

# Structural patterns of a coastal hermit crab–gastropod shell interaction network: new insights from a unique relationship

Gabriel Fellipe B. Rodrigues<sup>1,2,\*</sup>, Caio S. Ballarin<sup>3</sup>, Adilson Fransozo<sup>1,2</sup>,  
Felipe W. Amorim<sup>2,3</sup>

<sup>1</sup>Núcleo de Estudos em Biologia, Ecologia e Cultivo de Crustáceos - NEBECC, Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista 'Júlio de Mesquita Filho', 18618-689 Botucatu, São Paulo, Brazil

<sup>2</sup>Programa de Pós-graduação em Ciências Biológicas (Zoologia), Instituto de Biociências, Universidade Estadual Paulista 'Júlio de Mesquita Filho', 18618-689 Botucatu, São Paulo, Brazil

<sup>3</sup>Laboratório de Ecologia da Polinização e Interações – LEPI, Departamento de Botânica, Instituto de Biociências, Universidade Estadual Paulista 'Júlio de Mesquita Filho', 18618-689 Botucatu, São Paulo, Brazil

**ABSTRACT:** Hermit crabs are ideal organisms for assessing how species that share resources can coexist, as these crustacean species have an intimate relationship with gastropod shells and therefore compete for this particular resource. There is compelling evidence that hermit crabs do not interact with gastropod shells randomly, but few studies have investigated the community-level interactions between hermit crabs and shells. Here we used network analyses to present the first community-level assessment of the structure of a hermit crab–shell interaction network in a coastal region in southeastern Brazil in order to identify mechanisms that underlie hermit crab coexistence. Our results show that the hermit crab–gastropod shell interaction network was non-nested, specialized, and modular. The modular network structure revealed differences in resource use among hermit crab species. The network structure departs from those of free-living species in which the lack of interaction intimacy between species leads to a nested pattern. Thus, the morphological specialization of hermit crabs in relation to their host shells appears to play an important role in structuring the community-level interaction network. Future studies should evaluate the relative importance of abundance and functional traits in the structure of this unique interaction network.

**KEY WORDS:** Marine interaction network · Modularity · Species roles · Paguroidea · Mollusk · Crustacean · Coastal ecosystem

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## 1. INTRODUCTION

The relationship between resources and species abundances is important in understanding biological diversity patterns (Pohle et al. 2011, Miloslavich et al. 2013, Zajac et al. 2013). Resource competition generates negative interactions between individuals of different species due to the reduction of available resources that both organisms require (Tilman 2004). Species traits (e.g. body shape and size, feeding habits, etc.) are related to the ecological role (i.e. their pattern of direct

and indirect interactions with other species) a species plays in a given community (see Cirtwill & Eklöf 2018). In this sense, within ecological communities, species with similar functional traits often compete for the same kind of resources, which may result in competitive exclusion or in resource-use specialization, allowing coexistence of multiple species (Kellogg 1977, Alcaraz & Kruesi 2019). Hence, the outcome of competition will shape community structure (i.e. species richness, composition, and relative abundance), and, therefore, will also determine community functioning.

Hermit crabs are ideal organisms for assessing how functionally similar species coexist in an ecological community. These crustaceans have an intimate relationship with gastropod shells (Hazlett 1981, Tricarico & Gherardi 2007, Gorman et al. 2018), which represent an important niche dimension throughout their life history. Survival, growth, and reproduction of hermit crabs strictly depend on the occupancy of empty gastropod shells of appropriate size and shape (Kellogg 1976). Hermit crabs must continually obtain new suitable shells throughout their development, either because of their growth (Herrnkind & Hazlett 1980) or alteration in the condition of their current shell caused by sessile epibionts (Hazlett 1981, McLean 1983). Hence, this dependence on shells creates competition, because hermit crab individuals cannot obtain shells directly from living gastropods (Laidre 2011) and therefore need to compete for suitable empty shells available in the environment. These crustaceans exchange shells by fighting, bargaining, or by a chain reaction caused by a single empty shell (Peres et al. 2018).

