Team 2019), with "stats" for univariate tests (R Core Team 2019) and "bipartite" for all network analyses (Dormann et al. 2008). The following network metrics were calculated to describe each location (Ilhéus and Itacaré):

1. Weighted nestedness (wNODF) quantifies whether specialized species interactions represent subsets of interactions of more generalist species, for which values close to 0 indicate a non-nested pattern and those close to 100 indicate a perfect nested pattern (Almeida-Neto and Ulrich 2011);
2. Niche overlap (R_0) using Horn's index (Horn 1966). Niche overlap index varies from 0 to 1, and low values of R_0 indicate that the ontogenetic groups of *C. tibicen* are partitioning their usage of empty gastropod shells;
3. Modularity (Q') calculates whether species (or any group) from the same subset interact more with each other than with species (or any group) composing other subsets. This index was calculated using the QuanBiMo algorithm, which measures modularity in an iterative approach (Dormann and Strauss 2014). Therefore, we ran the algorithm 15 times to find the module conformation with the highest value of Qw'. For this, the number of Markov Chain Monte Carlo (MCMC) moves was set to 109 (Dormann and Strauss 2014; Maruyama et al. 2014).

In order to assess the significance of all network indexes, we compared the observed values to those generated by a null model. To generate the simulated matrices, we used the Patefield algorithm (Patefield 1981) through the function *r2dtable* in R (Dormann et al. 2008, 2009), which maintains the total number of interactions by fixing the marginal totals. Hence, this algorithm maintains the network size and species richness. We estimated a 95% confidence interval (CI) for each metric from the simulated values by assessing the significance of the calculated indexes.

Species-level metrics

To understand the specialization of each ontogenetic group (for both locations), we applied species-level specialization (d') ranging from 0 to 1, in which values closer to 1 denote higher specialization, meaning that of all possible interactions, a given species chooses just a few, regardless of their availability (Blüthgen et al. 2006; Dormann et al. 2008). In addition, we calculated partner diversity (PD), i.e., Shannon diversity applied to species interactions, to evaluate the diversity of resources used by the ontogenetic groups of *C. tibicen*. In addition, to evaluate whether ontogenetic stages and sex affect species-level specialization, we performed a generalized linear mixed model (GLMM), considering d' and PD as a response variable, ontogenetic stages and sexes as fixed factor and locality as a random effect.

Shell adequacy index (SAI)

We assessed shell adequacy by modifying the Shell Adequacy Index (SAI) (Vance 1972) to check whether *C. tibicen* were occupying adequate gastropod shells by location and ontogenetic group. SAI was calculated using the equation SAI = "optimal" SL/"real" SL. When SAI = 1, it indicates that the animal occupies a shell of adequate size, while when SAI $\neq$ 1, the hermit crab is in a shell that is larger (SAI > 1) or smaller (SAI < 1) than the adequate size. Under the same environmental conditions, we calculated the optimal SL, based on linear regressions of the hermit crab species ($R^2 > 0.6$, p value < 0.05, Fig. S1).

We calculated SAI indexes using both height (SAIh) and width (SAIw) of shell aperture. In order to compare SAI indexes between both location and ontogenetic groups, we performed a Mann–Whitney test and a Kruskal–Wallis test (p value < 0.05), respectively, since our data were nonparametric. A post hoc multiple comparison test (Dunn's test) was then performed to identify specific differences between the ontogenetic groups.

Results

In Ilhéus, shells of 6 gastropod species were occupied by 687 specimens of *C. tibicen,* of which 240 were males, 224 non-ovigerous females, 146 ovigerous females and 77 juveniles including males and females. In Itacaré, shells of 16 gastropod species were occupied by 643 specimens of *C. tibicen* (183 males; 190 non-ovigerous females; 225 ovigerous females; and 45 juveniles, including males and females).

