

# A host-endoparasite network of Neotropical marine fish: are there organizational patterns?

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## SUMMARY

Properties of ecological networks facilitate the understanding of interaction patterns in host-parasite systems as well as the importance of each species in the interaction structure of a community. The present study evaluates the network structure, functional role of all species and patterns of parasite co-occurrence in a host-parasite network to determine the organization level of a host-parasite system consisting of 170 taxa of gastrointestinal metazoans of 39 marine fish species on the coast of Brazil. The network proved to be nested and modular, with a low degree of connectance. Host-parasite interactions were influenced by host phylogeny. Randomness in parasite co-occurrence was observed in most modules and component communities, although species segregation patterns were also observed. The low degree of connectance in the network may be the cause of properties such as nestedness and modularity, which indicate the presence of a high number of peripheral species. Segregation patterns among parasite species in modules underscore the role of host specificity. Knowledge of ecological networks allows detection of keystone species for the maintenance of biodiversity and the conduction of further studies on the stability of networks in relation to frequent environmental changes.

Key words: network, endoparasites, nestedness, modularity, co-occurrence, null models.

## INTRODUCTION

The heterogeneity and asymmetry of inter-species interactions are important properties of ecological networks, mainly through the promotion of community coexistence, with a reduction in competitive interactions between species and an increase in resistance to stochastic extinction (Bascompte *et al.* 2006; Bastolla *et al.* 2009). Two patterns stand out in this context: (i) nestedness, in which a group of generalist species (i.e. with many interactions) interact with each other and specialist species (i.e. with few interactions) preferentially interact with generalist species and rarely with each other (Bascompte *et al.* 2003); and (ii) modularity, in which the networks exhibit subsets of species interacting more with one another within a larger group of species (Lewinsohn *et al.* 2006a).

These two patterns are not mutually exclusive. There are nested networks with modular networks (Olesen *et al.* 2007; Fortuna *et al.* 2009, 2010) and modular networks may have nested structures within the modules (Lewinsohn *et al.* 2006a). In modular networks, it is possible to determine the functional

role of each species based on its pattern of intra-module and inter-module connections, which assists in understanding how species are connected (Guimerà and Amaral, 2005a,b; Olesen *et al.* 2007). The connectance (i.e. proportion of the number of actual interactions divided by the number of possible interactions) of a network has been identified as one of the factors that determine the degree of nestedness and modularity, as the most highly connected networks tend to exhibit only one or neither of these two properties (Fortuna *et al.* 2010).

The evaluation of the properties of a host-parasite network and the characterization of the functional roles of species demonstrate the importance of parasite specificity to the network topology. This specificity is evidenced by a high number of species that perform few links with other species of the network. Host-parasite networks are a good model for understanding the interaction structure of organisms and its effects on natural communities (Gotelli and Rohde, 2002; Vázquez *et al.* 2005, 2007; Tello *et al.* 2008). However, the interaction between hosts and parasites in a host-parasite network does not directly reveal the interaction pattern between parasite species, as the networks seem to link hosts with parasites regardless of whether they co-occur in the community within an individual host (i.e. infracommunity; Bush *et al.* 1997). Thus, parasites of a host species and within the same subgroup or module do

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not always coexist in all individual hosts. Therefore, the analysis of possible co-occurrence patterns among parasite species allows the recognition of patterns in structuring modules and component community (i.e. *all parasite* species exploiting the same *host* population; Bush *et al.* 1997).

A number of studies report that the absence of competition between parasites in certain species of hosts is a reflection of an unsaturated community (Rohde *et al.* 1995; Rohde, 1998; Morand *et al.* 1999). Furthermore, null model analysis of species co-occurrence patterns has revealed scant evidence of non-randomization in the structuring of communities (Gotelli and Rohde, 2002; Mouillot *et al.* 2005). However, it is understood that the different degrees of interaction among the parasites of a host species require these communities to be in a continuum of interactionist to isolationist communities (Holmes and Price, 1986). Thus, modules could either be sets of species that have minimized the effects of competitive exclusion through the differentiation of some components of their niches or random sets of species, which is less likely.