Previous studies found that hermit crabs have developed precise mechanisms to obtain information about the resource value of their own shell (Tricarico & Gherardi 2007) and in what context they may or may not abandon their shells (Turra & Gorman 2014). Hermit crabs have evolved the ability to make fine distinctions between the quality and suitability of a shell found in the habitat and the current domicile shell (Hazlett 1981). Thus, a given hermit crab species can exploit certain gastropod shell species based on its morphology in relation to the shells, leading to resource-use specialization. Resource-use specialization may also arise through morphological mismatching between hermit crab and gastropod shell species. In these cases, the disproportionate relation between hermit crab body size and shell morphology may prevent shell occupation (Alcaraz et al. 2015). In this sense, key functional traits, such as hermit crab and shell morphologies, play an important role in determining local community structure, because they affect a species' potential to obtain resources (De Bie et al. 2012, Borthagaray et al. 2014). Thus, species with different traits are expected to play different roles in a given community, leading to different resource utilization patterns (Cirtwill et al. 2018)

Graph theory applied to ecological networks can help us to unravel community-level mechanisms that allow functionally similar species to coexist. The examination of the structure of an ecological network, i.e. the interactions among species in a com-

munity, allows the understanding of which mechanisms may shape community structure (see Vázquez et al. 2009, Delmas et al. 2019). For instance, the existence of clearly defined groups of species with many intragroup links (i.e. interactions) and few intergroup links is the main characteristic of a modular network, which may reflect niche specialization in a given community. On the other hand, interaction networks may also present a nested structure wherein specialists interact with proper subsets that represent the core of generalist species, which in turn potentially interact with all available species in the community (Bascompte et al. 2003). While modularity and nestedness are not mutually exclusive patterns, they can reveal distinct properties about community structure and functioning (Lewinsohn et al. 2006, Fortuna et al. 2010), since they reflect different mechanisms that underlie species coexistence.

Over the last few decades, several population-level studies have focused on patterns of shell selection and utilization by hermit crabs (e.g. Scully 1979, Bertini & Fransozo 2000, Mantelatto et al. 2007, Vale et al. 2017, de Oliveira et al. 2018), but few studies have investigated the community-level interactions between hermit crabs and occupied shells (e.g. Teoh et al. 2014, Vale et al. 2017). To date, no studies have applied network theory to assess and describe community-level structural patterns of hermit crab–gastropod shell interactions. In this context, here we used ecological network analyses to present the first community-level assessment of the structure of a hermit crab–shell interaction network in a coastal, southeastern region of Brazil. Since it is widely known that shell selection by hermit crabs is a non-random process, because hermit crabs actively evaluate shell quality and morphology (Hazlett 1981, Asakura 1995, Vale et al. 2017, Alcaraz & Kruesi 2019), and interspecific competition plays an important role in shell usage patterns (Vale et al. 2017), in this study we hypothesized that community-level hermit crab–gastropod shell interactions are specialized and modular. Finally, we applied species-level descriptors to assess the species roles of both hermit crabs and gastropod shells to evaluate how they affect the overall network structure.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study was carried out at Ubatuba Bay (23° 26' S and 45° 02' W), which is located along the northern

coast of São Paulo State in southeastern Brazil. Ubatuba's coastal range exhibits small bays and headland-embayed beaches with variable orientation due to its proximity to the Serra do Mar mountain range. This region houses mixed fauna including tropical, temperate, and sub-Antarctic species, which are supported by the thermal regime of the coastal water (Coelho & Ramos 1972).

## 2.2. Animal sampling

Animals were sampled (trawled) using a fishing boat equipped with double-rig nets (4.5 m wide at the mouth, 25 mm mesh, and a cod-end mesh diameter of 15 mm). Each trawl lasted 30 min, covering an estimated area of 18 000 m<sup>2</sup>. Samples were taken monthly on 3 consecutive days from September 2016 to August 2017. A GPS was used to record the location of the sampling site in order to ensure that the sampling was conducted at the same site for all surveyed months. In the boat, the hermit crabs were kept in plastic bags and stored inside coolers with crushed ice. In the lab, each hermit crab was removed from its shell by carefully cracking the shell with a bench vice, and identified according to Melo (1998), while the gastropod shells were identified according to Rios (1994). Hermit crabs without shells or within deteriorated gastropod shells (impairing species-level identification) were excluded from the analysis (in total, they corresponded to less than 2% of the sampling effort). Hermit crabs were preserved in 70% ethyl alcohol solution, and all specimens were subsequently stored in the scientific collection of the Department of Zoology, São Paulo State University (UNESP, Botucatu).