Network-level metrics

The network structure of *C. tibicen* varied between locations. In Ilhéus, the interaction network between *C. tibicen* and gastropod shells revealed a nonsignificant nested pattern (wNODF = 30.47, 95% CI 22.38–62.22; Fig. 1). The network, in turn, was more modular than expected by chance based on the null distribution of Q_w' ($Q_w' = 0.057$, 95% CI 0.017–0.049). The niche overlap was lower than expected by chance ($R_O = 0.97$, 95% CI 0.98–0.99), indicating that hermit crab species exhibited niche partitioning and thus use a certain subset of shell species available in the community. In contrast, in Itacaré, the interaction network was less nested than expected by chance (wNODF = 40.93, 95% CI 45.42–61.81, Fig. 2), revealing a non-nested structure. The network was more modular than expected by chance based on the null distribution of Q_w' ($Q_w = 0.13$, 95% CI 0.04–0.08) and the niche overlap was lower than expected by chance ($R_O = 0.88$, 95% CI 0.95–0.99). Overall, both locations showed a modular structure and a low degree of niche partitioning. In Itacaré the modular structure formed four groups (modules), with each ontogenetic stage representing a single module. In Ilheus, we found three modules, grouping non-ovigerous females and ovigerous females together.

Species-level metrics

The largest ontogenetic groups of *C. tibicen* were males (M) in Ilhéus and ovigerous females in Itacaré, comprising 240 and 225 interactions, respectively. The degree of resource specialization was higher among juveniles in both locations (d' Ilhéus = 0.05; d' Itacaré = 0.21) (Table 1). In addition, ovigerous females displayed a greater diversity of interactions (partner diversity = 0.47) in Ilhéus, while males achieved a higher value in Itacaré (partner diversity = 0.74) (Table 1).

We observed that ontogenetic stages influenced species-level specialization (GLMM, $p < 0.05$). However, we did not find the same pattern for sex. Also, ontogenetic stages and sex did not influence Partner diversity (GLMM, $p > 0.05$).

Shell adequacy index (SAI)

SAI was calculated using both aperture height (SAIh) and aperture width (SAIw), based on the regression analyses (Fig. S1). We found no differences in SAIh

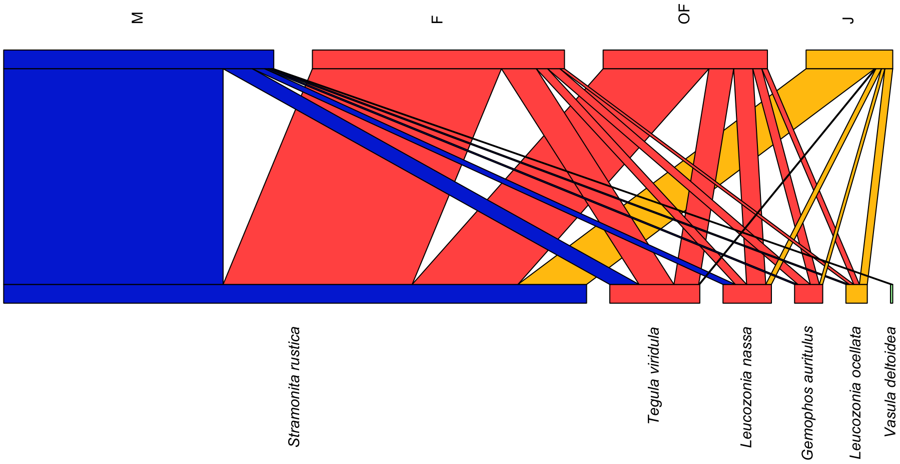

Fig. 1 Weighted network of ontogenetic groups and gastropod shells sampled for 1 year on rocky shores of Ilhéus. The upper level shows the ontogenetic groups of *Calcinus tibicen* with males (M), females (F), ovigerous females (OF) and juveniles (J). The lower level indicates gastropod species of the occupied shell and the relative density of each species is illustrated by the width of its block. Three different modules are indicated by three different colors (females and ovigerous females are within the same module)