The aim of the present study was to determine characteristics of the community structure of gastrointestinal helminths of an assemblage of 39 species of marine fish collected in the state of Rio de Janeiro, Brazil, revealing the network patterns as well as the real interaction patterns of species in the community. For such, the following questions are addressed. (i) Is the ecological network nested, modular or both? (ii) What is the degree of network connectance? (iii) What is the functional role of network species with respect to their position among and within modules? (iv) What are the parasite species co-occurrence patterns?

#### MATERIALS AND METHODS

A total of 2493 infracommunities of gastrointestinal parasites of 39 species of marine fish representing 10 orders and 21 families were collected and analysed. All fish were caught by local fishermen in coastal waters off the state of Rio de Janeiro, Brazil (latitude 21 to 23°S) between 1991 and 2006. Fish identification was based on the protocols of Figueiredo and Menezes (1978, 1980, 2000) and Menezes and Figueiredo (1980, 1985). The valid names for each species were based on those reported by Froese and Pauly (2010). All dissections and the collection of the parasites were performed using the same methods. Parasite identification was either performed or confirmed by the same researcher (J. L. L.). Thus, the data do not suffer from problems associated with datasets compiled from different sources and/or based on different methods. The parasites belonged to 170 taxa of trematodes, cestodes, nematodes or acanthocephalans. The presence-absence matrix was used for

analysis, with '1' denoting that a species was found in a particular host and '0' denoting its absence.

The degree of nestedness of the network was evaluated using the NODF metric (Almeida-Neto *et al.* 2007, 2008). The randomness of matrix nestedness was assessed by the analysis of null models. The hypothesis of randomness of matrix nestedness was tested by calculating the proportion (P) of NODF values obtained from null matrices equal to or greater than that observed among a total of 999 random matrices. The calculation of the NODF metric ('nestednodf') (Oksanen *et al.* 2010) and the simulation of the null model were conducted using the R program (version 2.11) with the 'oecosimu' function of the Vegan package (Oksanen *et al.* 2010) and the swap algorithm ('SIM9' and 'Fixed-Fixed') (Gotelli, 2000; Joppa *et al.* 2010). There is intense debate in the literature regarding which null model should be used to test for the significance of nestedness (Ulrich and Gotelli, 2007; Ulrich *et al.* 2009; Fortuna *et al.* 2010; Joppa *et al.* 2010). In the present study, the decision was made to use the swap null model, as studies have demonstrated that this model is more conservative and realistic and offers a lesser probability of type I statistical errors (Joppa *et al.* 2010).

The investigation of the existence of modules in network interactions and the functional role of species was conducted with an optimization routine of the Netcarto program (Guimerà and Amaral, 2005a,b). This procedure generates a value of modularity (M) for the interaction matrix. The hypothesis of M randomness was calculated by generating 99 null matrices which, together with the M value of the real matrix, totals 100 values for the construction of the null distribution of the statistical test (Manly, 2004).

To determine the functional role of the species, the classification described by Olesen *et al.* (2007) was employed, which considers the degree  $z$  of the species within a module and the connectivity  $c$  between modules (Guimerà and Amaral, 2005a,b). Based on  $cz$  scores, species are considered peripheral ( $z \leq 2.5$  and  $c \leq 0.62$ ) (i.e. with few links to other species), connectors ( $z \leq 2.5$  and  $c > 0.62$ ) (i.e. linking several modules), module hubs ( $z > 2.5$  and  $c \leq 0.62$ ) (i.e. highly connected and linked to many species within their own module) or network hubs ( $z > 2.5$  and  $c > 0.62$ ) (i.e. both connectors and module hubs). Connectance (C) was measured for entire networks as well as for each module.