## 2.3. Ecological network analysis

To analyze the structural pattern of the community-level hermit crab–gastropod shell interactions, associations between a given hermit crab and a gastropod shell were compiled into a quantitative interaction matrix, where rows ( $i$ ) represent gastropod shell species and columns ( $j$ ) represent hermit crab species. To compose a quantitative matrix, we considered the number of times that a gastropod shell  $i$  was found being occupied by a hermit crab  $j$ , as the interaction frequency for each pair of species ( $a_{ij}$ ) in the matrix. Further, to describe the structure of the hermit crab–shell interaction network and the level

of specialization, we used frequency data to calculate some network quantitative indexes, since quantitative analyses show less influence of the sampling effort (Fründ et al. 2016, Vizentin-Bugoni et al. 2016).

### 2.3.1. Network-wide specialization

We calculated the community-wide specialization index ( $H_2'$ ), which describes the overall selectiveness of the species within the interaction network (see Blüthgen et al. 2006). The  $H_2'$  specialization index varies from 0 to 1, and the more selective the species are, given the availability of partners in the whole community, the larger the specialization for the whole network.

### 2.3.2. Niche overlap

To measure the degree of interaction overlap between a pair of hermit crab species in the community, we calculated the niche overlap ( $R_0$ ) using the Horn index (Horn 1966). The niche overlap index also varies from 0 to 1, and a low value of  $R_0$  indicates that hermit crab species are partitioning their usage of available species of gastropod shells.

### 2.3.3. Nestedness

We also calculated nestedness using the weighted nestedness metric based on overlap and decreasing fill (wNODF). 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 nestedness pattern (see Almeida-Neto et al. 2007, Almeida-Neto & Ulrich 2011). Thus, a highly nested structure means that peripheral species tend to interact only with the more generalist ones (Bascompte et al. 2003, Vázquez et al. 2009).

### 2.3.4. Modularity

To identify whether interactions between hermit crabs and shells are organized in modules, i.e. a particular subset of co-occurring hermit crabs that interact preferentially with a specific subset of gastropod shells in the community, we calculated the

weighed modularity index ( $Q_w'$ ). This index calculates whether species from the same subset interact more with each other (considering species from different trophic levels) than with species composing other subsets. Modularity was estimated using the DIRTLPAwb+ algorithm (Beckett 2016), which calculates modularity in an iterative approach. Thus, the value of  $Q_w'$  might vary among sequential algorithm runs. Therefore, we ran the algorithm 10 times to find the module conformation with the highest value of  $Q_w'$ . For this, the number of Markov chain Monte Carlo moves was set to  $10^9$  (Dormann & Strauss 2014, Maruyama et al. 2014, 2015).

### 2.3.5. Significance of network indices

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. In order to assess the significance of the calculated indexes, we estimated a 1-tailed 99% confidence interval (CI) for each metric from the simulated values. All analyses were performed with the R programming language version 3.5.3 (R Core Team 2019).

## 2.4. Species-level metrics

Since species traits are related to the ecological role a species plays within the community (see Cirtwill & Eklöf 2018), we used some species-level metrics to describe species' roles within the interaction network. Considering that we hypothesized that community-level hermit crab–gastropod shell interactions are specialized and modular, and to better understand the species' contributions to the overall network specialization and modularity, we calculated the following species-level indexes.

Species-level specialization ( $d'$ ), which indicates how the distribution of interactions of a given species occurs in relation to the availability of the interacting species in other trophic levels. Values of  $d'$  range from 0 to 1, and values closer to 1 denote higher specialization, that is, from all possible interactions, a given species interacts with just a few counterparts regardless of their availability (Blüth-

gen et al. 2006). The generalization of  $d'$  values for the entire network produces the community-wide specialization index ( $H_2'$ ), which means that the greater the number of specialist species, the higher the specialization of the whole web. While there are other available indexes to describe ecological specialization, we opted to use  $d'$ , since it is highly robust (Poisot et al. 2012). Also, despite the availability of other equally robust, and even more informative measures, such as the paired difference index (see Poisot et al. 2012 for more details), we choose  $d'$ , because it is the most widely used index to describe both commensalistic and mutualistic networks, making comparison across different biological systems more accessible.