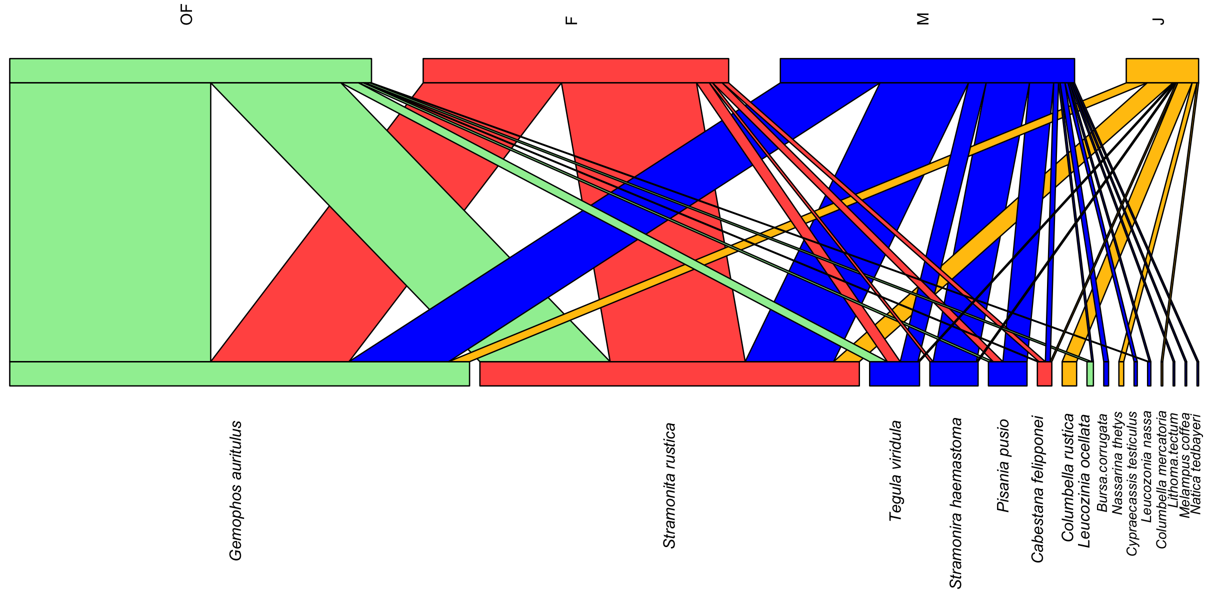

Fig. 2 Weighted network of its ontogenetic groups and gastropod shells sampled for 1 year on a rocky shore of Itacaré. The upper level shows the ontogenetic groups of *Calcinus tibicen* with males (M), females (F), ovigerous females (OF) and juveniles (J) of hermit crabs. The lower level indicates the gastropod species of the occupied shell and each species has its relative density illustrated by the width of its block. Four different modules are indicated by four different colors

Table 1 Species-level metrics and shell adequacy for each ontogenetic group of *Calcinus tibicen* in both locations

Localities	Ontogenetic groups	SAIw	SAIh	d'	PD
Itacaré	J	0.8266^{c}	1.0103^{ab}	0.2192	0.6806
	M	0.9309^{bc}	1.0541^{ab}	0.1176	0.743
	OF	1.0688^{a}	1.1855^{a}	0.0987	0.4365
	F	1.0013^{b}	1.1508^{a}	0.053	0.4739
Ilhéus	J	1.0414^{a}	0.974^{b}	0.0552	0.3313
	M	0.9347^{b}	1.0252^{b}	0.0226	0.3041
	OF	1.0068^{b}	1.1193^{a}	0.024	0.475
	F	0.9867^{b}	1.0158^{b}	0.0102	0.3683

SAIw shell adequacy index based on shell width, *SAIh* shell adequacy index based on shell height, *F* females, *OF* ovigerous females, *M* males, *J* juveniles, d' species-level specialization, *PD* partner diversity

^{abc}Different letters indicate significant differences among ontogenetic groups (Dunn test)

between Ilhéus and Itacaré (*p-value* =0.294); however, we found differences in SAIw (*p-value* =< 0.001) (Fig. 3). Regarding the ontogenetic groups, we found differences in SAIh in the shells from Ilhéus (KW = 43.38, $p < 0.001$) and Itacaré (KW = 71.81, $p < 0.001$). Similar results were found for SAIw in both locations (Ilhéus: KW = 36.96, $p < 0.001$; Itacaré: KW = 12.95, $p = 0.004$) (Table 1 and supplementary material Fig. S2). We found significant differences in both SAIh and SAIw between males and ovigerous females from Itacaré, while only SAIh was different from Ilhéus (Dunn test, $p < 0.05$) (Table 1).

Discussion

To date, most empirical studies about hermit crab shell-usage patterns have focused on descriptive