To determine the influence of evolutionary relationships among fish in host-parasite interactions, the association between the host taxonomic distance matrix and parasitic fauna dissimilarity matrix (generated by the 'vegdist' function of the Vegan package with a Mantel test (Legendre and Legendre, 1998; Manly, 2004)) was determined by the R program, using the correlation coefficient  $r$  as a test statistic (Manly, 2004).

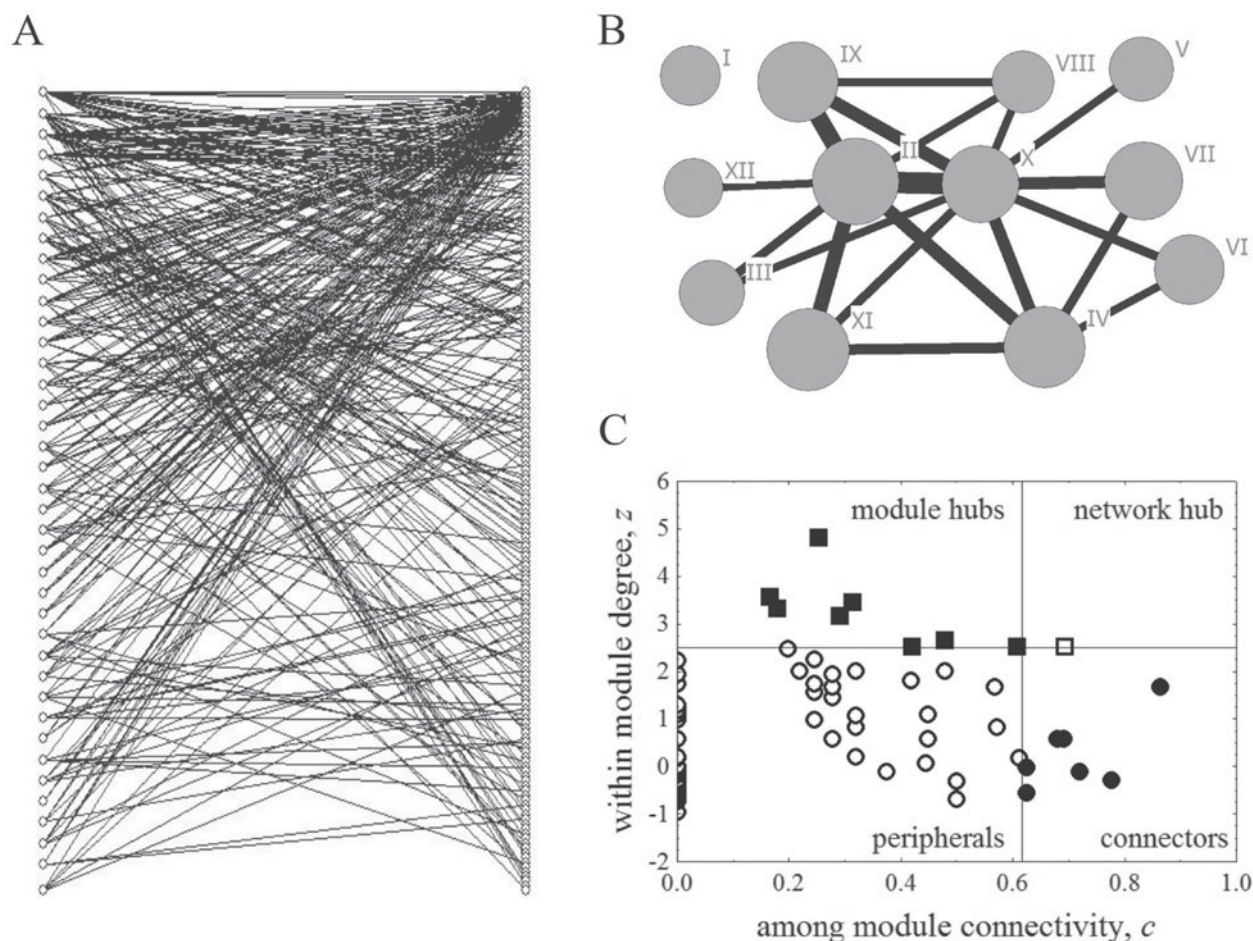


Fig. 1. (A) Bipartite graph (left edges are host species and right edges are parasite species, the species are ordered from top to bottom in order of decreasing interactions). (B) Graph of modules (line thickness corresponds to the number of links between the modules, and the circle diameter corresponds to the number of species in module). (C) Species roles according to a  $c$ - $z$ -plot for host-endoparasite matrix.