To understand the species role of hermit crabs and gastropod shells within the modular network, we calculated 2 different indexes: the within-module degree ( $z$ ), which indicates the number of connections a species has within its own module relative to other species in that module, and the among-module connectivity ( $c$ ), which describes how well a given species is connected to species from other modules (Olesen et al. 2007). According to their  $c$ - and  $z$ -values, we can classify the species roles as peripherals (low values of both  $c$  and  $z$ ), connectors (high  $c$ - and low  $z$ -values), module hubs (high  $z$ - and low  $c$ -values), or network hubs (high values of both  $c$  and  $z$ ). We defined the threshold using the standard deviation of both  $c$ - and  $z$ -values in order to preserve an equal probability of a given species relying on these 4 categories.

## 3. RESULTS

### 3.1. Species interactions

We recorded a total of 625 interactions between 6 hermit crab species and 15 gastropod shell species, with a connectance as high as 0.41 (Fig. 1). The hermit crab *Dardanus insignis* occupied 13 shell species (59% of all interactions), followed by *Pagurus exilis*, which occupied 8 shell species (20.8%). The most frequently occupied shell was *Buccinanops cochlidium*, with 208 interactions (33% of the total) and hosting all hermit crab species. This species was followed by *Olivancillaria urceus*, which was involved in 137 interactions (21.92% of the total) and hosted 3 hermit crab species.

The hermit crab–shell interaction network was less nested than expected by chance (wNODF = 50.48, 99% CI: 56.84–80.73; Fig. 1), revealing a non-nested

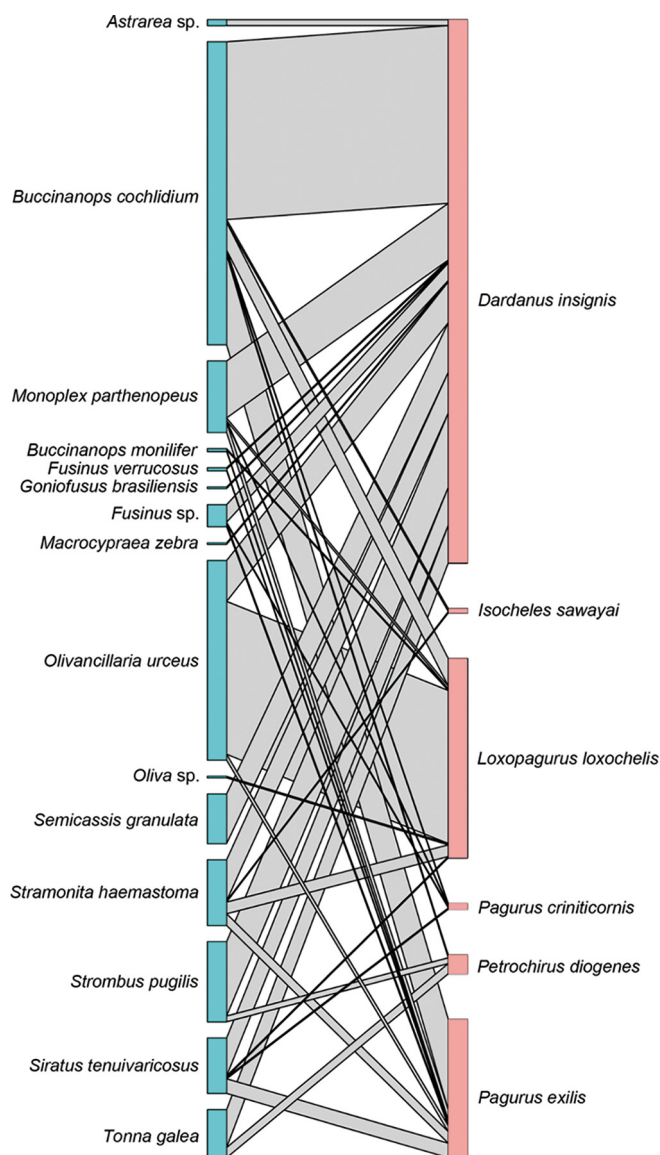


Fig. 1. Quantitative hermit crab–gastropod shell interaction network at Ubatuba Bay, located on the northern coast of São Paulo State in southeastern Brazil. Gastropod shells are represented by blue vertices, hermit crabs by red vertices, and interactions between them by gray lines. Line thickness indicates interaction frequency of each pair of species

structure. The network, in turn, was more specialized and modular than expected by chance based on the null distribution of  $H_2'$  ( $H_2' = 0.32$ , 99% CI: 0.01–0.07) and  $Q_w'$  ( $Q_w' = 0.28$ , 99% CI: 0.03–0.11) values. The interaction network presented 3 modules (Fig. 2), and the niche overlap of hermit crabs was lower than expected by chance ( $R_0 = 0.47$ , 99% CI: 0.54–0.88), indicating that hermit crab species present niche partitioning; therefore, they use a certain subset of shell species available in the community.