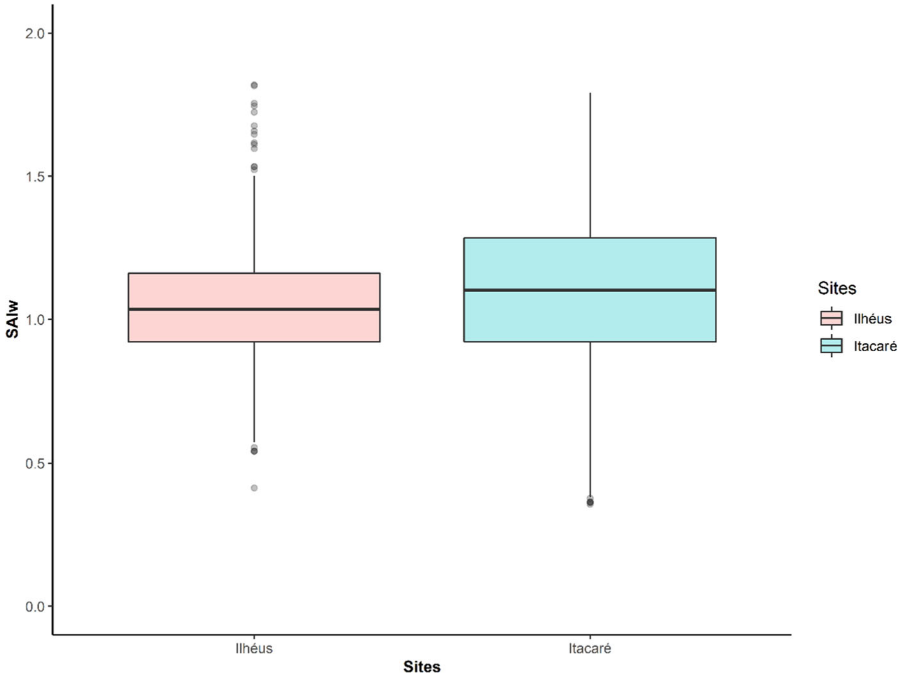

Fig. 3 Boxplots showing median, quartiles and outliers of adequacy index in each location. SAIw = Shell Adequacy Index based on shell width; SAIh = Shell Adequacy Index based on shell height

analyses of the relative abundance of shells occupied (Bertini and Fransozo 2000; Tricarico et al. 2009; Sant'Anna et al. 2012) and on linear regression/multivariate analyses exploring how shell morphology can modulate the pattern of shell occupation (Kuris and Brody 1976; Scully 1979; Bertness 1980; Sant'Anna et al. 2006; Ayres-Peres et al. 2012; Teoh and Chong 2014; Frameschi et al. 2015; Rodrigues and Martinelli-Lemos 2016; Lima et al. 2018; Steibl and Laforsch 2020). In this study, we described the resource usage pattern of gastropod shells by distinct ontogenetic groups of *C. tibicen*. By analyzing the resource usage patterns, we found that (1) intraspecific shell utilization differed between sexes and throughout ontogeny (modular pattern); (2) shell adequacy varied among ontogenetic groups, with juveniles occupying shells smaller than ideal size and ovigerous females occupying shells larger than ideal size; and (3) aperture width adequacy (SAIw) differed between locations. Considering that the survival, growth, and reproduction of hermit crabs strictly depends on occupying gastropod shells of appropriate size and shape (Hazlett 1981), a partition in resource use among different ontogenetic groups minimizes intraspecific competition, allowing local coexistence. Such niche partitioning plays a major role in ecology by reducing competition for resources.

Network structure

The modular pattern found in a species-specific hermit crab–shell network suggests that the ontogenetic groups of *C. tibicen* are using different subsets (modules) of shells. Modularity may reflect habitat heterogeneity (Lewinsohn et al. 2006), and resource partitioning (Augustyn et al. 2016), leading to a non-random pattern of interaction that is not mediated by their abundances. Since we found modularity in both locations (no spatial variation), resource partitioning to avoid competition could be a major driver of the modular pattern observed in these interaction networks,

Several species-level studies indicate differences in the shell-usage pattern among different ontogenetic groups (Bertini and Fransozo 2000; Mantelatto and de Meireles 2004; Ribeiro et al. 2015; Vale et al. 2017). Despite the high similarity found among ontogenetic groups, resource overlap (R_0 = 0.88) was still lower than expected by chance, indicating that distinct ontogenetic groups of *C. tibicen* partitioned the occupation of empty shells. Thus, even in a generalist resource-using species, we found differences in the empty shells occupied by ontogenetic groups.