Organization patterns of the infracommunities of gastrointestinal parasites were analysed using the checkerboard score (C-score) co-occurrence index (Stone and Roberts, 1990) and the swap algorithm ('SIM9') (Gotelli, 2000). Co-occurrence analyses were carried out with all infracommunities of all host species together, as well as within each module, and on the component community, totaling 52 matrices. For each matrix analysed, 30000 randomizations were performed using the Ecosim 7 program (Gotelli and Entsminger, 2001). These analyses were conducted for each component community to determine whether these were intrinsic characteristics determining co-occurrence patterns within the modules.

## RESULTS

Among the 170 parasite species analysed in the present study, only 51 were associated with more than 1 host and, among these parasites, only 3 were found to occur in more than 10 host species. Fish species had between 5 and 22 parasite species in their component communities, but only 6 fish species had

more than 10 parasite species. The most generalist parasite was *Lecithochirium microstomum* (degree = 21) and the fish with the most interactions was *Pseudoperca numida* (degree = 22). *Scolex polymorphus* have a high degree (24) but it is a cestode larval stage species complex.

A nested pattern was found in the host-parasite network (NODF = 5.491,  $P < 0.001$ ) (Fig. 1A) and modules were found in the network interaction ( $M = 0.680$ ,  $P < 0.001$ ). Twelve modules with 5–31 species were identified (see Supplement material, Online version only). Fig. 1B displays the interaction patterns among the modules.

Most species were peripheral ( $N = 92.820\%$ , Fig. 1C). Only 7 species were connectors and, among these, 5 were parasite species (*Bucephalus margaritae*, *Hysterothylacium* sp. 1, *Lobatostoma ringens*, *Procamallanus macaensis* and *Scolex polymorphus*) and 2 were host species (*Paralonchurus brasiliensis* and *Menticirrhus americanus*). Connector parasite species were from modules II and X, except *Lobatostoma ringens*, which was from module XI. Seven species were module hubs and, among these, only 1 was a parasite species (*Parahemius merus*;

Table 1. Observed values and mean of the values expected at random of the index C-Score applied for parasite species in each network module of the coastal area of Rio de Janeiro, Brazil

(HS, number of host species; N, number of analysed hosts; PS, number of parasite species; Obs., value observed; Exp., value expected; s.d., standard deviation; \* significant data.)

Modules	HS	N	PS	C-Score			
				Obs.	Exp.	s.d.	P <sup>#</sup>
I	1	29	5	14·500	15·084	0·906	0·727
II	10	531	21	728·528	706·484	4·837	<0·001*
III	1	150	10	400·622	389·611	2·578	<0·001*
IV	6	616	20	1330·347	1296·136	3·108	<0·001*
V	2	132	8	45·500	46·622	1·257	0·816
VI	2	77	13	138·371	115·731	1·283	<0·001*
VII	4	216	19	358·327	321·071	2·087	<0·001*
VIII	1	30	7	8·238	7·596	0·708	0·176
IX	3	159	22	105·311	104·417	1·082	0·201
X	5	246	17	334·529	319·849	3·309	<0·001*
XI	3	273	24	210·387	200·181	0·962	<0·001*
XII	1	34	4	19·333	19·643	1·289	0·505

# Probability that the observed number of pairs of species that do not co-occur ≥ simulated number of pairs of species that do not co-occur, inside the null hypothesis of random structure of parasite species in each module.

module II) and all others were host species (*Balistes capriscus*, *Dactylopterus volitans*, *Lophius gastrophysus*, *Merluccius hubbsi*, *Mugil platamus* and *Pseudoperca numida*). Only the digenean *Lecithochirium microstomum* from module II was a network hub (see Supplement material, Online version only, for identification of the functional role of all species). Overall network connectance (C) was 4·796% and mean module C ± s.d. was 61·050% ± 31·680%. Host-parasite interactions were influenced by the taxonomic distance of the host (Mantel r = 0·404; P < 0·001); in other words, phylogenetically close hosts tended to share parasite species.