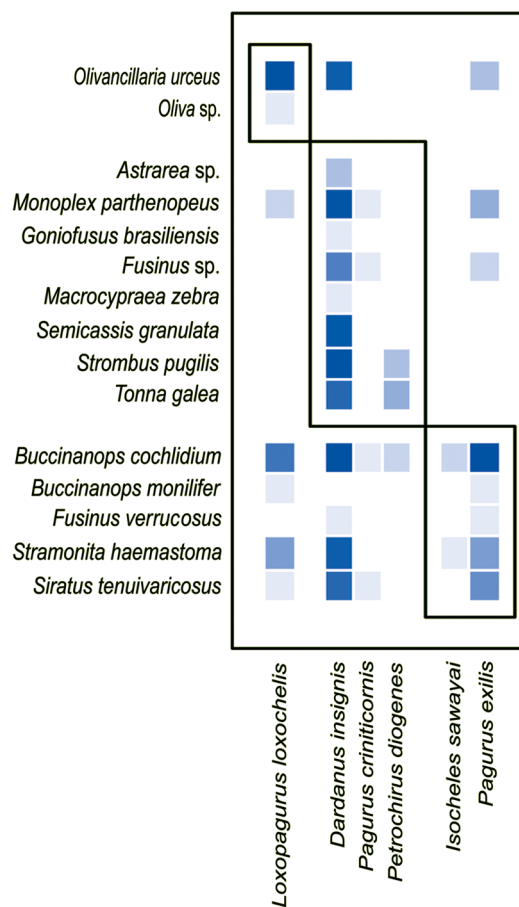


Fig. 2. Module conformation (niche specialization pattern) of the hermit crab–gastropod shell interaction network at Ubatuba Bay. Modules are represented by the small boxes inside the panel, and interaction frequency between hermit crabs and gastropod shells is shown by the intensity of the color in the modular network

### 3.2. Species-level metrics

Species-level descriptors are summarized in Table 1. The hermit crab species with the largest number of interactions was *D. insignis*, followed by *Loxopagurus loxochelis*. For gastropods species, *B. cochlidium* and *O. urceus* had most of the interactions in the network. *L. loxochelis* was the most specialist hermit crab, showing the most unique interaction links ( $d'$ ) with gastropods shells, followed by *Petrochirus diogenes*. Most hermit crabs were classified as 'connectors' (Fig. 3). The hermit crab *D. insignis* was classified as a 'network hub,' while *Pagurus criniticornis*, *L. loxochelis*, *P. exilis*, and *Petrochirus diogenes* were 'connectors,' and *Isocheles sawayai* was 'peripheral.' No such trend was observed for gastropods (Fig. 3). Also, only gastropod shell species acted as 'module

Table 1. Species-level specialization ( $d'$ ) of hermit crabs and gastropod shells at Ubatuba Bay

Species	$d'$
<b>Gastropod shell species</b>	
<i>Astraea</i> sp. (Röding, 1798)	0.089
<i>Buccinanops cochlidium</i> (Dillwyn, 1817)	0.098
<i>Monoplex parthenopeus</i> (Salis Marschlins, 1793)	0.064
<i>Buccinanops monilifer</i> (Kiener, 1834)	0.126
<i>Fusinus verrucosus</i> (Gmelin, 1791)	0.033
<i>Goniofusinus brasiliensis</i> (Grabau, 1904)	0.000
<i>Fusinus</i> sp. (Rafinesque, 1815)	0.090
<i>Macrocypraea zebra</i> (Linnaeus, 1758)	0.000
<i>Olivancillaria urceus</i> (Röding, 1798)	0.455
<i>Oliva</i> sp. (Bruguière, 1789)	0.169
<i>Semicassis granulata</i> (Born, 1778)	0.173
<i>Stramonita haemastoma</i> (Linnaeus, 1767)	0.015
<i>Strombus pugilis</i> Linnaeus, 1758	0.201
<i>Siratus tenuivaricosus</i> (Dautzenberg, 1927)	0.074
<i>Tonna galea</i> (Linnaeus, 1758)	0.238
<b>Hermit crab species</b>	
<i>Dardanus insignis</i> (de Saussure, 1857)	0.193
<i>Isocheles sawayai</i> Forest & de Saint Laurent, 1968	0.081
<i>Loxopagurus loxochelis</i> (Moreira, 1901)	0.526
<i>Pagurus criniticornis</i> (Dana, 1852)	0.144
<i>Petrochirus diogenes</i> (Linnaeus, 1758)	0.382
<i>Pagurus exilis</i> (Benedict, 1892)	0.238