Shell adequacy and specialization among ontogenetic groups

This investigation found significant differences in SAIh and SAIw between males (M) and ovigerous females (OFs) in Itacaré, while in Ilhéus only SAIh was different. SAIh and SAIw in OF achieved values greater than one, which indicates that OFs are occupying shells that are larger than ideal size. These results could be explained by OF's need to occupy shells that provide better protection and internal volume to store their eggs (Fotheringham 1976; Abrams 1988; Angel 2000; Mantelatto and Garcia 2000). In addition, juveniles (J) showed higher species-level specialization (d') in both locations. The higher d' of juveniles may be connected to the exclusive use of certain shell species (d' *Ilhéus* = 0.05; d' *Itacaré* = 0.21) and/or by juveniles being a less abundant ontogenetic group (Figs. 1, 2). In Itacaré, it is important to highlight that juveniles occupied shells that were smaller than the ideal size (SAIw parameters). These results differ from what was found by Domiciano and Mantelatto (2004), where juveniles occupied shells larger than the suitable size. They suggesting that this might be considered a strategy to allow the growth of juveniles inside the shells. Alternatively, we suppose that in Itacaré might to be occurring an intense intra- and inter- specific competition for shells, disfavoring juveniles to occupy an ideal size of shells. Several studies have reported inadequate shell use (Bertness 1981; Turra and Leite 2003; Alcaraz and Kruesi 2009; Mantelatto et al. 2016; Peres et al. 2018). Aside from inter- and intraspecific competition, shell occupancy is affected by limitation (inadequate adequacy shell) and availability of shells. On a sheltered rocky shore, such as Itacaré, the diversity and richness of Anomura are higher than those from an exposed rocky shore due to the low impact of waves, which forms complex microhabitats, accommodating more species and which consequently may increases the interspecific competition among hermit crab species for empty gastropod shells (Giraldes et al. 2012; Silva et al. 2019).

Shell adequacy and specialization between locations

Some studies have shown different shell occupancies among populations of the same species of hermit crabs that live in different habitats (Leite et al. 1998; Mantelatto et al. 2007, 2010; Ayres-Peres et al. 2012; Ribeiro et al. 2015). The population dynamics of hermit crabs, as observed by Mantelatto and Garcia (2000), are intrinsically associated with the gastropod species that inhabit the same or adjacent habitats. The differences in shell occupation may be a result of a latitudinal effect, as well as the geographic distribution of mollusks and their relative abundance, with consequences on gastropod diversity (Mantelatto and Garcia 2002; Mantelatto et al. 2010).

The structural complexity and degree of habitat heterogeneity (consisting of crevices, algae cover, hydrodynamics, slope of the rocky coast and substratum type) are environmental factors that can alter the availability of empty gastropod shells, even on shores that are close to each other. Consequently, the set of environmental factors affect the occupation of shells by hermit crabs (Leite et al. 1998; Mantelatto and Garcia 2002; Teoh et al. 2014), who tend to pick heavier shells in areas with higher wave action to adhere better to the substrate (Argüelles et al. 2009). Thus, in sheltered shores (Itacaré) more gastropod species may occur due to habitat heterogeneity and environmental stability (Pandey et al. 2018). In contrast, shores that are exposed (Ilhéus) due to strong wave action prevent certain gastropod species form occupying these harsh environments. As expected, we found higher gastropod richness in Itacaré than in Ilhéus, which may explain the higher values of specialization and partner diversity for all ontogenetic groups.

Finally, we found differences in SAIw between Ilhéus and Itacaré. Gastropods that live on sheltered and exposed rocky shores (e.g., Itacaré and Ilhéus, respectively) have different morphological characteristics and life histories. These differences can occur within a species under distinct environmental pressures in both types of rocky shores (Boulding 1990; Boulding et al. 1999). In exposed rocky shores, gastropods tend to be smaller and their shells more fragile with larger apertures. These morphological adaptations reduce the risks of being swept away by waves (Yamada 1972; Trussell et al. 1993; Boulding et al. 1999). On the other hand, in sheltered shores, it has been suggested that hermit crab shells tend to be larger, more durable and their apertures smaller due to higher predations risks (Heller 1976; Atkinson and Newbury 1984; Boulding et al. 1999).

Conclusion

Ecological network analyses enabled us to view intraspecific niche partitioning from a new perspective. SAI analyses indicated different adequacy between locations and among ontogenetic groups of the studied populations. These strategies reduce intraspecific competition and allow local coexistence of different ontogenetic groups, which may benefit the population as a whole, having significant implications for this species.

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Author contributions All authors contributed to the study conception and design. MPS, GFBR, VR and MLN-F carried out the material preparation, data collection and analysis. MPS and GFBR elaborated the first draft of the manuscript. After that, all authors commented and suggested alterations or adaptations on previous versions of the manuscript. All authors have read and approved the final version of the manuscript.

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

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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