The observed C-score for the matrix with all infracommunities was higher than the expected value (C-score<sub>observed</sub>: 711·551; C-score<sub>expected</sub>: 703·668; P < 0·001), revealing a negative co-occurrence pattern and demonstrating the segregation of parasite species. Table 1 displays the observed values and mean values expected at random of the C-score index applied to each module. Among modules with more than one host species, only modules V and IX displayed random co-occurrence patterns, which was similar to the modules with a single host species, except module III. Negative co-occurrence patterns were observed in the other modules. Considering the 39 matrices analysed for infracommunities of each fish species, only 7 had non-random patterns and these were negative (P<sub>observed</sub> ≥ P<sub>expected</sub>) (Table 2).

DISCUSSION

Host-parasite networks have a nested structure similar to mutualistic networks (Poulin, 2010).

However, antagonistic predator-prey or, in the present case, host-parasite co-evolution leads to differences in network structures in comparison with the majority of mutualistic networks, thereby producing modules with greater frequency that depend on more specialized network interactions, mainly governed by co-evolutionary processes (Lewinsohn et al. 2006b; Thompson, 2005, 2006; Olesen et al. 2007; Fortuna et al. 2010; Thébault and Fontaine, 2010; Stouffer and Bascompte, 2011). The data of the present study corroborate these notions.

A large number of generalist species tends to increase network connectance, reduce nestedness and modularity (Fortuna et al. 2010) and promote homogenization (Borrett and Salas, 2010), which makes the network more susceptible to disturbances (Olesen et al. 2007). Generalist parasite species tend to reduce biodiversity through competition, unlike specialist species (Hudson et al. 2006), which are frequent in communities with a low degree of connectance. In contrast, low connectance in networks promotes nestedness and modularity patterns simultaneously, as observed in the present study, although these patterns may have some dependence on the null model and the measure employed (see Fortuna et al. 2010). In the present study, the large number of peripheral species and low degree of network connectance reflected the high degree of specialization of the host-parasite interactions.

Determining factors that lead to parasite specialization requires the combination of phylogenetic and ecological approaches (Poulin, 2005). The variation of the parasite species richness of network host species and its functional role might be a reflection of ancient associations between fish and parasite

Table 2. Observed values and mean of the values expected at random of the index C-Score applied for infracommunities of gastrointestinal parasites of 39 species of marine fish collected in the coastal area of Rio de Janeiro, Brazil

(N, number of analysed hosts; S, parasite richness; Obs., value observed; Exp., value expected; s.d., standard deviation; \* significant data.)