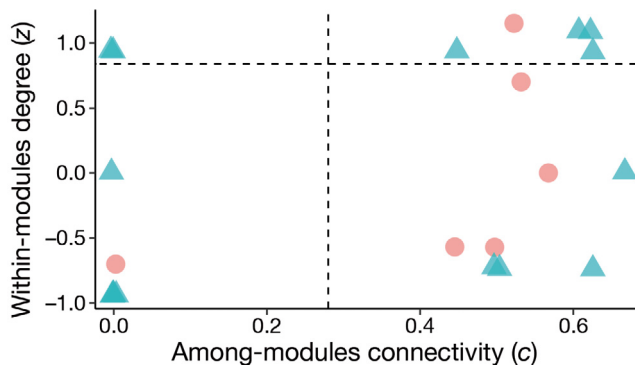


Fig. 3. Distribution of gastropod shell (blue triangles) and hermit crab (red circles) species according to their values of 'among-module connectivity' ( $c$ ) and 'within-module degree' ( $z$ ) at Ubatuba Bay. The threshold values of  $z = 0.84$  and  $c = 0.28$  were based on standard deviations of  $c$  and  $z$  scores

hubs' in the community, such as the large gastropod shell *Tonna galea*, *Strombus pugilis*, and the spiral shaped *Fusinus* sp. The most frequent shell species *B. cochlidium* was a 'network hub.' Among the hermit crab species, only *D. insignis* was as a 'network hub,' occupying a wide diversity of gastropods shells. The gastropod shells of *O. urceus* and *T. galea* were occupied by a restricted group of hermit crabs, presenting the highest values of species-level specialization (Table 1).

#### 4. DISCUSSION

Previous studies have shown that interaction intimacy, i.e. the degree of biological association between individuals of different species (sensu Guimarães et al. 2007), affects the structure and dynamics of ecological networks, since interaction networks formed by free-living (nonsymbiotic) species tend to be nested (Bascompte et al. 2003, Guimarães et al. 2007, Dáttilo et al. 2014, Fagundes et al. 2017), while those of symbiotic ones tend to be modular and more specialized (see Guimarães et al. 2007, Benítez-Malvido & Dáttilo 2015). Although interactions between hermit crabs and gastropod shells are unlike most interaction networks where both interacting species are living organisms, we found structural patterns that were similar to symbiotic interacting species (Guimarães et al. 2007, Benítez-Malvido & Dáttilo 2015), in which interaction intimacy affects specialization patterns of the network structure (Thompson 2005). Our results showed a non-nested, specialized, and modular network structure, indicating that hermit crabs interact with a clear subset of gastropod shell species. It is important to highlight that modularity and nestedness, despite not being mutually exclusive structural patterns, are poorly correlated at high a connectance (see Fortuna et al. 2010), and reflect distinct mechanisms underlying species coexistence.

However, just like nonsymbiotic species, each individual hermit crab has the opportunity to interact with multiple shells of different species during its lifetime. In such interaction networks between free-living species, due to the low interaction intimacy, network structure commonly has a nested pattern (Guimarães et al. 2007). Nevertheless, some particular networks of free-living species, such as those involving plants and hummingbirds, may be non-nested and highly modular due to coadaptation that leads to morphological specialization between groups of species (see Maruyama et al. 2014, Vizentin-Bugoni et al. 2014). Similarly, we found a specialized and modular structure in the hermit crab–shell interaction network; thus, we suggest that morphological specialization of crabs in relation to their host shells may play an important role in structuring community-level interactions.