Host species	N	S	C-Score			
			Obs.	Exp.	s.d.	P <sup>#</sup>
<i>Aluterus monoceros</i>	39	5	47.000	47.173	1.391	0.515
<i>Archosargus rhomboidalis</i>	29	5	14.500	15.041	0.870	0.715
<i>Aspistor luniscutis</i>	69	6	12.266	11.945	0.386	0.230
<i>Balistes capriscus</i>	66	11	48.181	39.604	1.406	<0.001*
<i>Balistes vetula</i>	30	7	21.047	19.324	0.554	0.006*
<i>Caranx hippos</i>	60	6	53.066	51.908	1.428	0.196
<i>Caranx latus</i>	55	7	33.000	30.485	1.255	0.044*
<i>Cynoscion guatucupa</i>	72	7	93.619	92.954	1.544	0.322
<i>Dactylopterus volitans</i>	78	21	46.980	46.222	0.541	0.085
<i>Euthynnus alletteratus</i>	46	6	68.666	66.885	1.571	0.133
<i>Genidens barbatus</i>	63	5	48.000	48.767	1.874	0.626
<i>Gymnothorax moringa</i>	30	5	26.500	24.757	0.764	0.032*
<i>Haemulon steindachneri</i>	80	8	91.392	91.726	1.706	0.549
<i>Lophius gastrophysus</i>	30	10	5.333	4.992	0.415	0.191
<i>Macrodon ancylodon</i>	31	7	12.533	11.425	0.659	0.084
<i>Menticirrhus americanus</i>	115	9	125.527	125.595	1.576	0.489
<i>Merluccius hubbsi</i>	31	10	16.777	16.083	0.447	0.075
<i>Micropogonias furnieri</i>	100	10	53.688	56.085	1.912	0.915
<i>Mugil platanus</i>	150	12	295.560	285.550	2.064	<0.001*
<i>Mullus argentinae</i>	100	5	337.300	336.854	3.480	0.408
<i>Oligoplites palometa</i>	84	6	65.066	66.907	2.334	0.794
<i>Oligoplites saliens</i>	36	5	12.100	12.918	1.301	0.746
<i>Oligoplites saurus</i>	37	6	34.866	36.225	1.266	0.877
<i>Orthopristis ruber</i>	162	9	744.555	709.679	3.470	<0.001*
<i>Paralichthys isosceles</i>	36	5	37.900	38.095	1.263	0.525
<i>Paralanchurus brasiliensis</i>	93	6	100.533	100.591	1.735	0.452
<i>Parona signata</i>	31	6	2.866	3.060	0.639	0.578
<i>Peprilus paru</i>	81	5	140.300	146.113	4.105	0.944
<i>Pinguipes brasilianus</i>	31	15	18.761	19.045	0.306	0.825
<i>Prionotus punctatus</i>	80	5	232.100	224.398	2.192	0.004*
<i>Pseudopercis numida</i>	62	22	33.870	33.925	0.455	0.520
<i>Pseudopercis semifasciata</i>	66	19	42.918	42.205	0.573	0.115
<i>Selene setapimmis</i>	89	9	78.357	77.067	1.927	0.232
<i>Trichiurus lepturus</i>	55	7	4.714	4.616	0.678	0.437
<i>Tylosurus acus acus</i>	31	5	15.100	14.378	0.441	0.079
<i>Umbrina canosai</i>	81	7	54.571	53.825	1.945	0.327
<i>Uraspis secunda</i>	34	5	23.600	22.436	1.206	0.179
<i>Urophycis brasiliensis</i>	75	9	182.083	180.586	1.196	0.111
<i>Urophycis mystacea</i>	55	6	78.666	78.999	1.814	0.542

# Probability that the observed number of pairs of species that do not co-occur  $\geq$  simulated number of pairs of species that do not co-occur, inside the null hypothesis of random structure of infracommunities.

species, and not only a consequence of the ecological traits, e.g. diet or host habitat (Luque and Poulin, 2004). *Scolex polymorphus* was the parasite with the largest number of interactions; however, this is a larval stage and possibly a complex of species (Chandler, 1935; Chambers *et al.* 2000; Braicovich and Timi, 2008) and thus is not possible to verify the host specificity. *Lecithochirium microstomum* (Hemiuridae) was the parasite adult species with the highest number of interactions and occurred in fishes with a high range of parasite species richness, such as *Pseudopercis numida* (Perciformes), *Gymnothorax*

*moringa* (Anguilliformes), *Oligoplites saliens* (Perciformes) and *Paralichthys isosceles* (Pleuronectiformes) (see Supplementary material, Online version only). *Lecithochirium microstomum*, was the only network hub species observed and was parasitizing unrelated fishes. The other non-peripheral parasite species has a low specificity tendency (see Bush *et al.* 2001; Cribb *et al.* 2002; Torres and Soto, 2004; Marchiori *et al.* 2010).