Also, there is compelling evidence that hermit crabs actively choose morphologically suitable shells rather than randomly using what is available (Bertini & Fransozo 2000, Benvenuto & Gherardi 2001, Teoh et al. 2014, Vale et al. 2017, Ragagnin et al. 2018). Shell distribution among different hermit crab com-

munities has been explained through interspecific differences in exploitation and fighting abilities (Sant'Anna et al. 2012, Alcaraz & Kruesi 2019). Thus, the niche partitioning observed among hermit crab species could be derived from intensive resource competition and selective exploitation for optimal shells (Gherardi & Vannini 1993, Squires et al. 2001, Peres et al. 2018, Alcaraz & Kruesi 2019). However, in a community context, abundance can also influence the structural pattern of interaction networks, since the chance of interaction is higher when interacting species have higher abundances (Jordano 1987, Bascompte et al. 2003, Vázquez et al. 2009). Therefore, shell choice, which determines the structural pattern of hermit crab–shell community-level interactions, despite being influenced by niche-based processes (e.g. behavior, morphology, sex), may also be influenced by a neutral process, i.e. abundance (Dowds & Elwood 1985, Barnes 1999, Oba & Goshima 2004, Hazlett et al. 2005). Hence, future studies should investigate the relative influence of both processes in hermit crab–gastropod shell network structure.

Species-level descriptors provided information for both hermit crab and gastropod shell species contributions for network structure. The large-bodied hermit crab *Petrochirus diogenes*, for instance, has a clear preference for large shells, occupying only 3 shell species in the community including mainly *Tonna galea*, which has a large aperture width. However, juveniles are known to occupy a wide diversity of shell species of very different shapes (Bertini & Fransozo 2000), while adults tend to compete for the more restrict larger shells. Moreover, small hermit crabs such as *Pagurus criniticornis* and *P. exilis* were not found in heavier shells like *Strombus pugilis* and *Semicassis granulata* as found in other studies (Mantelatto et al. 2007, 2016, Sant'Anna et al. 2012). Carrying heavier shells could delay growth, reproduction, and survival (Alcaraz et al. 2015). Also, the generalist hermit crab *Dardanus insignis*, which reaches an intermediate size when compared to the other members of the community, was found in a wide array of shells with different features, revealing that shell traits do not impose any morphological constraint, i.e. 'forbidden link' (see Vázquez et al. 2009, Vizentin-Bugoni et al. 2014) for some hermit crab species.

We highlight the importance of *D. insignis* for being responsible for a large amount of the realized links of very different gastropod species. The ability to occupy a wide diversity of shells allows *D. insignis* to reach higher abundances in many soft-sediment habitats in the Ubatuba Bay region (Fransozo et al.

1998, Gregati et al. 2011, Frameschi et al. 2013). From a resource perspective, the shell of the gastropod *Buccinanops cochlidium* plays the most important role in the interaction network, since it was occupied by all hermit crab species found in the community and was responsible for a great number of interactions. On the other hand, we found some specialized relationships, such as that between *Loxopagurus loxochelis* and *Olivancillaria urceus*. *O. urceus* has a narrow, elongated aperture that facilitates the protection of *L. loxochelis* due to the well-developed and elongated left chela fitting well with the shell aperture (Meireles et al. 2003, Mantelatto et al. 2004, Frameschi et al. 2013). This reveals the importance of traits, such as behavior, in the structure of the hermit crab–gastropod shell interaction network.

In sum, our results suggest that functional traits of hermit crabs, such as morphology, behavior, and active selection of shell species, rather than random choices determined by abundance, may structure hermit crab–gastropod shell interaction networks. However, availability of shells may also contribute to the network structure, since more abundant species tend to have higher encounter rates. Also, we argue that hermit crab–shell interactions should be more thoroughly investigated in distinct environments, since species roles for both hermit crabs and gastropod shells might change spatially and temporally across different seasons. Thus, future studies should not only evaluate the interactions between hermit crabs and shells, but should also investigate the relative importance of abundance and functional traits in the structure of this unique interaction network. Moreover, considering the anthropogenic disturbance scenarios affecting marine ecosystems, and, consequently, species interactions within these communities (Griffith et al. 2012), a crucial issue that should also be investigated is the causality between the structural patterns of interaction networks and the stability of these ecological communities (Thébault & Fontaine 2010). The non-nested and modular pattern observed in this unique interaction system resembles those observed in other studies (e.g. Vizentin-Bugoni et al. 2014, Ballarin et al. 2020). Hence, future studies should also analyze the processes behind the patterns (see Vázquez et al. 2009) structuring hermit crab–gastropod shell interaction networks, which would help to better understand some overlooked factors determining hermit crab species distribution and community structure across different habitats and geographical regions.

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