Factors such as habitat heterogeneity, divergent selection regimes and phylogenetic groups of related species could promote modularity, contributing to

complexity in ecological networks (Pimm and Lawton, 1980; Lewinsohn *et al.* 2006b; Olesen *et al.* 2007). In mutualistic networks, the presence of species from different families in the same module may be indicative of convergence between non-related species (Thompson, 1994, 2005). In contrast, in host-parasite networks like the one analysed here, the acquisition of parasites is linked to the food chain (ingestion of intermediate hosts), in which the presence of phylogenetically distant hosts in the same module may indicate a reduction in competitive pressure or adaptation to an abundant resource (Rezende *et al.* 2009), whereas the presence of related host species in different modules may avoid niche overlap. The highest similarity of the parasite fauna of related host species in the network and the presence of congeneric hosts in the same module are an indicator of the conservation of phylogenetic niches by the hosts, through feeding of the same preys (intermediate hosts of parasites). Nevertheless, the presence of fish species from different taxonomic orders in the network modules could suggest that in some cases the host ecology could be more important than host phylogeny to determine the similarity of their parasite faunas (Chávez *et al.* 2011) and in the formation of modules.

Interactions among modules typically occur with generalist species (Olesen *et al.* 2007), and these species when removed from the system could exhibit the fragility of the network structure forming several isolate modules (Solé and Montoya, 2001). For instance, the non-peripheral hosts overfishing could result in a decrease in parasite diversity affecting the stability of the network and the functionality of the ecosystem (Scheffer *et al.* 2005; Wood *et al.* 2010). In the present study, modules II and X were fundamental to the topology of the network as these modules contained the majority of non-peripheral generalist parasite species. Additional studies about the other hosts of the life cycle of these parasite species might give important information about diet overlapping in the network fish species. Moreover, the presence of few generalist parasites in a few modules enables greater complexity in the network and could indicate a low degree of competition for resources. This low degree of competition is also suggested by the few component communities that exhibited non-random patterns of co-occurrence.

Gotelli and Rohde (2002) stressed that metazoan ectoparasites of marine fish exhibit little evidence of non-randomization in the interactions of their component communities, as demonstrated for the endoparasites in the present study. Non-randomization may occur due to intrinsic characteristics of the component communities, indicating hosts from different demographic groups with some particular sex or age classes (Fellis *et al.* 2003) or hosts from different locations (Krasnov *et al.* 2010). In the present study, a negative pattern of co-occurrence was found when

all component communities were analysed together, grouping different species of fish.

A host individual is a habitat for its parasites and, although there are genetic and physiological differences between populations of the species of this host, the individuals are basically homogeneous (Rossin *et al.* 2005). This may have benefitted the predominant random distribution pattern in modules with one host species and those with hosts belonging to the same family (module V – Ariidae; and module IX – Pinguipedidae) as well as in the component communities analysed. Moreover, the low number of parasite species with prevalence equal to or greater than 60% reported by Poulin and Luque (2003) for 30 of the host species examined in the present study may explain the random distribution pattern observed, as parasites of low prevalence are less likely to co-exist in their hosts. According to the same authors, the CC<sub>50</sub> interactivity index revealed that the 7 component communities with a negative co-occurrence pattern are in an isolationist-interactive continuum, thereby supporting the notion that competition or some other type of interaction is not deterministic in the component communities. Thus, these characteristics may indicate that even host-parasite interactions with a high degree of specialization in the network may be governed by randomness within the component communities.

Host-parasite interactions in ecological networks or component communities allow the understanding of factors related to host biology and ecology. Moreover, endoparasites could be an indicator of the organization of trophic networks in terms of host diversity (intermediate or definitive) involved in their life cycles. With detailed knowledge on ecological networks, it is possible to detect key species for the maintenance of biodiversity and carry out future studies on the stability of networks in the face of frequent environmental changes as well as the effect of overfishing.

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